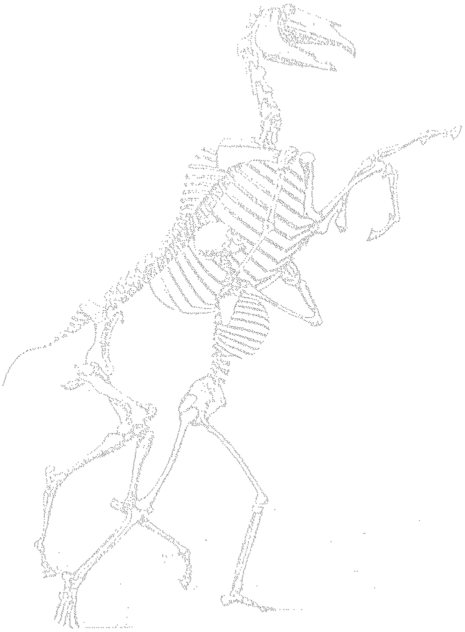
OSSA

International Journal of Skeletal Research



VOLUME 6 1979

FESTSCHRIFT ALBERT DAHLBERG

Papers in:
Human and Animal Osteology
Forensic Osteology and Applied Techniques
Paleopathology, Prehistoric Environment
Interdisciplinary Studies

Osteological Research Laboratory
University of Stockholm
S-171 71 SOLNA — Sweden

OSSA

International Journal of Human
and Animal Osteology

SPONSORS

Volume 6 1979
The Swedish Natural Science Research Council
The Swedish Council for Research in the Humanistic and Social Sciences

EDITORS

General Editor: *Nils-Gustaf Gejvall,* Ph.D., Prof. Em. Past Dir. Osteological Research Laboratory, University of Stockholm, Gnejsvägen 1, S-310 40 Harplinge — Sweden
Prof. Dr. *Joachim Boessneck,* Head of Institut für Paleoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München, Schellingstrasse 10/II, 8 München 40, BRD
Antje T. Clason, Ph.D., Biologisch-Archaeologisch Instituut der Rijksuniversiteit, Poststraat 6, GRONINGEN — The Netherlands
Lennart Diener, Dr. Med Ass. Prof., Chief Physician, Department of Radiology, Central Dispensary of Stockholm, Box 17202, S-104 62 STOCKHOLM — Sweden
István Kiszely, Ph.D., Archaeological Institute of the Hungarian Academy of Science, Uri Utca 49, 1250 BUDAPEST 1 — Hungary
Philip Rightmire, Ph.D., Ass. Prof., State University of New York at Binghamton, Department of Anthropology, BINGHAMTON, 13901 USA
Torstein Sjøvold, Ph.D., Prof. Dir. Osteological Research Laboratory, University of Stockholm, S-171 71 Sweden
Herbert Ullrich, Dr. rer. nat., Zentralinstitut für Alte Geschichte und Archäologie, Akademie der Wissenschaften der DDR, Leipziger Strasse 3—4, 108 BERLIN — DDR
Gerrit Nanning van Vark, Ph.D., Anatomisch-Embryologisch Laboratorium der Rijksuniversiteit, Oostersingel 69, GRONINGEN, The Netherlands
Translations into Russian — Dipl. Ing. Ada Kolman. Typing of this volume by Mrs. Ulla-Britta Ekstrand

PROGRAM

OSSA is a nonprofit journal directed to all experts and scientists in interrelated fields of human and animal osteology.
OSSA is intended to deal with such material from an interdisciplinary point of view, theoretically, methodologically and practically, in order to use skeletal remains for the exploration of prehistoric and present man, his domestic animals, his environment and its changes, diseases and genetical interrelations, to mention some few aspects.
OSSA is mainly printed in English, but papers in German are also accepted. Each article starts with an English abstract, followed by a resumé in Russian. Summaries should be written in English.
OSSA is *not* delivered on exchange basis.

MANUSCRIPT and BUSINESS ADDRESS

Manuscripts, conforming with the rules on page 3 of this cover as well as communications regarding accepted manuscripts, proofs, orders of reprints, subscriptions, etc. should be addressed to Professor Nils-Gustaf Gejvall, Gnejsvägen 1, S-310 40 HARPLINGE — Sweden.

REPRINTS

Authors will receive 50 reprints free of charge. Further reprints for non-commercial circulation may be ordered by fifties or hundreds according to average prices set by the publisher on a non-profit basis.

SUBSCRIPTION PRICE, including postage

OSSA, volume 1, 1974 (1 issue), Swedish kronor 30:— (US $7: 50) few copies still available
OSSA, volume 2, 1975 (1 issue), Swedish kronor 30:— (US $7: 50)
OSSA, volume 3/4, 1976—1977 (1 issue), Swedish kronor 115: (US $25)
OSSA, volume 3, 1976 supplement 1, Swedish kronor 30:— (US $7: 50)
OSSA, volume 4, 1977 supplement 1, Swedish kronor 30:— (US $7: 50)
OSSA, volume 5, 1978, Swedish kronor 65:— (US $15)
OSSA, volume 6, 1979, Swedish kronor 125:— (US $30:—)

OSSA

International Journal of Skeletal Research

Berlings, Arlöv 1980

Photo by David Brill

To Albert Dahlberg on his 70th birthday –
November 20, 1978

Editor's Introduction

It is my very special pleasure to have had the opportunity to assemble a collection of papers in honour of Dr. Albert Dahlberg's 70th Birthday. It is only a small tribute to the indefatigable efforts of a truly outstanding international scholar and humanitarian.

Dahlberg's name is synonymous with Dental Anthropology. He has contributed close to 100 publications, including a number of books, which cover a wide variety of research interests. Al's influence in virtually all branches of dental science is adequately reflected in the broad range of topics covered by the contributors to this volume. His research and teaching have reached many students in the fields of dental medicine, biology, zoology and anthropology. Those who have learned from him have come to have a fuller understanding and appreciation of human evolution and variation.

I recall most vividly my first encounter with Al in December 1966 when I was contemplating enrolling in the graduate school of the University of Chicago. Immediately his warmth and his genuine interest in my intentions placed me at ease. He strongly suggested that I consider joining the graduate program and, as an incentive, offered me a National Institute of Dental Research Traineeship. It was during the ensuing years at Chicago that I learned to appreciate Al, not only as a well respected scholar, but also as one of the kindest and sincerest people I had come to know. His Dental Anthropology Laboratory served as a major focus for graduate students in Physical Anthropology and was always open for study, research, seminars, and conversation - no doubt there are many who share with me warm memories of those days.

On behalf of the contributors to this volume, and all of those colleagues, students and friends who have had the fortune to know you, Al Dahlberg, I would like to express our deepest congratulations and gratitude for all you have accomplished and inspired. We, who have had the opportunity to know you and to have been encouraged by your knowledge, generosity and dedication to intellectual enrichment and individual enlightenment, are the fortunate ones. From all of us, our very sincerest wishes for all future endeavors and may you continue to prosper in the years ahead.

Donald C Johanson, Editor
Cleveland Museum of Natural History
Cleveland, Ohio, U.S.A.

Acknowledgements

I would like to express my appreciation to my Administrative Assistant, Ms. Doris Harman, for her substantial assistance in making the completion of this FESTSCHRIFT possible. The editorial assistance of Mr. William H. Kimbel is gratefully acknowledged.

Special thanks are due Dr. N-G. Gejvall, General Editor of OSSA, for providing the means for publishing this FESTSCHRIFT. Finally, the contributing authors should be congratulated for their patience and understanding throughout the editorial process.

Introduction by the editor of OSSA

It was indeed a great event when Dr. D. C. Johanson suggested through Dr. P. O. Pedersen that FESTSCHRIFT ALBERT DAHLBERG should appear in this journal.

I first met Al during my time as keeper of the Osteological Collections of the Museum of National Antiquities in Stockholm in the sixties. Thelma and Albert Dahlberg came to study the neolithic skull material, part of which was published by Gustaf Retzius in "Crania Suecica Antiqua" already in 1899.

Everybody who has the privilege of meeting and working with Al is fascinated by his captivating personality, his stringent methods of research and his enterprise. I remember him showing his new abrasion casts of human jaws which he had used on his Jericho material. - In those days visits from afar were rather rare at the osteological section, we were all preoccupied with the bite of the 'ancient Swedes', time flew, and I was called to the telephone and kept from returning to the store-room and the Dahlberg family for hours. I quite forgot the conservative way in which we Swedes receive foreigners, even most distinguished ones, not even enthrusting to them a key for personal use. - After this I was afraid Thelma and Al would never return, having been trapped in a cold distant museal store-room. But Al kept sending me his many important publications, although we have had very few opportunities to meet again.

In 1967 H. M. the late King Gustaf VI. Adolf, our great tutor of Archaeology, inaugurated the Osteological Research Laboratory of the University of Stockholm. This was a great moment for osteology in our country, and it had been the intention all my life. My wife worked as my laboratory engineer till 1977.

In 1974 I started OSSA as a forum for osteology - see cover - and will try to keep it alive although I retired in 1978.

I hereby venture to present volume 6 apologizing for the errors that invariably appear in any publication of this kind.

When this volume is now handed over to Dr. Albert Dahlberg, I know I share my great admiration for him and his unbelievable life-work with all my friends and colleagues in the field of dental research all over the world, and I would like to congratulate and thank him on behalf of thousands of students for the inspiration he has given us all.

Nils-Gustaf Gejvall
Harplinge Sweden

Bilateral hypoplasia of the mandibular condyles in an ancient Polish skull

VERNER ALEXANDERSEN, KRYSTYNA SZLACHETKO AND ALINA WIERCINSKA

OSSA

A medieval Polish skull of a ca. 20 years old - probably male - with bilateral hypoplasia of the mandibular condyles is described. They are small, deformed, the mandible has short rami with antegonial notching, shortened body and considerable symphyseal height.

The most severe degenerative changes occur in the surfaces of the TM-joints, the occipital condyles, in atlas and axis, but changes are observed in other parts of the cervical and thoracical columna and in some small joints of the feet.

Already during early childhood this mandible has rotated posteriorly, its anterior facial height has increased considerably and some of the teeth with long path of eruption developed very long roots. A change in head posture to secure free air passage contributed to the severe arthritic changes in the two uppermost vertebrae.

Etiological factors discussed: congenital defect, trauma or systemic disease. Conclusion: Symmetric hypoplasia of the mandibular condyles plus widespread degenerative articular changes in such a young individual is most likely due to juvenile rheumatoid arthritis (Still's disease).

В статье описан средневековый польский череп, принадлежавший человеку в возрасте примерно 20 лет,- возможно, мужчине - с билатеральной гипоплазией нижнечелюстных мыщелков. Мыщелки малы и деформированы; нижняя челюсть имеет короткие отростки с антагониальной вырезкой, укороченную форму тела и довольно высокий симфизис.

Наиболее сильные дегенеративные изменения встречаются на поверхности ТМ-суставов, у затылочных мыщелков, у атланта и второго шейного позвонка. Кроме того, изменения наблюдались и в других частях шейного и грудного отделов позвоночника и в некоторых малых суставах ступней.

Уже в течение раннего детского возраста нижняя челюсть испытала заднюю ротацию; ее передняя лицевая высота значительно возросла, и некоторые зубы при прорезывании развили очень длинные корни. Это, по-видимому, привело к изменению в положении головы, давшему свободное прохождение воздуха, и содействовало сильным артритическим изменениям в двух самых верхних позвонках.

Обсуждаются этиологические факторы: врожденный дефект, травма или заболевание. Заключение: симметричная гипоплазия нижнечелюстных мыщелков плюс широко распространенные дегенеративные суставные изменения у такого молодого человека зависят, с большой вероятностью, от ревматического артрита, перенесенного в юном возрасте /болезнь Стилла/.

Verner Alexandersen, Department of Anthropology, Anatomical Institute, University of Copenhagen, Nørre Allé 63, 2100-Copenhagen, Denmark.

Krystyna Szlachetko, Alina Wiercinska, State Archaeological Museum, ul. Dluga 52, Arsenal, 00-950 Warsaw, Poland.

Vol. 6, pp. 7-22, Lund. ISSN 0345-8865.

Hypoplasia of the mandibular condyles with mandibular retrognathia and a convex facial profile is a rare facial deformity. This condition was observed by Dr. Alina Wiercinska in the skull of an incomplete skeleton kept in the State Archaeological Museum in Warsaw. The skeleton is dating from the Middle Ages. It was found in Grodzisk voivodship Siedlce in Poland.

The documentation of malformations, diseases and different types of injuries in ancient populations is important. This demonstrates the disease pattern in a given population. In fact, the chief reason for the study of paleopathology is to discover the intricate relationship between a people' s way of life and the diseases they endure (Wells, '64).

Pathological changes of ancient bones are readily observed but often difficult to interpret. The diseased or malformed bones show the end result of an illness which may have been of long duration. The soft tissues of the body are missing and so is the "patient' s history". In spite of these disadvantages, however, a description of the diseased bones can be achieved and an opinion ventured about etiology and pathogenesis.

Determination of the sex and age

The skull shows relatively small dimensions. The forehead is only slightly inclined backwards, the glabellar region is moderately prominent but the one preserved mastoid process is rather large. In general the skull has a moderately developed relief. The additional traits from the rest of the incomplete skeleton suggest, although not conclusively, that the individual was of male sex.

The epi- and diaphyses of the long bones are united and the spheno-occipital synchondrosis is closed. Postmortally a reopening of the basal sutures has occurred between the temporal and occipital bones and a post mortal fracture of the sphenoid bone is found anterior to the spheno-occipital synchondrosis. All the sutures of the cranial vault are open. The skeleton belonged to a young adult.

This age estimate is supported by the stage of dental development. The third molars are not fully formed. The roots of the third molars are almost completely formed but the apical foramina are wide open (Fig. 1).

Johansson (' 71) observed a developmental stage of third molars called "root-length 3/4" at the age of 18± 2.6 years (1 S.D.) in a combined sample of recent Swedish males and females. The upper and lower third molars did not show any developmental differences in Johansson' s material. Miles (' 63) observed that by 18 years the roots of M_3 are usually nearly complete in length and the apical canals are beginning to close; by 20 years the apical canals are usually closed although apical canals large enough to be seen with the naked eye are not uncommon. Miles based his observations on a sample of recent British teeth.

The mandibular third molars are fully erupted in the Polish skull and so is the left maxillary third molar. The right maxillary molar is partly erupted. The fully erupted molars show some occlusal wear of the enamel indicating they had been in occlusion.

According to Rantanen (' 67) eruption of mandibular third molars in recent Finns (males) occurs at the average age of 18.5 years, while eruption of the maxillary third molars tends to come at the average age of 19.5 years. The mean eruption age for third molars in recent European populations is 20.8 years for males (Hurme, ' 49) but theire is a considerable range of variation from 16.2 to 27.2 established arbitrarily at ± 3.5 S.D. from the mean (N = 93 000) (Horowitz and Hixon, ' 66). Hence it is concluded that the dental age of the Polish dentition is about 20 years.

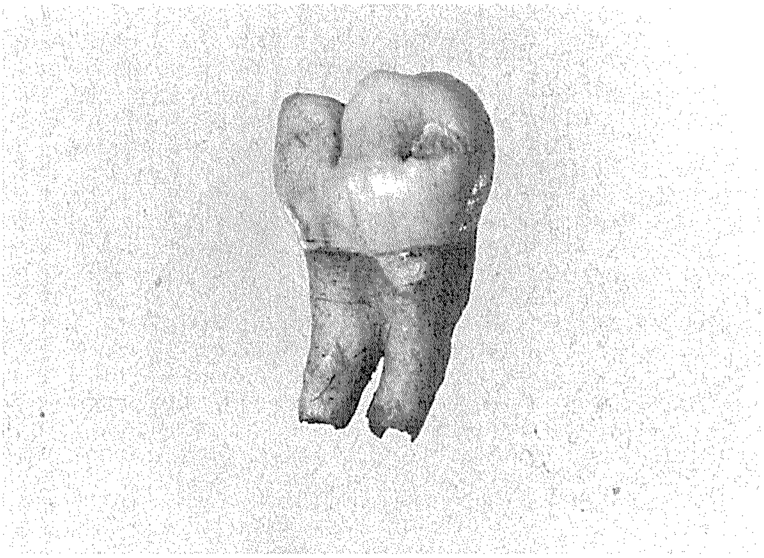


Fig. 1. The mandibular right third molar showing incomplete root formation.

Description of the skull and the dentition

The cranial vault is normally developed. The glabellar and occipital regions show faint relief. The right mastoid process is of moderate size, while the left mastoid process is completely destroyed. There are post-mortem changes of the left temporal region and it is likely that the left mastoid region was also damaged post-mortem (Fig. 2b). In the occipital region of the skull there is a bipartite Inca bone (Fig. 3a). Wormian bones are present at lambda, asterion and in the right side of the coronal suture. An epipteric bone is formed on the left side of the skull.

The calvaria has been somewhat distorted post-mortem. In a basal view of the skull the previously mentioned reopening of sutures and fracture of the sphenoid bone are visible. It is also noticed that foramen lacerum is large on both sides (Fig. 2b).

The anterior view of the skull shows no major asymmetries. Minor bilateral asymmetries are found between the two nasal bones, the supra-orbital borders and the size of the infraorbital and zygomatic foramina (Fig. 2a).

The zygomatic bones are well developed but the right zygomatic arch has been broken post-mortem. There are no visible malformations of the external auditory meatus. The maxilla is of normal width and anterior height. The occlusal plane is sloping backwards and upwards when the skull is oriented according to the Frankfurt Horizontal plane (Fig. 3b).

The skull shows relatively small dimensions (Table 1). It reveals moderate brachycephaly, a very high cranial vault, a very high face with a narrow nose and relatively low orbits. Cranioscopically the following features are worth mentioning: medium high and broad nasal root, probably medium prominent nose with slightly doubled lower margin of the nasal aperture and moderately prominent nasal spine. The orthognathous face has shallow canine fossae and slightly developed maxillary incisura.

Such a combination of quantitative and qualitative traits corresponds in the Polish anthropological terminology to Subnordic type /AL/ of its nordoid fraction (cf. Wiercinski, '62). This type was not very common in the racial composition of Medieval Poland. It began to increase in frequency in late medieval times and is now the most numerous component of the Polish population.

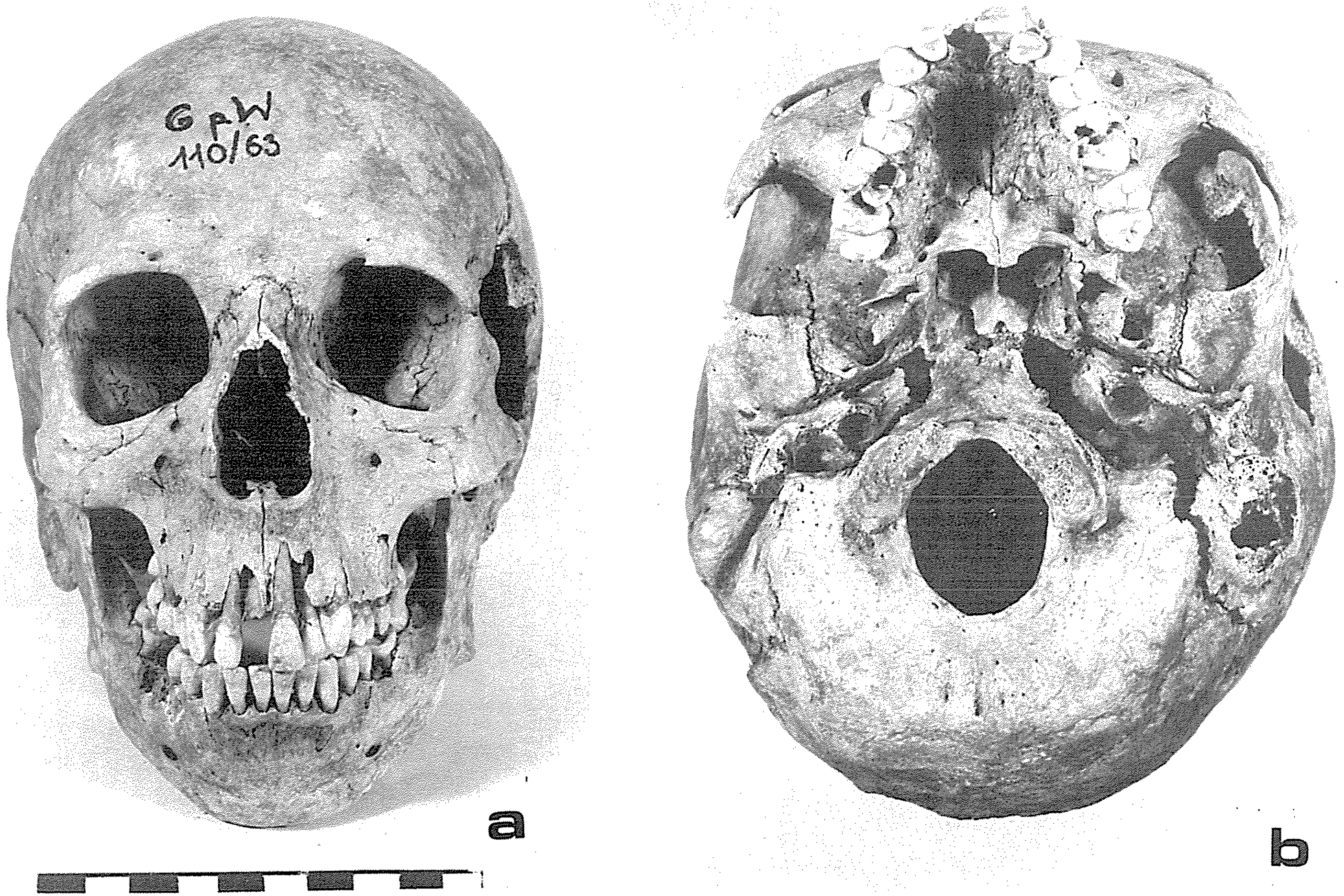


Fig. 2. Anterior (a) and basal (b) views of the skull. Note: (a) Bilateral asymmetry in size and shape of the facial foramina. The maxillary central incisor is one of several teeth with very long roots. (b) Crowding of the anterior teeth, dental caries in the left second premolar and in three of the molars. In the temporal parts of the TM-joints anterior - posterior oriented grooves are formed with osteoporosity at the anterior ends of the grooves. The occipital condyles are severely affected by osteoporosity and osteophytes. Postmortem changes include fracture of the cranial base, loss of the right zygomatic arch, a part of the left temporal bone, the left mastoid process and the maxillary right

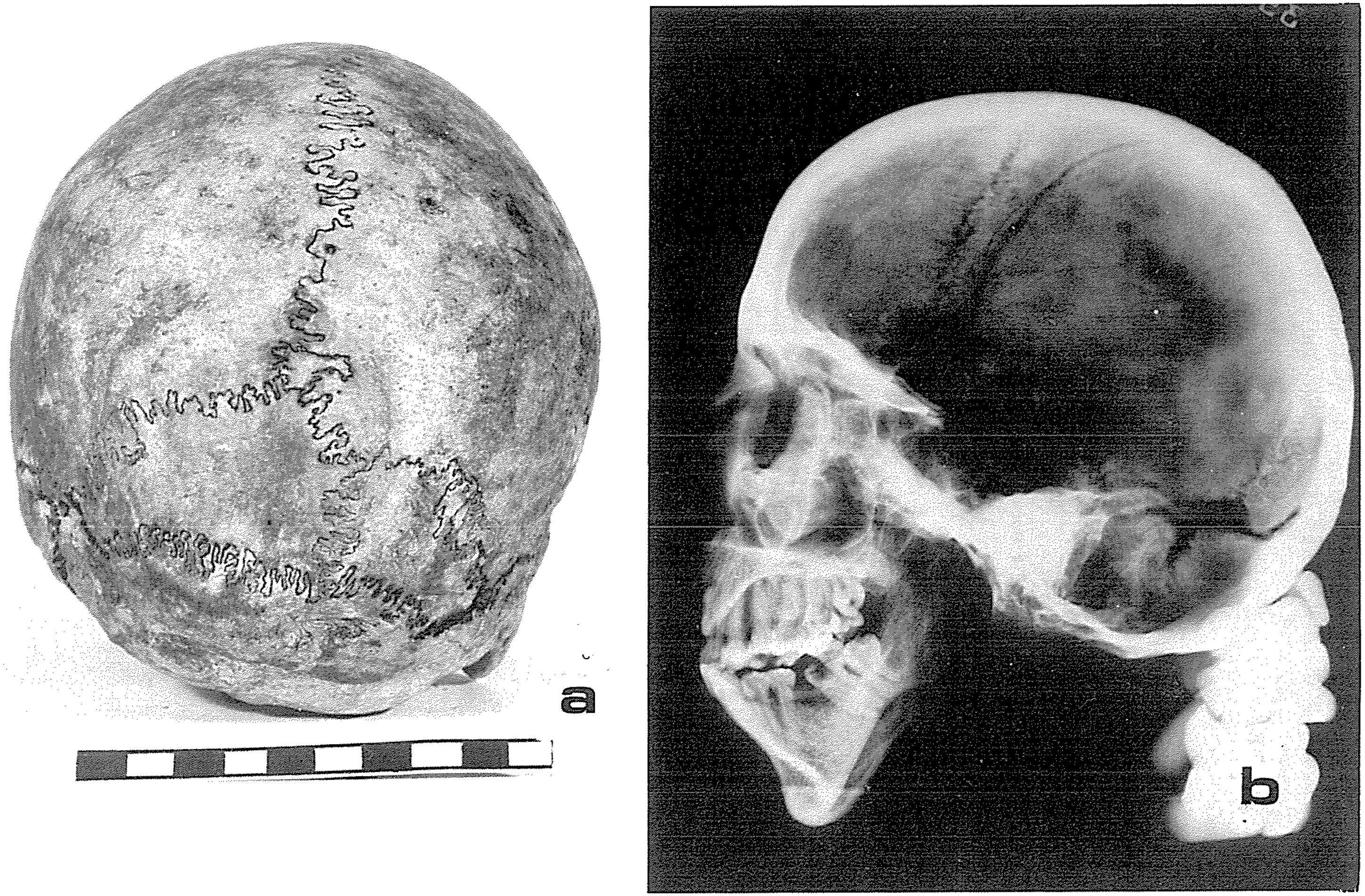


Fig. 3. (a) Occipital view of the skull showing bipartite Inca bone, Wormian bones at lambda and along the lambdoid suture. The bilateral asymmetry of the skull is to some extent of postmortem origin. (b) Lateral x-ray cephalogram of the skull with the mandible in occlusal position to show the mandibular retrognathia.

The mandible belonging to the skull is malformed. The condylar processes are very short, tilted posterior and the condyles are abnormally small with irregular surfaces (Fig. 4). The coronoid processes are of normal size. The incisura is incipiently developed. The mandibular rami are short with prominent angular processes. The mandibular basal contour from the condyles to the chin is shorter than normal.

When the mandible is placed in occlusion the chin is very retruded relative to the maxilla. The symphyseal height of the lower jaw is remarkably large. Antegonial notching is found on both sides of the jaw.

The temporal parts of the temporomandibular joints are of abnormal shape. The articular eminences have been replaced by grooves oriented in anterior-posterior direction. With the dental arches in normal position the mandibular condyles are placed under the now missing articular eminences, i.e. in an anterior position. The bony surface at the anterior ends of the grooves exhibits some porosity.

The maxillary teeth are present with exception of the right central incisor, which was lost post-mortem. In the mandible the two first molars were lost ante-mortem. All the other mandibular teeth are present. The loss of the first molars happened some time before death, because the second and third molars in the mandible have migrated forwards and the right maxillary first molar is somewhat elongated.

The mesiodistal and buccolingual diameters of the tooth crowns are close to the mean values of medieval Danish teeth (Tables 2 and 3). The lengths of the roots, however, are large. Compared with data published by Black ('02) some of the Polish teeth have root lengths exceeding the range of variation observed by Black (Table 4).

The shape of the teeth is normal. In the dental arches there is crowding of the teeth in the anterior regions. The occlusion appears to be normal in the anterior and in the premolar regions. In the molar regions the previously mentioned migrations of the molars have occurred.

The teeth are slightly worn. Dental pathology includes fractures of the occlusal enamel and dentine on four molars, i.e. the mandibular second molars, the maxillary left first molar and right second molar. Dental caries with formation of large cavities are found in five teeth, i.e. in the maxillary right first and second molars, in maxillary left second premolar and first molar and in the mandibular left second molar. The ante-mortem loss of the mandibular first molars is probably the result of tooth fractures or dental caries.

Other skeletal changes

The occipital condyles are the site of osteoarthritic degenerative changes with porosity of the joint surfaces and periphereal osteophytes (Fig. 5a).

The preserved cervical vertebrae - atlas and axis - show corresponding degenerative changes. In the atlas extensive changes are found in the atlanto-occipital joints and moderate changes of the atlanto-axoid joint (Fig. 5b). In the axis no pathological changes are found in the dorsal intervertebral joints (Fig. 5c).

Minor osteoarthritic changes are found in the thoracic vertebrae where 11 out of 36 examined small joints showed osteoarthritic porosity (Fig. 5d).

A few preserved bones belonging to the feet also showed porosity of the joint surfaces in the interphalangeal joints. The small bones of the hands were not available for examination. A few of the long bones of the extremities were examined. They did not reveal any osteoarthritic changes.

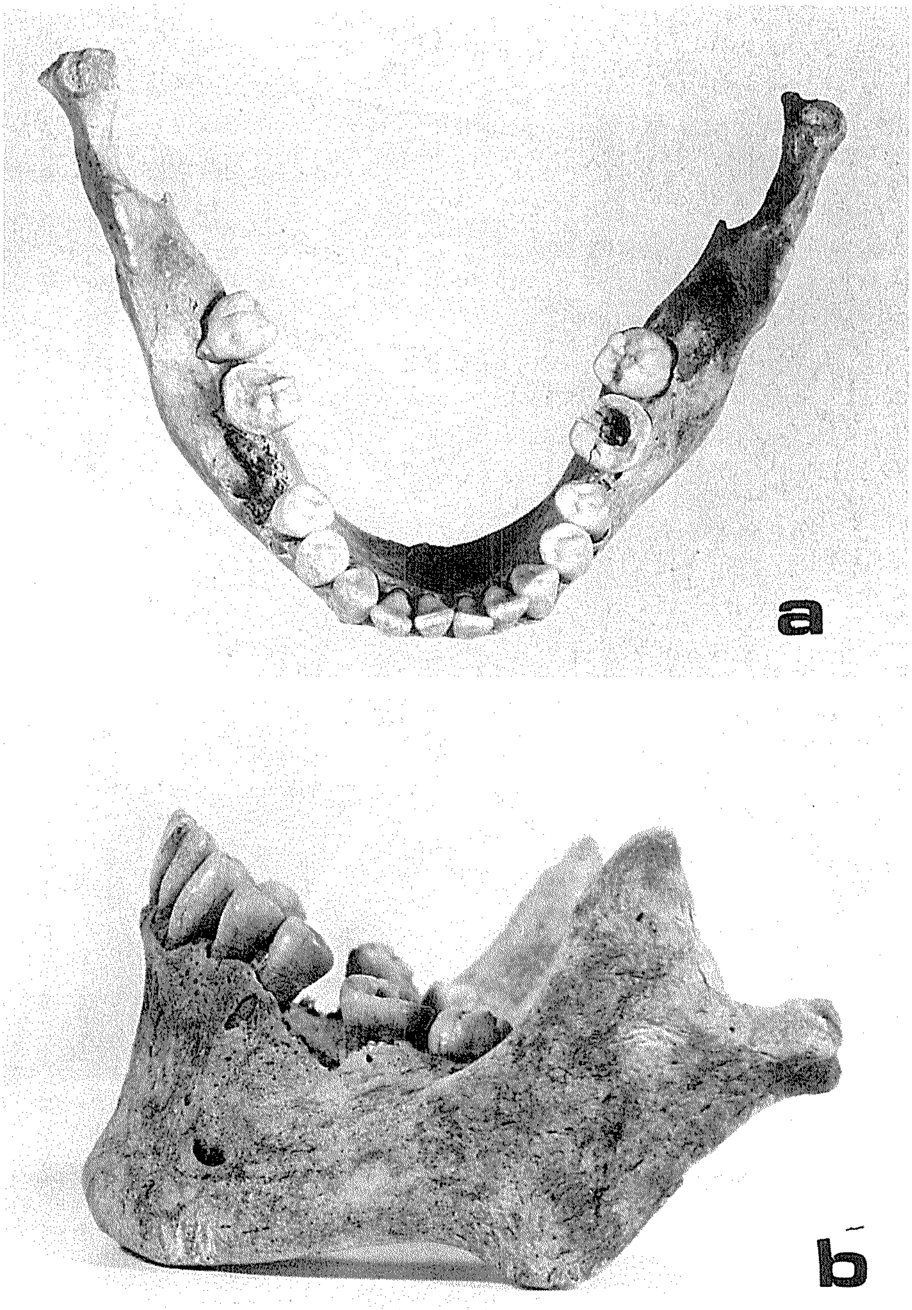


Fig. 4. (a) Occlusal view of the mandible. The mandibular condyles are reduced in size with irregular osteoporotic surfaces. The mandibular first molars were lost ante-mortem. The second molars show evidence of dental caries and fractures. (b) Lateral view of the mandible showing the hypoplastic condyle, the posteriorly directed condylar process, the antegonial notching and the large anterior height of the lower jaw.

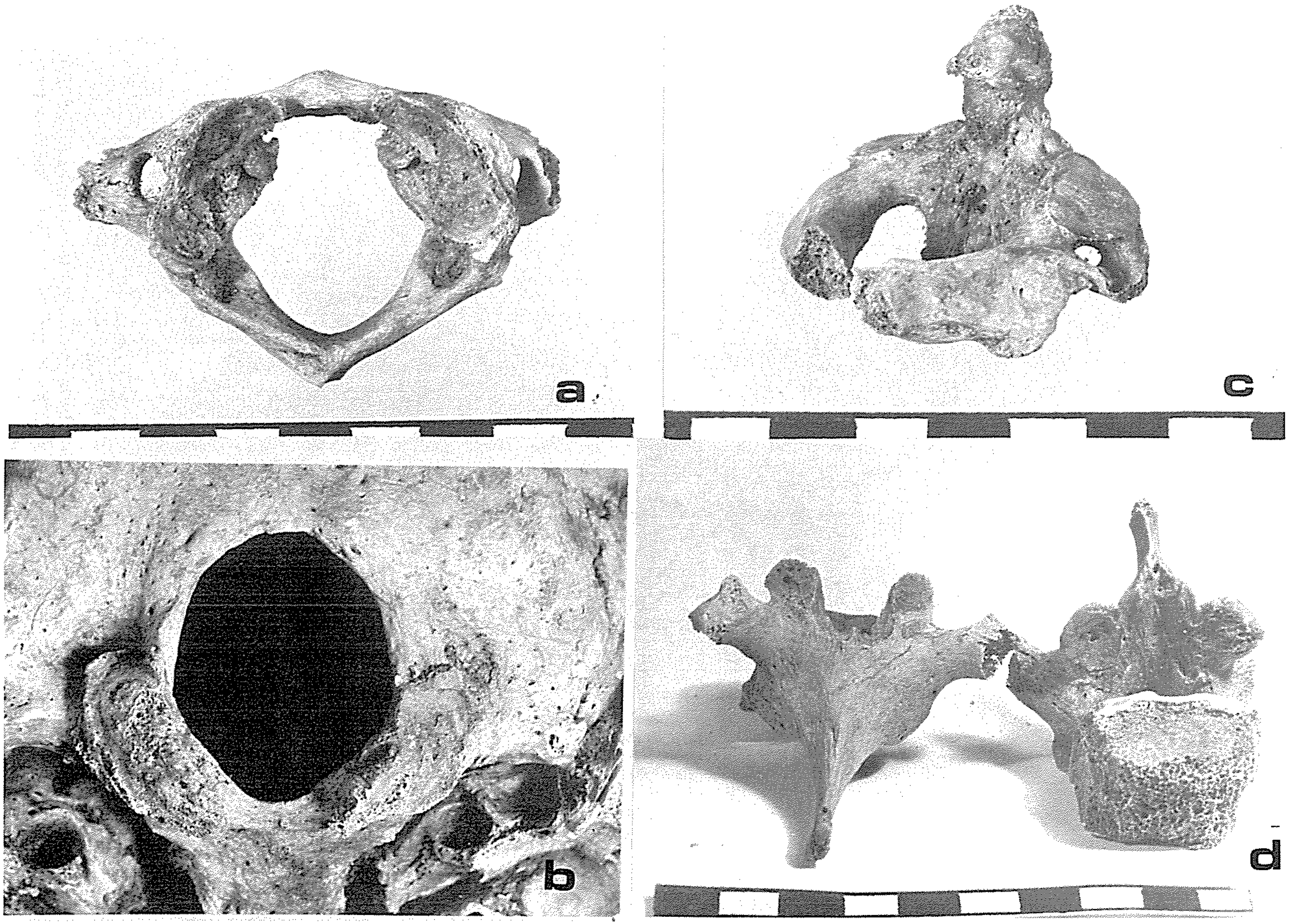


Fig. 5. (a) and (b) show severe osteoarthritic changes of the occipital condyles and the superior articular surfaces of the atlas. (c) The axis showing pathological changes of the odontoid process. (d) Thoracic vertebrae with osteoporotic changes of the small joints as well as postmortal changes of the vertebral body and the processes.

Discussion

The most conspicuous feature of this Polish skull is the malformed mandible. There is bilateral hypoplasia of the mandibular condyles associated with reduced size of the mandibular basal arch.

The facial deformity developed over a period of years. The retardation of the condylar growth was initiated before the age of 5 or 6 years. Otherwise there would not have been sufficient time for the observed remodeling of the jaws.

The shape of the cranial vault is normal. The cranial base appears to be bent to a marked degree. The maxilla shows the evidence of a vertically directed growth with short anterior-posterior size and increased anterior vertical height. The shape of the maxilla is related to the growth pattern of the mandible which rotated posteriorly during the period of growth. The rotation of the lower jaw occurred around a center located at the occluding molars. Anterior open bite did not develop because of compensatory growth of the anterior parts of the jaws.

What is the cause of the mandibular malformation? This type of symmetric malformation is found in cases of congenital syndromes of the first branchial arch, in some cases of injuries to the temporomandibular joints early in childhood and in cases of juvenile rheumatoid arthritis (Still' s disease).

Congenital syndromes derived from pertubations of the first branchial arch usually lead to defective development of many structures. Some of the facial and cranial bones aside from the jaws develop abnormally. The soft tissues such as the ears, eyes, muscles etc. are often involved (Gorlin and Pindborg, '64; Klein, '74; Dahl, Kreiborg and Björk, '75). According to Hövels ('53), the weakest manifestation of a syndrome related to the first branchial arch is a micrognathic mandible.

In the Polish skull the major malformation is located in the mandible. The accumulation of minor bony anomalies such as sutural bones, supernumerary facial foramina and bilateral asymmetries may be part of an intrauterine developmental anomaly.

Hess ('46) found that formation of several Wormian and epipteric bones can occasionally be related to a metabolic disorder of the mesoderm. In the Polish skull there is a tendency to early development of osteoarthritic degenerative changes especially in the cervical spine. These can partly be explained by the altered head posture observed in patients with mandibular micrognathia. Solow and Kraiborg ('77) showed that the continued extension of the head in patients suffering from mandibulofacial dysostosis to counteract the restriction of the naso-oropharyngeal airways caused by the micrognathia altered the head posture in relation to the cervical spine.

The osteoarthritic changes of the small joints in the spine are similar to the ones described by Ingelmark ('63) in a Danish population from the Middle Ages. Such changes were found in 27% of the juvenile skeletons and in 44% of the adult skeletons. The number of affected joints was very low in the juvenile group (0.08% ± 0.4),while the percentage of small joints affected in adults was 6.5% ± 0.79. In the Polish skeleton the limited number of vertebrae examined showed a very high frequency of small joints affected (11 out of 36).

There is no convincing evidence for a postnatal traumatic origin of the mandibular hypoplasia but the fractured molars observed in the dentition require consideration of this possibility. A severe blow to the jaw could have fractured the teeth and caused damage to the joints but there are no bony changes indicating fractures of the condylar necks, no malunions or bony ankylosis. Injuries of the mandibular condyles resulting in mandibular retrognathia usually occur before age 6 (Szlachetko et al., '74). In this case the injury occurred after the second molars had erupted at age 12. The symmetry of the present mandibular deformity also reduces the possibility of a trauma being the cause of the malformation.

The bilateral symmetry of the abnormality suggests a systemic cause - a hematogenous spread of infection to the temporomandibular joints or a polyarthritic collagenous disease.

No primary sites of inflammation were found in the incomplete skeleton under examination. Among the systemic collagenous diseases juvenile rheumatoid arthritis is known to affect the temporomandibular joints with a frequency varying from 14% to 65% according to various surveys (Bache, '64; Schönberger, '67; Georgot et al., '75). When the temporomandibular joints are attacked early in childhood, micrognathia is often the end result (Björk, '62). The temporomandibular joints may be among the first joints to be attacked (Rönning et al., '74) and micrognathia has been observed in different series with a frequency varying from 4% to 30% (Sairanen, '64).

In juvenile rheumatoid arthritis involvement of the cervical spine was noted in 70% of the cases and confirmed radiologically in 54% by Barkin (' 52). In other series the involvement of the cervical spine occurred in 27% to 47% of the children (Laaksonen, '66). Secondary osteo-arthritis is a comparatively common phenomenon in children and juvenile patients. It is found in particular in active and weight-bearing joints (Laaksonen, '66).

The mandibular micrognathia and the arthritic changes of the temporomandibular joints and in the cervical spine are interrelated and compatible with the diagnosis: juvenile rheumatoid arthritis.

Literature cited

Barkin, R. E. 1952 Juvenile rheumatoid arthritis: a long-term follow-up. Ann. rheum.Dis., 11: 316.

Bache, C. 1964 Mandibular growth and dental occlusion in juvenile rheumatoid arthritis. Acta Rheum. Scand., 10: 142-153.

Björk, A. 1962 Facial growth in bilateral hypoplasia of the mandibular condyles. In: Vistas in Orthodontics. Kraus, B. S. and R. A. Riedel, eds. Lea & Febiger, pp. 347-358.

Black, G. V. 1902 Descriptive Anatomy of the Human Teeth. 4th Ed. Philadelphia.

Dahl, E., S. Kreiborg and A. Björk 1975 A morphologic description of a dry skull with mandibulofacial dysostosis. Scand. J. Dent. Res., 83: 257-266.

Georgeot, C., L-N. Neyer, M. Hassan, J. Laufer, F. Hayem and P. Mozziconacci 1975 L' Arthrite Temporo-maxillaire dans la Polyarthrite chronique infantile. Signes cliniques et radiologiques. Ann. Pediat., 22: 477-487.

Gorlin, R. J. and J. J. Pindborg 1964 Syndromes of the Head and Neck. McGraw-Hill Book Company, New York-Toronto-London.

Hess, L. 1946 Ossicula Wormiana. Human Biol. 18: 61-80.

Horowitz, S. L. and E. H. Hixon 1966 The Nature of Orthodontic Diagnosis. The C. V. Mosby Company, St. Louis.

Hurme, V. 1949 Ranges of normalcy in the eruption of permanent teeth. J. Dent. Childr. 16: 11-15.

Hövels, O. 1953 Zur Systematik der Missbildungen des 1. Visceralbogen unter besonderer Berücksichtigung der Dysostosis mandibulo-facialis. 1. Mitteilung. Zeitschr. f. Kinderheilkd. 73: 532-567.

Ingelmark, B. E. 1959 Function of and pathological changes in the spinal joints. Acta Anat. Suppl. 36 = 1 ad Vol. 38, pt. 4: 12-60.

Johansson, G. 1971 Age Determination from Human Teeth. A critical evaluation with special consideration of changes after fourteen years of age. Odont. Revy, Suppl. 21. Diss. Lund.

Klein, D. 1971 Genetic factors and classification of cranio-facial anomalies derived from a pertubation of the first branchial arch. In: Moyers, R. E. and W. M. Krogman, eds. Cranio-facial Growth in Man. Pergamon Press, Oxford. pp. 193-204.

Laaksonen, A.-L. 1966 A Prognostic Study of Juvenile Rheumatoid Arthritis. Analysis of 544 cases. Acta Pædiat. Scand. Suppl. 166.

Lunt, D. 1969 An odontometric study of mediaeval Danes, Acta odont. Scand., vol. 27, Suppl. 55.

Miles, A. E. W. 1963 Dentition in the assessment of individual age in skeletal material. In: Dental Anthropology. Symposia of the Soc. for the Study of Human Biology. D. R. Brothwell, ed. Pergamon Press, Oxford. pp. 191-210.

Rantanen, A. V. 1976 The age of eruption of the third molar teeth. Acta odont. Scand. 25: suppl. 48.

Rönning, O., M.-L. Väliaho and A.-L. Laaksonen 1974 Involvement of Temporomandibular Joint in Juvenile Rheumatoid Arthritis. Scand. J. Rheumatol. 3: 89-96.

Sairanen, E. 1964 On micrognathia in juvenile rheumatoid arthritis. Acta Rheum. Scan. 10: 133-141.

______ 1970 On the etiology of growth disturbance of the mandible in juvenile rheumatoid arthritis. Acta Rheum. Scand. 16: 136-143.

Schönberger, A. 1967 Untersuchungen über Kiefergelenksbeteilungen beim entzündlichen Rheumatismus. Deutsche Zahn-, Mund- u. Kieferheilkd. 49: 150-157.

Solow, B. and S. Kreiborg 1977 Soft-tissue stretching: a possible control factor in craniofacial morphogenesis. J. Dent. Res. 56: Special issue A, A 49 (Abstract).

Szlachetko, K., M. Jackowska, and B. Czarnecka 1974 Disturbances in the structure and functions of the mandible following trauma in childhood. Czas. Stomat. 27: 1369-1376. (In Polish.)

Wells, C. 1964 Bones, Bodies and Disease. Ancient Peoples and Places. Vol. 37. Thames and Hudson, London.

Wiercinski, A. 1962 The racial analysis of human populations in relation to their ethnogenesis. Curr. Anthrop. 3: 2-46.

TABLE 1.

Measurements of the cranium No. 110/63.

Cranial length /g-op/	170
cranial breadth /eu-eu/	142
bregmatic height /ba-b/	140
minimum frontal breadth /ft-ft/	95
upper facial height /n-pr/	77
total facial height /n-gn/	127
bizygomatic breadth /zy-zy/	122?
zygomaxillar breadth /zm-zm/	87
nasal height /n-ns/	53
nasal breadth	22
orbital breadth /mf-ek/	39
orbital height	31
biauricular breadth /au-au/	119
frontal length /n-b/	109
parietal length /b-l/	107
sagital arc /g-op/	271
frontal arc /n-b/	125
parietal arc /b-l/	120
transversal arc /au-au/	302
cranial index	83,5
height-length index	82,3
height-breadth index	98,6
fronto-parietal index	66,9
upper-facial Kolm. ind.	63,1
upper-facial Virch. ind.	88,5
total facial ind.	104,1
nasal index	41,5
orbital index	79,5
sagittal globulling index.	159,4
frontal " "	114,7
parietal " "	112,1
transversal" "	253,8

TABLE 2.

Mesiodistal diameters of maxillary and mandibular teeth in cranium 110/63 and in Medieval Danes

Tooth	Cranium 110/63	Medieval Danes			
		$\bar{x}$	s	n	sex
I^1	8.4	8.80	0.49	24	M
		8.28	0.52	54	F
I^2	6.4	6.78	0.55	33	M
		6.37	0.58	70	F
C	7.6	7.76	0.39	62	M
		7.44	0.35	97	F
P^1	6.4	6.73	0.32	58	M
		6.54	0.33	97	F
P^2	6.3	6.52	0.37	49	M
		6.33	0.36	87	F
M^2	9.8	9.63	0.62	72	M
		9.17	0.58	105	F
M^3	9.2	8.87	0.80	88	M
		8.47	0.68	77	F
I_1	5.5	5.53	0.23	7	M
		5.29	0.25	28	F
I_2	5.9	6.12	0.42	16	M
		5.76	0.32	45	F
C	6.2	6.93	0.35	50	M
		6.51	0.37	82	F
P_1	7.1	6.77	0.43	54	M
		6.62	0.39	94	F
P_2	7.5	6.87	0.39	54	M
		6.64	0.38	81	F
M_3	10.6	10.56	1.07	66	M
		9.97	0.69	71	F

In cranium 110/63 the teeth from the right side of the jaws were measured whenever possible.
The Danish teeth were measured by D. Lunt (Tables XX and XXI, '69).

TABLE **3.**

Buccolingual diameters of maxillary and mandibular teeth in cranium 110/63 and in Medieval Danes

Tooth	Cranium 110/63	Medieval Danes $\bar{x}$	s	n	sex
I^1	7.3	7.33	0.42	40	M
		6.92	0.38	76	F
I^2	6.7	6.46	0.43	43	M
		6.09	0.42	83	F
C	8.9	8.47	0.52	62	M
		8.00	0.48	102	F
P^1	8.9	8.99	0.52	81	M
		8.68	0.50	118	F
P^2	9.25	9.16	0.55	84	M
		8.77	0.54	111	F
M^2	11.4	11.29	0.72	94	M
		10.92	0.66	112	F
M^3	10.5	10.63	0.77	95	M
		10.14	0.84	79	F
I_1	5.8	5.96	0.34	8	M
		5.71	0.29	23	F
I_2	6.1	6.38	0.42	9	M
		6.15	0.39	37	F
C	7.8	7.87	0.48	34	M
		7.34	0.47	74	F
P_1	7.9	7.62	0.45	63	M
		7.33	0.41	95	F
P_2	8.4	8.15	0.50	69	M
		7.84	0.42	95	F
M_3	9.85	9.76	0.73	74	M
		9.33	0.53	75	F

In cranium 110/63 the teeth from the right side of the jaws were measured, except M^2 and I^1, where the left-sided teeth were measured.
The Danish teeth were measured by D. Lunt (Tables XXII and XXIII, '69).

TABLE 4.

Tooth	Root Length		
	Cranium 110/63	Recent American Whites $\bar{x}$	 range
LI^1	17.1	12.0	8.0 - 16.0
LI_1	21.6	17.3	11.0 - 20.5
RM^1	15.5	13.2	10.0 - 16.0
RI_1	15.0	11.8	9.0 - 16.0
RI_2	17.0	12.7	11.0 - 17.0
RC	18.8	15.3	11.0 - 21.0
RP_1	17.3	14.0	11.0 - 18.0
RP_2	16.7	14.4	11.5 - 17.5

Root lengths of selected teeth from the Polish skull compared with root lengths of recent American Whites published by Black (1902).

Some morphological observations on unerupted human deciduous molars

P. M. BUTLER

OSSA

The occlusal morphology of human teeth is greatly influenced by enamel thickness. The dentin surface exhibits conservative features present on the more thinly enamelled crowns of the lower primates. This study reveals unsuspected details of crown morphology which are seen on developing teeth dissected out of fetuses. This paper is concerned with the deciduous molars, especially the first deciduous molars. The first deciduous molars are of special interest because they differ taxonomically in their degree of molarization and have important phylogenetic implications.

The following aspects are described for m^1 and m^2: (1) basal outline and apical foramina; (2) the ectoloph; (3) mesial fovea and mesial marginal ridge; (4) distal marginal ridge and oblique ridge. The following aspects are described for m_1 and m_2: (1) basal outline and apical foramina; (2) protoconid and mesial marginal ridge; (3) metaconid and trigonid basin; (4) talonid. Molarization of all the deciduous molars is considered as well as the Delta variation.

Толщина эмали оказывает сильное влияние на окклюзионную морфологию человеческих зубов. Поверхность дентина обнаруживает установившиеся черты, отмечаемые у более тонко покрытых эмалью коронок низших приматов. Данное исследование выявляет неожиданные детали морфологии коронки, которые наблюдаются у развивающихся зубов в период утробной жизни. Статья посвящена большим коренным молочным зубам, в особенности, первым большим коренным зубам. Эти зубы вызывают особый интерес, поскольку они отличаются таксономически по отношению к степени формирования постоянных зубов и имеют важное филогенетическое значение.

Следующие аспекты описаны для m^1 и m^2 : 1/ базальное очертание и верхушечное отверстие корня зуба; 2/ эктолоф; 3/ медиальная полость и медиальная краевая складка; 4/ дистальная краевая складка и косая складка. Следующие аспекты описаны для m_1 и m_2 : 1/ базальное очертание и верхушечное отверстие корня зуба; 2/ протоконид и медиальная краевая складка; 3/ метаконид и тригональная вдавленность; 4/ талонид. Рассматривается формирование коренных зубов, а также - Дельта вариации.

P.M.Butler, Department of Zoology, Royal Holloway College. Egham, Surreu, England.

Vol. 6, pp. 23-38, Lund. ISSN 0345-8865.

Introduction

The morphology of human teeth is greatly influenced by the thickness of their enamel, which masks many of the finer details of crown structure. The sharp cusps and open valleys of the dentin surface are represented on the enamel surface by low, rounded cusps, separated by narrow grooves or fissures. The dentin surface thus shows conservative features present on the more thinly enamelled crowns of lower primates (Korenhof, 1960, 1961). Studies of developing teeth dissected out of fetuses revealed unsuspected details, such as the presence of minor cusps that are not visible on the completed crowns (Jordan, 1962; Kraus, 1963; Kraus and Jordan, 1965).

This paper is concerned with the crown patterns of the deciduous molars, and especially the first deciduous molars (referred to as m^1 and m_1). The deciduous molars may be regarded as the anterior members of the molar tooth district (Dahlberg, 1950). m^1 and m_1, standing in the most anterior position, are particularly variable, like the third permanent molars at the posterior end of the series. From a phylogenetic point of view, the first deciduous molars are of interest because they differ taxonomically in their degree of molarization. They are molariform in cercopithecids and australopithecines and relatively simple in pongids, while in modern man their molarization is variable (von Koenigswald, 1942; Broom, 1947; Jørgensen, 1956).

It therefore seemed desirable to make a study of the variation of the deciduous molars within a human population. For this purpose I obtained, through the generosity of Dr. M. V. Stack, a collection of calcified tooth caps of infants aged 0-19 weeks from Bristol, England. All are of white race. The collection contains associated m^1 and m_1 from 57 individuals; in 25 of these m^2 is preserved and in 23 also m_2. In addition there are 34 examples of associated m^1 and m_1 from which the enamel has been removed by a soft burr to show the shape of the dentin cap. During a visit to the United States in 1965-6 I was able to study the large collection of prenatal tooth germs made by the late Dr. B. S. Kraus and preserved in the Cleft Palate Center at the University of Pittsburgh. Only specimens in which calcification had begun on at least one cusp are used in the present investigation: 68 examples of m^1, 46 of m^2, 82 of m_1 and 58 of m_2. This collection, obtained from a wide area in the United States, is not racially homogeneous, but it is predominantly of white race.

The method adopted was to compare the two deciduous molars of each jaw, thus using the second molars to interpret the first. Developmental stages seen in the prenatal collection were of much value in understanding the final pattern. For ease of comparison, camera lucida drawings were made of all the specimens studied. In the crown views illustrated in this paper, the tips of cusps are conventionally indicated by small circles, ridges by solid lines and grooves by broken lines. When teeth are incompletely calcified, the area of calcification is shaded. Except in fig. 8, where teeth from both sides are drawn, the mesial side is to the left and the buccal side is above.

Comparison of m^1 with m_2

(i) Basal outline and apical foramina (Fig. 1A). m^1 is smaller than m^2 both in length and in width, but it is more reduced in length than in width. On both teeth the mesial marginal ridge overhangs the base, causing a projection of the outline. Both teeth are narrower distally than mesially, but the distal edge is proportionately more reduced on m^1 than on m^2. The mesiobuccal corner of m^1 is more acute in most specimens of m^1 owing to the development of the tuberculum molare. The lingual margin of m^1 is usually evenly rounded, but in specimens in which the hypocone is best developed the margin is somewhat flattened, though not as much as is normally the case on m^2.

In 32/60 (53%) of the prenatal American specimens of m^1 the distal interradicular tongue of Hertwig's sheath was very short or absent, so that the lingual and distobuccal primary apical foramina were united. In m^2 the proportion was much less: 5/42 (12%). According to Jørgensen (1956), in modern Danes the lingual and distobuccal roots are united more frequently: about 73% on m^1 and about 59% on m^2. Possibly the presence of the interradicular tongue does not prevent root fusion, or alternatively there may be a population difference. A right m^2 in the Kraus collection is abnormal in that the lingual part of the tooth is extended mesiodistally and there are two lingual apical foramina; the buccolingual diameter is reduced. Unfortunately the other teeth of this individual have not been preserved.

(ii) Ectoloph. The structure of the ectoloph (the longitudinal buccal ridge bearing the paracone and metacone) was studied in the American prenatal material.

On m^2 (fig. 2A) the mesial end of the ectoloph was occupied by the parastyle, which rose to form a distinct cusp in 18/36 (50%) cases. Between the parastyle and the paracone the mesial paracone ridge was elevated to form a convex shoulder in 11/36 (31%) cases, and in 3 (8%) it rose above the horizontal to form a small cusp. The distal ridge of the paracone nearly always formed a shoulder, and a cusp in this position was more frequent: 8/36 (25%). The mesial ridge of the metacone also frequently formed a shoulder but in only one case did it rise beyond the horizontal. Distal to the metacone, where the ectoloph turned to form the distal marginal ridge, a metastyle was present in 5/26 (14%) cases. The postnatal material from Bristol showed similar variations, but because of the presence of enamel the minor cusps were less apparent. However, these small cusps could be recognized as pits in the internal surface of the thin dentin caps.

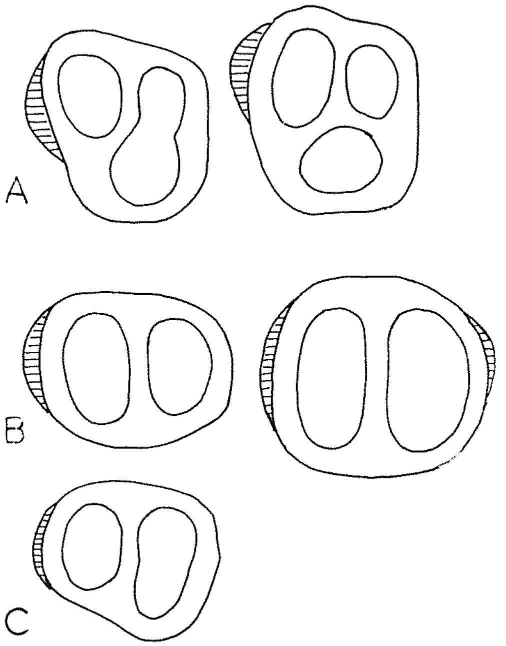


Fig. 1. Basal views of deciduous molars to show primary apical foramina. Overhang of crown over base shaded. A , m^1 and m^2. B, m_1 and m_2. C, Delta variant of m_1.

Out of 25 specimens, the parastyle was present in 11 (44%), the cusp on the mesial paracone ridge in 1 (4%), the cusp on the distal paracone ridge in 10 (40%), and the metastyle in 3 (12%).

The mesial part of the ectoloph (paracone + parastyle) of m^1 is about equal in mesiodistal length to the corresponding part of m^2: in 23 Bristol individuals the ratio of m^1/m^2 averaged 1.07, and ranged 0.9-1.2. The distal part (metacone + metastyle) of m^1 is however much reduced (mean ratio 0.60). In the Bristol specimens from which the enamel had been removed the parastyle was present in 17/34 (50%), the mesial paracone ridge formed a shoulder in 15/34 (44%), and the shoulder rose above the horizontal to form a cusp in 2/34 (6%). Of the enamel-covered specimens 24/50 (48%) showed the parastyle. Thus the variations of the ectoloph mesial to the paracone do not appear to differ significantly in frequency between m^1 and m^2.

One specimen from Bristol is abnormal in that the parastylar region is unusually prominent in a mesial direction. The cusp on the mesial shoulder of the paracone is large in this specimen. Both right and left m^1 show these characters, but m^2, m_1 and m_2 from the same individual are normal.

Distal to the paracone three cusps can develop on m^1: (1) a cusp on the distal paracone ridge, corresponding to that which frequently occurs on m^2, (2) the metacone and (3) the metastyle. Cusp (1) arises early in ontogeny, before calcification appears on the paracone. Jordan (1962) called it the distal parastyle, a name not altogether satisfactory as one thinks of the parastyle as a mesial cuspule; I propose to refer to it as the distal paracone shoulder cusp. Though it probably begins to calcify from a separate center, it rapidly becomes incorporated in the calcified area that spreads down from the paracone. The metacone arises more distally and is divided from the paracone by a deeper valley, so that it remains for a longer time as an independent area of calcification. The metastyle develops on the distal shoulder of the metacone and is only

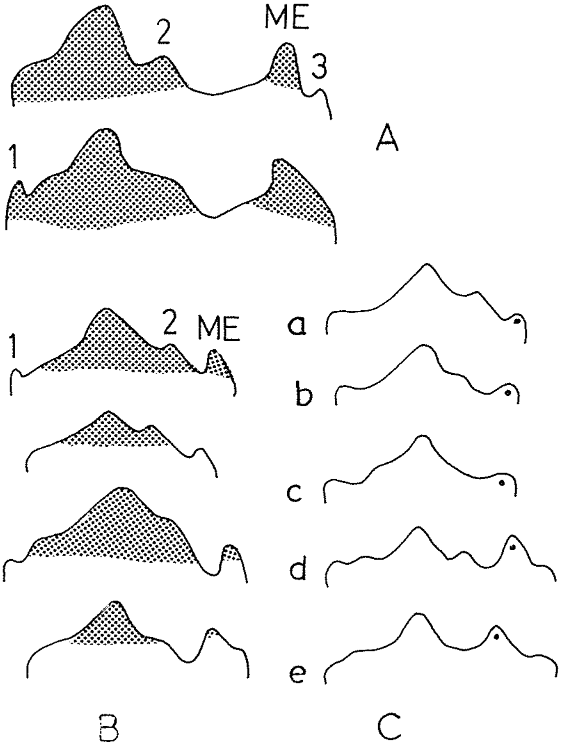


Fig. 2. Ectoloph of upper deciduous molars.
A, two variants of m^2 (prenatal)
B, prenatal examples of m^1, at a similar stage of development to A
C, postnatal specimens of m^1 with enamel removed, to show variations of the region distal to the paracone.
1, parastyle;
2, distal paracone shoulder cusp;
3, metastyle;
ME, metacone.
On the C the metacone is marked with a spot.

present when that cusp is relatively large. Often only two of these cusps are present and it is sometimes difficult to decide which is missing. A large distal shoulder cusp followed by a small metacone can easily be confused with a large metacone followed by a metastyle. Discrimination between these two conditions was based principally on the assumption that the valley mesial to the metacone is deeper than the valley between the metacone and metastyle, or that between the paracone and the distal shoulder cusp. In a few cases the presence of a strongly developed metastyle on m^2 was taken as evidence that the metastyle was present on m^1 of the same individual.

On this basis the Bristol material was classified as follows:- (fig. 2C)
(a) Metacone small, its mesiodistal length not more than 1/3 of the length of the paracone + parastyle; distal paracone shoulder cusp higher than the metacone; metastylar shoulder absent.
(b) As in (a), but the shoulder cusp small, or represented only by the shoulder.
(c) As in (a), but distal paracone shoulder absent.
(d) Metacone larger, its length 40% or more of the length of the paracone + parastyle; paracone shoulder present; metastyle usually present, sometimes developing a cusp.
(e) As in (d), but paracone shoulder absent.

The enamel-freed dentin caps (N=34) divided thus: (a) 6 (18%), (b) 5 (15%), (c) 6 (18%), (d) 6 (18%), (e) 11 (32%). When classifying the enamel-covered caps the state of the cusps was checked by examination of the internal surface of the dentin. This collection (N=47) divided as follows: (a) 8(17%), (b) 7(15%), (c) 3 (6%), (d) 15 (32%),

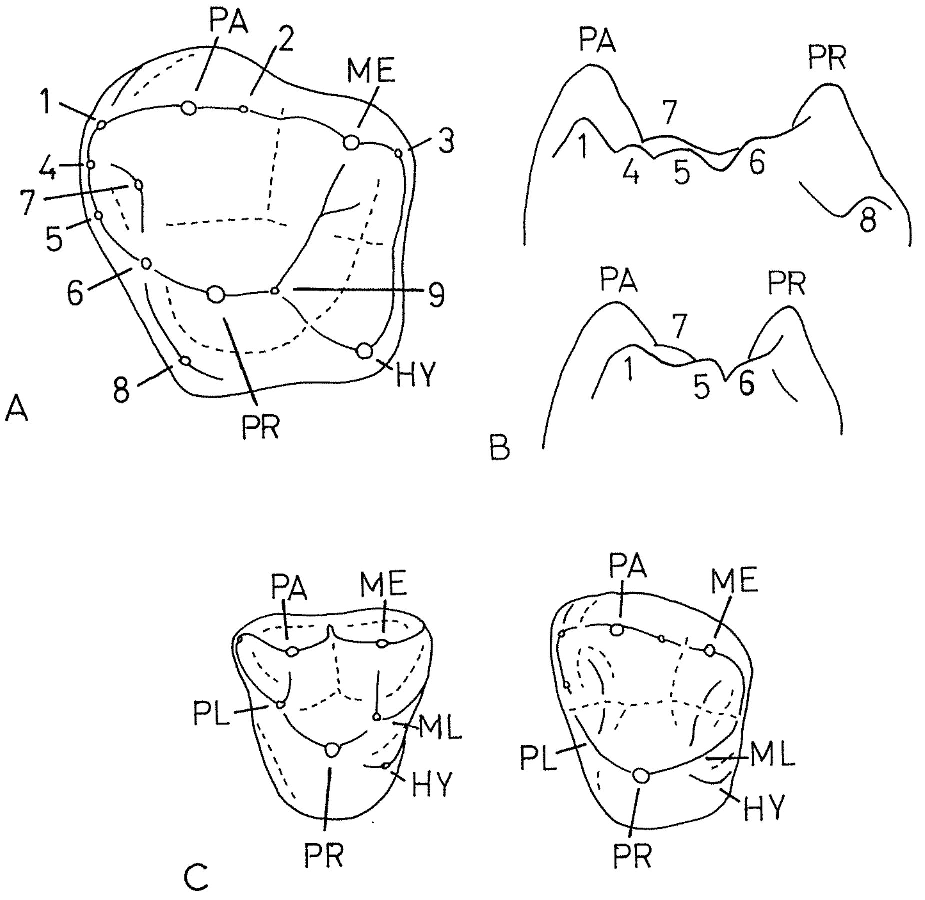


Fig. 3. A, Crown view of m^2 showing the most frequently occurring cusps. PA, paracone; ME, metacone; PR, protocone; HY, hypocone; 1, parastyle; 2, distal paracone shoulder cusp; 3, metastyle; 4 and 5, mesial marginal ridge cuspules; 6, paraconule; 7, foveal cuspule; 8, Carabelli's cusp; 9, metaconule.
B, Mesial views of m^2 and m^1. Labelling as A.
C, dm^4 of Plesiadapis gidleyi, compared with human m^1 with hypocone region of type (c). Labelling as A except ML, metaconule, PL, paraconule.

(e) 14 (30%). The difference between the two results in (c) and (d) may be ascribed to difficulty in determining the boundary between the paracone and the metacone in the enamel-free teeth, combined with difficulty in judging the development of the paracone shoulder in the enamel-covered teeth.

In three specimens the metacone was represented by two cusps of equal height, placed closely together.

(iii) Mesial fovea and mesial marginal ridge (Fig. 3). On m^2 some small cusps develop along the mesial marginal ridge, as described by Kraus (1963). They appear shortly before calcification spreads to the ridge, and for a short time they calcify separately. Study of specimens in the Kraus collection showed that there are normally two cuspules between the parastyle and the point where the marginal ridge is crossed by the main mesiodistal groove of the tooth. Beyond this point, a third cuspule arises where the mesial ridge of the protocone meets the mesiolingual (Carabelli) cingulum; this cuspule is the paraconule (= protoconule). On the enamel-covered teeth all these cuspules could be seen as minor elevations of the enamel surface.

Distal to the marginal ridge there usually develops another small cusp. which for a short time calcifies separately until it becomes joined with the paracone. I will refer to it as the foveal cuspule. It is usually connected by short ridge to the marginal cuspule that stands nearest to the parastyle, and lingually it extends as a ridge towards the paraconule. With the development of enamel, the foveal cuspule becomes the "drop-shaped swelling" of Jørgensen (1956:128). The valley between the foveal cuspule and the marginal ridge is the mesial fovea. Frequently the foveal cuspule fails to join the paraconule, and then the mesial fovea opens into the trigon basin.

On m^1 the mesial marginal ridge is strongly developed, and in about half the specimens it develops one cuspule lingual to the parastyle. This cuspule stands at the lingual end of the ridge, immediately buccal to the mesial end of the main longitudinal groove. It corresponds to the more lingual of the two cuspules that stand on the marginal ridge of m^2. The paraconule is represented on m^1 only by a shoulder on the mesial ridge of the protocone. The foveal cuspule is present on about half of the Bristol specimens, but it is frequently very small, and the American prenatal material showed that it does not calcify independently of the paracone. In a few cases the foveal cuspule is connected across the main mesiodistal groove to the mesial ridge of the protocone. On the internal dentin surface the foveal cuspule of m^1 is represented by a groove, showing that it is a feature of the enamel-dentin junction and not merely a localized enamel thickening.

On m^1 a groove in the enamel of the lingual surface marks off the rudimentary paraconule from the protocone, and in some cases a rounded ridge on the lingual side of the paraconule swells at the base to form the rudimentary equivalent of Carabelli's cusp.

(iv) Distal marginal ridge and oblique ridge. In some cases the oblique ridge of m^2 runs directly from the protocone to the metacone, but more usually it meets the distal ridge of the protocone at a point distal to the tip of the protocone (Fig. 3A). At the junction of the two ridges a cusp sometimes develops: this is the metaconule. The oblique ridge is usually continuous, but in some cases it is crossed by a faint groove in the enamel, continuous with the main longitudinal groove of the tooth. The hypocone is connected by its mesial ridge to the distal ridge of the protocone, the junction taking place at the position of the metaconule. The mesial ridge of the hypocone varies in prominence; when it is weak the hypocone is separated from the protocone by a groove that opens into the distal fovea. The distal marginal ridge connects the hypocone with the distal ridge of the metacone. The distal fovea, which lies between the distal ridge and the oblique ridge, is partly broken up in about 20% of the specimens by short ridges that branch off from the distal side of the oblique ridge.

The distal part of m^1 is reduced in comparison with m^2 and much more variable in structure (Fig. 4). The oblique ridge runs in a transverse direction. It is continuous in only 7/48 (15%) of the enamel-covered Bristol specimens: usually it is divided into buccal and lingual parts by the main longitudinal groove, but in 9/48 (19%) its buccal or lingual portions or both are absent. The hypocone is developed as a definite cusp in 11/48 (23%) of the Bristol specimens and in 17/68 (25%) of the prenatal American specimens.

There is considerable variation in the arrangement of ridges on the distolingual part of m^1. The specimens can be classified in four groups (Fig. 4):

(a) In the most molariform specimens of m^1 the hypocone stands directly distal to the protocone, to which it is connected by a ridge of variable strength; in some cases the ridge is weak and the cusps are separated by a groove.

(b) The distal protocone ridge runs directly distal to meet the edge of the crown in the position of the hypocone, but that cusp is not developed.

(c) The distal protocone ridge curves buccally, and the hypocone is represented by a short ridge or a swelling to the lingual side of the distal protocone ridge.

(d) No trace of the hypocone can be made out, the distal protocone ridge passing smoothly into the distal marginal ridge.

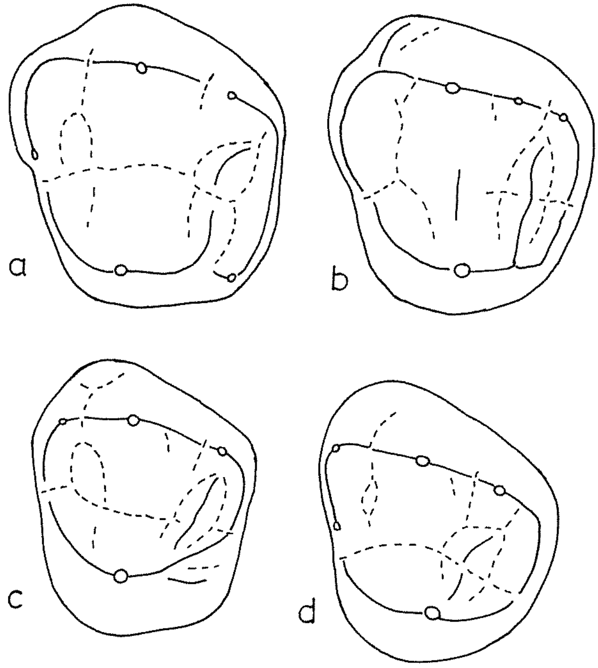


Fig. 4. Variations of the distolingual region of m^1.

The 48 Bristol specimens divided thus: (a) 11 (23%), (b) 17.5 (36%), (c) 16.5 (34%), (d) 4 (8%). (One specimen different on the two sides, the right tooth in group (b) and the left in group (c).)

Only in groups (a) and (b) is the distal marginal ridge continuous up to the distolingual corner of the crown; in groups (c) and (d) it is diverted towards the protocone (actually towards the position of the metaconule), and the hypocone rudiment in group (c) is marked off from it by a groove. Teeth of group (c) resemble primitive tribosphenic molars in which a ridge from the metaconule passes along the distal margin and the hypocone is represented by a distolingual cingulum (Fig. 3C).

In only 2/48 (4%) of the Bristol specimens does the buccal end of the oblique ridge join the metacone directly; in nearly all it points more distally, and in some cases it joins the distal marginal ridge. This connection may represent a ridge branching distally from the oblique ridge on m^2. Jørgensen (1956:149-50) referred to the buccal portion of the oblique ridge of m^1 as a "drop-like enamel formation", but it is represented in the enamel-dentin junction. He rightly rejected the view of Jones (1947) that it is homologous with the metaconule.

On 7/48 (15%) of the Bristol specimens (one on the left side only) the main longitudinal groove is interrupted by a transverse ridge between the bases of the protocone and the paracone (Fig. 4B). In two of these cases the oblique ridge is absent. On one specimen a ridge branches from the mesial side of the oblique ridge near its lingual end and crosses the basin towards the metacone.

Comparison of m_1 with m_2

(i) Basal outline and apical foramina. (Fig. 1B). m_1 is smaller than m_2, especially in buccolingual width. It is widest across the mesial part of the crown, at the level of the protoconid, whereas m_2 is widest near the middle, across the hypoconid. In prenatal specimens of m_1 the primary apical foramen for the mesial root is somewhat greater in buccolingual diameter than that for the distal root; whereas on m_2 the two primary apical foramina are equal or the distal one is slightly the larger. The mesiobuccal corner of the outline of m_1 is more prominent than the mesiolingual corner, due to the development of the tuberculum molare, but on m_2 the mesial border of the crown is evenly rounded. On the other hand, the distobuccal corner is more prominent on m_2 than on m_1 owing to the greater development of the hypoconulid.

m_1 sometimes departs markedly from its normal shape to produce the so-called Delta-form (Jørgensen, 1956). It is proportionately broader, approaching a triangle in outline, and the distal apical foramen is extended lingually (Fig. 1C). According to Jørgensen, a third root may be present. This variation, which does not occur in m_2, is described in a separate section.

(ii) Protoconid and mesial marginal ridge. The protoconid of m_1 is longer mesiodistally than on m_2 (mean ratio 1.22, range in 18 comparisons 1.1-1.4). The difference is mainly due to the greater length of the mesial protoconid ridge. This continues lingually to form the mesial marginal ridge as far as the base of the metaconid. On m_2 a cuspule may develop on the marginal ridge (Fig. 5A, B). It was found in about one-third of the older prenatal specimens in the Kraus collection. It occurs also on the first permanent molar, and it is represented on some specimens of m_1 by an elevation at the mesial end of the mesial protoconid ridge. This cuspule is very probably the paraconid.

On m_1 and m_2 the distal ridge of the protoconid nearly always develops a shoulder. On 15% of the enamel-free caps from Bristol the profile rises above the horizontal to form a small cusp, like the distal paracone shoulder cusp of m^1. This cusp was not observed on m_2 (Fig. 5C, D).

(iii) Metaconid and trigonid basin. The metaconid of m_1 is situated closer to the protoconid and in a more distal position than on m_2. As the trigonid becomes more molariform, the metaconid comes to occupy a more mesial position, and the angle between the mesial protoconid ridge and a line drawn through the tips of the protoconid and metaconid (the trigonid angle) becomes less obtuse (Fig. 7). The distal ridge of the metaconid develops a shoulder in nearly all specimens of m_2, and in 14/38 (37%) of the prenatal specimens in the Kraus collection the profile rises above the horizontal to form a cusp (Fig. 5F). This cusp is the metastylid (cusp 7). The shoulder is present in about half the specimens of m_1 but the cusp is rarely developed: it was seen on one prenatal specimen and on one of the Bristol teeth.

On m_2 a buccal ridge on the metaconid may join a lingual ridge on the protoconid, but both ridges fall steeply and their connection lies at a very low level, below that of the mesial marginal ridge. Together, the ridges are equivalent to the distal trigonid ridge that separates the trigonid and talonid basins (Fig. 6): In 10/17 specimens from Bristol the ridges do not meet, but end blindly, and the two basins are in communication. In 5 of these cases the metaconid ridge points not towards the protoconid but more distally, in one specimen ending opposite a lingual ridge on the distal shoulder of the protoconid. On m_1 the groove between the protoconid and the metaconid is interrupted by a ridge in 29/47 (62%) cases, and in all cases the groove lies at a much higher level than the mesial marginal ridge. This difference is reflected in the mode of calcification of the trigonid: on m_2 the calcified area of the metaconid unites with that of the protoconid first along the mesial marginal ridge, whereas on m_1 the junction between the two cusps is made directly, along the protoconid-metaconid ridge.

(iv) Talonid. On m_2 the length of the talonid, measured from the groove between the protoconid and the hypoconid, is about 60% of the length of the tooth. On m_1 the talonid is much smaller: on the most molarized examples the proportion is about 45%

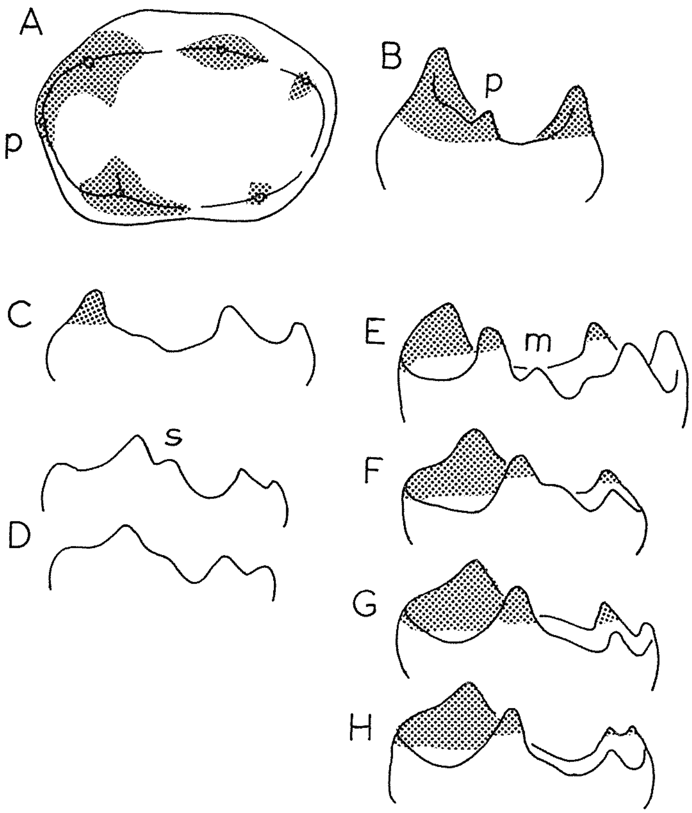


Fig. 5. A, Prenatal specimen of m_2 showing paraconid (p). B, the same, mesial view. C, Prenatal specimen of m_2, buccal view. D, postnatal specimens of m_1 with enamel removed, buccal view. One has a cusp (s) on the distal shoulder of the protoconid. E - H, prenatal specimens at a similar stage of development. E, m_2 with metastylid (m). F, m_1 with metastylid shoulder; hypoconulid absent. G, H, variations in the development of the hypoconulid.

and it may be as small as 31%. The talonid of m_2 normally bears three cusps, hypoconid and hypoconulid buccally and entoconid lingually, but an additional distolingual cusp (cusp 6) is present in 3/33 (9%) of the prenatal specimens and 2/15 (13%) of the Bristol specimens.

The talonid cusps of m_1 show more variation, particularly in the development of the hypoconulid. In a sample of 54 prenatal specimens in the Kraus collection the hypoconulid was absent in 10 (18%); situated very close to the tip of the hypoconid, which appeared to be twinned, in 5 (9%); distinct, but much nearer the hypoconid than the entoconid, in 22 (41%); and nearly equidistant between the hypoconid and the entoconid in 17 (31%). In the Bristol material the hypoconulid is absent on at least one side of the mouth in 7/50 (14%); the distal marginal ridge is marked off from the hypoconid by a groove (Fig. 7A). Two specimens show a slight elevation of the marginal ridge on one side of the mouth, representing a rudimentary hypoconulid. In 4/50 (8%) cases the hypoconulid is closely twinned with the hypoconid, so that there appears to

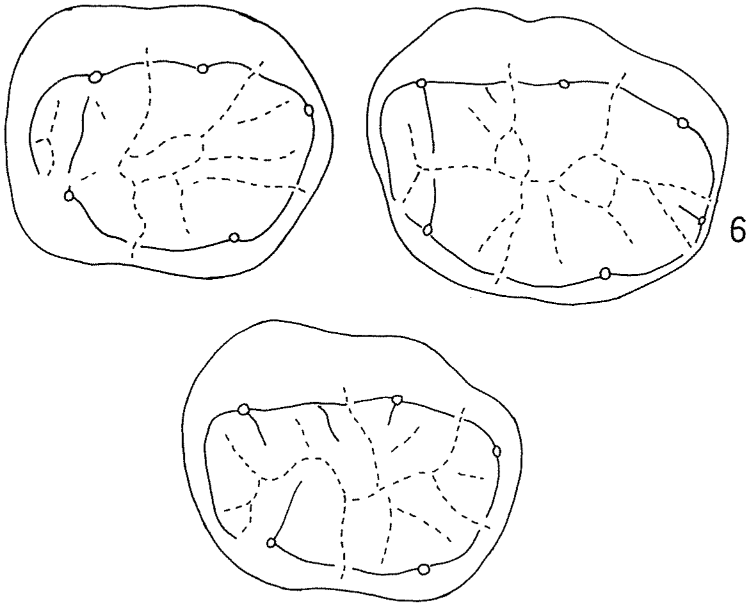


Fig. 6. Examples of m_2 to show variations in the development of the distal trigonid ridge. One specimen has cusp 6.

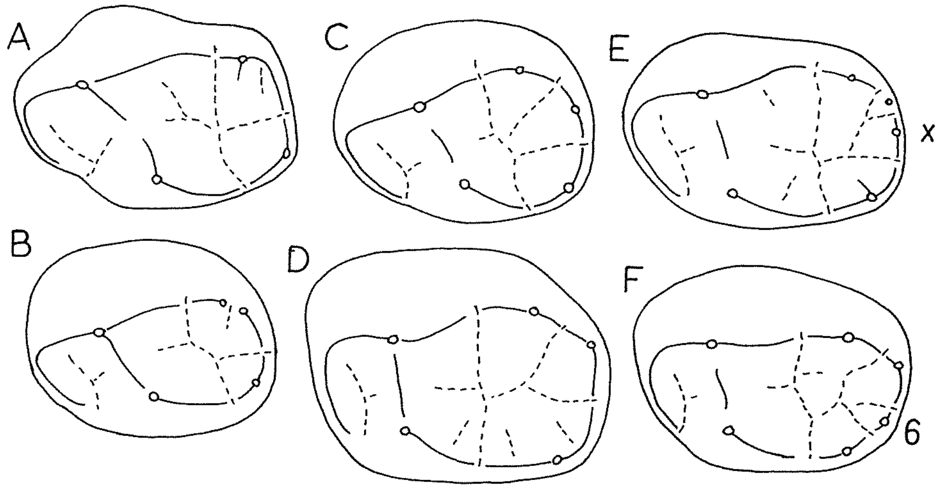


Fig. 7. Variations of the talonid of m_1. X, additional cusp, lingual to the hypoconulid.

be a single distobuccal cusp, divided by an enamel groove at the tip (Fig. 7B).

Jørgensen (1956) questioned whether the twinned hypoconulid of m_1 is homologous with the hypoconulid of m_2. Specimens of m_1 in the Kraus collection of 21-23 weeks fetal age already show a difference in the development of the hypoconulid. In some the hypoconulid and hypoconid are of equal height and calcify at the same time, soon becoming joined (Fig. 5H); in others the hypoconulid is smaller than the hypoconid and it calcifies later (Fig. 5G), as it always does on m_2. In a few cases the hypoconulid appears to be duplicated. Thus two specimens (fetal ages 26 and 31 weeks) have two cusps distal to the hypoconid, both well-separated from that cusp and not as high. One Bristol specimen (Fig. 7E) shows this structure on the right side of the mouth but not on the left. A Negro fetus aged 24 weeks has a double-tipped hypoconid, followed by a lower, uncalcified hypoconulid; m_2 of the same individual is abnormal in having a double-tipped hypoconulid. A specimen aged 35 weeks has three small cusps between the hypoconid and the entoconid. None of these cases provides convincing evidence that the two sorts of hypoconulid, illustrated in Figs. 5G and 5H, represent different cusps; they are better regarded as variations in the development of the same cusp, which corresponds to the hypoconulid of m_2.

The entoconid of m_1 varies considerably in size, often differing on the two sides of the mouth. Among the Bristol specimens, in 3/50 cases (6%) the entoconid is absent or extremely rudimentary. In 2 cases (4%) cusp 6 is present (Fig. 7F). Of the prenatal specimens, cusp 6 occurs in 6/54 (11%), and in one the entoconid is twinned.

Owing to their smaller size, the talonid cusps of m_1 are simpler in form than those of m_2. The mesial ridge of the hypoconid forms a shoulder in about 40% of the specimens of m_2 but only in about 10% of m_1. On the entoconid there is a mesial shoulder in about 85% of m_2 and about 20% of m_1. A distal shoulder is present in about 50% of m_2 and 10% of m_1. Ridges from the cusps and their shoulders pass down into the talonid basin, at the bottom of which are a number of minor elevations. These features of the interior of the basin are reflected on the internal surface of the dentin cap when this is thin, showing that they involve the dentin-enamel junction and are not merely localized thickenings of enamel. On both the deciduous molars the entoconid is the last cusp to remain independent as a calcified area. The last part of the talonid basin to calcify is situated opposite the groove between the metaconid and the entoconid, somewhat to the lingual side of the midline of the tooth.

Molarization

The two deciduous molars of each jaw can be compared in considerable detail. By changing the relative development of the parts, the pattern of one tooth can easily be conceived as transformable into the pattern of the other. Moreover, variations of the second molars are repeated on the first molars, sometimes with similar frequency (e.g. parastyle, cusp 6), or sometimes with a different frequency (e.g. metastylid). The morphogenetic processes involved in the development of the two deciduous molars must be essentially similar.

Compared with m^2, m^1 is most reduced at the distal end (metacone and hypocone regions) and least reduced, or even enlarged, in the mesiobuccal (paracone) region. Likewise, m_1 has a smaller talonid and a larger protoconid than m_2. Much of the variation of the first deciduous molars is towards or away from the pattern of the second deciduous molars. Thus on m^1 the metacone may be larger or smaller, and the hypocone may be present as a cusp or it may be rudimentary or absent; on m_1 the talonid may be longer or shorter, with larger or smaller hypoconulid, and the trigonid may be shorter and more transversally developed or elongate with a distally placed metaconid. Thus the difference between the two deciduous molars is to an extent bridged by their variations. In mammals generally it is a common phenomenon that teeth tend to vary and evolve so as to become more or less like adjacent teeth. To explain this it was postulated (Butler, 1937, 1963) that there exists in the jaw of the embryo a morphogenetic gradient or "field" which controls the development of the teeth. Variations in the mesial extent of the molar region of the field, for example, would lead to the first deciduous molars coming to a variable degree under its influence, and so varying in their degree of molarization.

If this were so it would be expected that those distal parts of m^1 and m_1 which differentiate them most from the second deciduous molars would vary correlatively, as all would be affected by the same field. Inspection of the teeth shows, however, that the metacone, hypocone and talonid to a large extent vary independently: for example, a relatively molarized hypocone is associated in some individuals with a small metacone or with a small talonid. A 2 x 2 test was made, in which the metacones were divided into more molarized (types d and e) and less molarized (types a, b and c), and the hypocones into more molarized (types a and b) and less molarized types c and d). The association was significant only at the 10% level (chi^2 = 2..76). Nevertheless, in the cases both of the metacone and the hypocone, the higher level of molarization is associated with a greater average talonid development on the lower tooth (Table 1). The correlation coeffient of metacone length with talonid length was also calculated: it was found to be weak (r= 0.34) but significant at the 5% level.

TABLE 1.

	metacone		
	a + b + c	d + e	
hypocone			
a + b	7.5	18	
c + d	10	8.5	chi^2 = 2.76

	talonid length / total length, m_1			
	N	mean	S. D.	t
metacone, m^1				
a + b + c	17	0.372	0.056	2.81
d + e	26	0.413	0.032	
hypocone, m^1				
a + b	25	0.411	0.039	2.73
c + d	19	0.370	0.060	

In a study of molarization of the deciduous molars in the order Perissodactyla (Butler, 1952) it was found that the teeth evolved as if they were a mosaic of a number of parts which molarized at different times and at different rates. Thus the talonid could become molariform before the trigonid, and the hypocone could be better developed than the protocone. It was suggested that the cusps might differ in their sensitivity to the molarization gradient, i.e. in the threshold level of the gradient at which they make their appearance. A similar idea was put forward by Dahlberg (1948, 1950, 1971). The genes responsible for dental traits differ, not only in the frequency with which they affect any one tooth but in the range of teeth in which they find expression. Under the action of modifiers a gene might extend its range forward, being able to produce an effect lower in the molarization gradient. If the pattern of the teeth were controlled by several genes which vary independently in their relation to the gradient, the poor correlation between elements of the tooth during molarization might be explained.

Interaction between the parts of the developing tooth cannot however be left out of account. Some evidence for this is provided by a negative correlation between the length of the metacone and the length of the paracone + parastyle. In 55 specimens, r was found to be -0.38, significant at the 1% level. Perhaps enlargement of the paracone

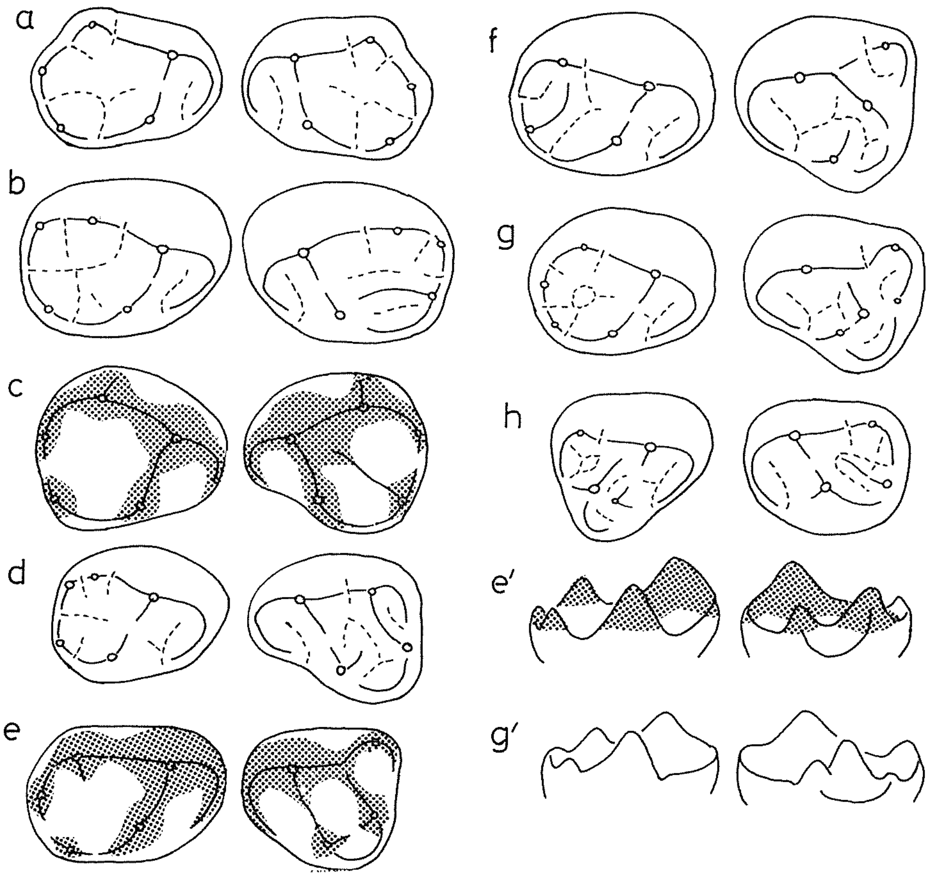


Fig. 8. The Delta variation of m_1 . e′ and g′ are lingual views.

inhibits the development of the metacone. Mechanical factors may also play a part; this is indicated by a consideration of the Delta variation of m_1, described below.

The Delta variation

Jørgensen (1956:92-3) gave the following characteristics of a deviant form of m_1 which he called the Δ form: (1) the occlusal surface is broadly triangular, tapering to a lingual point at the groove between the metaconid and entoconid; (2) the metaconid and entoconid are closer together and sometimes united; (3) the hypoconid shows a tendency to buccal displacement, so that the groove separating it from the protoconid is deepened; (4) there is a tendency for the variation to occur unilaterally. This form of m_1 occurred in 3.1% of the medieval Danish specimens studied by Jørgensen.

In the Bristol collection 4/57 specimens (7%) conform to this definition; 3 are from the right side and one from the left (Fig. 8 d, f, g, h). Two prenatal examples were found in the Kraus collection. In one of these the right side is affected and the left side is normal (e); in the other, both sides are moderately affected, the right more than the left (c).

In all cases the protoconid and the mesial marginal ridge are normal. In four cases (e, f, g, h) the metaconid is reduced in height and the entoconid is enlarged, so that the entoconid is higher than the metaconid. In the two least modified cases (c, d) the entoconid is not enlarged and it stands as far away from the metaconid as on the contralateral tooth; however, the talonid basin extends lingually between the two cusps, and the marginal ridge that connects them is bent in a lingual direction. In the remaining four cases (e, f, g, h) the metaconid and entoconid are connected by a ridge directly, and the curved ridge of the milder cases remains to form a cingulum ledge. The two cusps approach each other in various degrees, the entoconid becoming displaced from the margin of the crown to occupy a more central position. In the two most extreme cases (g, h) the metaconid appears as a minor cuspule on the mesial side of the entoconid. A constant feature of these teeth is a strong ridge running mesiobuccally from the entoconid. In one specimen (d) the ridge runs towards the hypoconid, and in five it is connected to the distal ridge of the protoconid. The hypoconid in the least modified case (c) is in a normal position, but it possesses a strong buccal ridge. In the remainder the cusp is displaced buccally so that its buccal slope is more vertical than normal. Specimen c has a normal, but small hypoconulid; in the other specimens this cusp is missing, unless it is represented in g by a cuspule situated distal to the entoconid.

The contralateral teeth show abnormal features in some cases. The left m_1 of the least modified specimen (c) is widened across the talonid as much as on the right side. It also possesses a buccal ridge on the hypoconid, but there is no mesiobuccal ridge on the entoconid. This last ridge is present on the contralateral teeth of f and h: in f it is connected to the hypoconid. Most of the contralateral teeth are broader than normal, but not all.

Two cases were noticed which, though classified as normal, possessed some of the characters of the Delta-form. In one of these (Fig 8 b) the entoconid on the right side is connected to the base of the metaconid by a ridge which cuts the talonid basin in two; the left tooth is normal. In a second case (a), on both sides, the talonid is widened and the hypoconid is displaced buccally.

Jørgensen (1956) suggested that the Delta-form of m_1 might be produced by pressure due to lack of space in the jaw during growth. Certainly these teeth have the appearance of having been distorted by coming up against an obstruction at the distal end during their growth, perhaps m_2. The two prenatal specimens had already developed calcification on all the cusps (fetal ages 29 and 30-31 weeks respectively), so they throw no light on this question. The unilateral incidence of the abnormality and the absence of similar modifications of the other teeth suggests a localized environmental cause. Whatever this may be, it is interesting to note that it results in considerable changes in the relative size and position of the cusps and the development of ridges. One prenatal specimen (e), in which the metaconid is reduced in size, has an abnormal calcification pattern: the entoconid has joined with the protoconid and hypoconid while the metaconid is still separate. Jørgensen noted that the more advanced cases had three roots. If these departures from the norm can be produced by an environmental factor such as pressure, it may be safely assumed that also in normal development environmental factors play a significant part.

References

Broom, R. 1947 The upper milk molars of the ape-man. Plesianthropus. Nature 159: 602.

Butler, P. M. 1937 Studies of the mammalian dentition. Differentiation of the post-canine dentition. Proc. zool. Soc. Lond. 109B: 1-36.

______ 1952 The milk molars of Perissodactyla, with remarks on molar occlusion. Proc. zool. Soc. Lond. 121: 777-817.

______ 1963 Tooth morphology and primate evolution. In: D. R. Brothwell (ed.) Dental Anthropology. Symp. Soc. Study hum. Biol. 5. Pergamon Press, Oxford, pp. 1-14.

Dahlberg, A. A. 1945 The changing dentition of man. J. Am. dent. Ass. 32: 676-690.

______ 1950 The evolutionary significance of the protostylid. Am. J. phys. Anthrop. (N. S.) 8: 15-25.

______ 1971 Penetrance and expressivity of dental traits. In: A. A. Dahlberg (ed.), Dental Morphology and Evolution, Univ. Chicago Press, Chicago. pp. 257-262.

Jones, H. G. 1947 The primary dentition in Homo sapiens and the search for primitive features. Am. J. phys. Anthrop. (N. S.) 5: 251-281.

Jordan, R. E. 1962 Fetal primary molar development in American Whites, Negroes and Indians: a morphological analysis. M. Sc. thesis, Univ. of Washington.

Jørgensen, K. D. 1956 The deciduous dentition. A descriptive and comparative anatomical study. Acta odont. Scand. 14, suppl. 20: 1-202.

von Koenigswald, G. H. R. 1942 The South African man-apes and Pithecanthropus. Publ. Carneg. Inst. Washington 530: 205-222.

Korenhof, C. A. W. 1960 Morphogenetical aspects of the human upper molar. A comparative study of its enamel and dentine surfaces and their relationship to the crown pattern of fossil and recent primates. Acad. proefschrift, Utrecht, Uitg. mij. Neerl. 368 pp.

______ 1961 The enamel-dentine border: a new morphological factor in the study of the(human) molar pattern. Proc. K. ned. Akad. Wet. (B) 64: 639-664.

Kraus, B. S. 1963 Morphogenesis of deciduous molar pattern in man. In: D. R. Brothwell (ed.), Dental Anthropology. Symp. Soc. Study hum. Biol. 5. Pergamon Press, Oxford. pp. 87-104.

Kraus, B. S. & R. E. Jordan 1965 The Human Dentition Before Birth. Lea & Febinger, Philadelphia, 218 pp.

Age changes in facial morphology of an Alaskan Eskimo population

ROBERT CEDERQUIST[1] AND ALBERT A. DAHLBERG[2]

OSSA

This investigation describes, cephalometrically, the craniofacial morphology of the Wainwright Eskimo population. The influence of sex and age was examined to help explain the adaptive significance of some of the characteristic morphological features of the Eskimo face. Further, in order to find possible indicators of changes in functional adaptation, the contemporary Eskimo face was compared with those of two Eskimo skeletal populations, one of precontact origin consisting of 55 skulls (data from Hylander, '72, and one dated about 1860 A. D. comprising 35 skulls (data from Dahlberg, '68).

The Wainwright sample consisted of 188 individuals, 96 males and 92 females. Roentgenographic cephalograms were used for analysis. They were divided into five groups, based on the age of the individual at the time of the examination. A digitizing system and a FORTRAN IV program were employed for the calculation of linear and angular measurements. Significance tests were performed for sexual dimorphism and for differences associated with age.

In the Wainwright population males exhibit more facial flatness than females, even though flatness increases with age for both sexes. Anterior mandibular rotation and mandibular basal prognathism increase with advancing age for both males and females, with concomitant reduction of apical base relation and dental overjet and closing of the gonial angle. No statistically significant differences were detected in midfacial flatness between the Wainwright sample and the skeletal material. The data from this study support the interpretation that midfacial flatness is an adaptation to biomechanical demands. The pronounced and progressive uprighting of the anterior dentition is also seen as an indicator of heavy mechanical function.

The anteroposterior dimension of the frontal sinus becomes progressively larger with age in both males and females from Wainwright. When compared with the skeletal material from Hudson Bay, the frontal sinus of the contemporary Eskimo is significantly larger. The Wainwright sample also has significantly more cranial base flexion. It is suggested that frontal sinus form is a bifactorial consequence, where the determinants are neurocranial form and biomechanical requirements in response to sinus function as space-framed structures (cf. Badoux, '66).

Keywords: Face, Eskimo, Age changes, Functional adaptation, Cephalometrics.

В исследовании цефалометрически описана морфология лицевого черепа эскимосского населения из области фиорда Вайнрайт. Было изучено влияние пола и возраста с целью объяснения адаптивного значения некоторых характерных морфологических черт эскимосского лица. Далее, для того, чтобы найти возможные индикаторы изменений функциональной адаптации, сравнивали современное эскимосское лицо со скелетными данными двух групп эскимосского населения. Первая группа - раннего происхождения - состояла из 55 черепов /Хиландер, '72/, вторая, датированная примерно 1860 г. н.э., включала 35 черепов /данные Дальберга, '68/.

Образец из Вайнрайта включает 188 индивидов, 96 мужчин и 92 женщин. Для анализа были использованы рентгенографические цефалограммы. Они были разделены на пять групп, основанных на возрасте индивидов и времени проводимого исследования. Счетно-вычислительная машина и программа ФОРТРАН 1V были применены для вычисления линейных и угловых измерений. Проводили тест статистической значимости для полового диморфизма и для различий, связанных с возрастом.

У мужчин из Вайнрайта наблюдаются более уплощенные лица, чем у женщин, хотя плосколицость возрастает также с возрастом у обоих полов. Передняя челюстная ротация и прогнатизм нижней челюсти возрастают по мере старения как у мужчин, так и у женщин, наряду с сопутствующим уменьшением апикального соприкосновения, перекрывания зубов и замыкания челюстного угла.

Не обнаружено статистически значимых расхождений между плоской лицевой частью у вайнрайтского образца и скелетного материала. Данные этого исследования поддерживают предположение, что уплощенность лица является результатом приспособления к биомеханическим потребностям. Резко выраженное и прогрессирующее вертикальное положение передних зубов также рассматривается как показатель тяжелой механической функции.

Продольные разрезы лобной пазухи прогрессивно увеличиваются с возрастом как у мужчин, так и у женщин из Вайнрайта. По сравнению со скелетным материалом из Гудсон Бей, лобная пазуха современных эскимосов значительно больше. Вайнрайтский образец имеет также значительно большую гибкость основания черепа. Предполагается, что форма лобной пазухи является следствием воздействия двух факторов, а именно, : формы мозгового черепа и биомеханических потребностей в ответ на функцию пазухи в качестве пространственно построенной структуры.

Ключевые слова: лицо, эскимос, возрастные изменения, функциональная адаптация, цефалометрия.

[1] *Robert Cederquist, Department of Orthodontics, School of Dentistry, Case Western Reserve University, Cleveland, Ohio, 44106 U.S.A.*

[2] *Albert A. Dahlberg, Department of Anthropology, University of Chicago, Chicago Illinois, 60637 U.S.A.*

Vol. 6, pp. 39-68, Lund. ISSN 0345-8865.

Facial form is of considerable interest in studies of both living and skeletal human populations. Numerous investigations of the craniofacial area have been conducted, and these have resulted in a large volume of anthropometric information. Several populations have been studied, with repeated findings of significant differences in size and shape of craniofacial structures. Many investigators have not extended their efforts beyond the collection and tabulation of measurements, or metric data have been used for comparative purposes to determine degree of variation in the attempt to define biologic distance between various populations.

Some emphasis has also been focused on the functional adaptation of craniofacial morphological features, and on the identification of functional factors that may be of significance for morphological adjustment. However, the number of investigations is relatively few, e.g. Coon et al. ('50), Wolpoff ('68), Steegman (' 70, ' 72), Beals (' 72), Koertvelyessy (' 72), Shea (' 77).

Similarly, the investigation and analysis of human facial growth, has yielded a large amount of anthropometric data, either for clinical use in orthodontic or pediatric practice, or for comparative analysis, by which population differences of growth events have been established, with variation in differential growth pattern, timing, and direction of growth vectors (Hellman, ' 27; Conolly, ' 28; Broadbent, ' 37; Björk, ' 47, ' 50; Craven, ' 58; Sarnäs, ' 57; Brown et al. ' 71; Colby and Cleall, ' 74). Efforts have been made to explain adaptation of facial form to functional demands as a regulating mechanism for variation in growth patterns. Important contributions have been made by Bolk (' 23), Weidenreich (' 41), van der Klaauw (' 46), Moss (' 62), Moss and

Young ('60), Moss and Rankow ('68), Moss and Salentijn ('70, '71), Linder-Aronson ('70), Harvold et al. ('72, '73), McNamara ('72).

The physical characteristics of Eskimo populations have attracted considerable attention from physical anthropologists and comparative anatomists. In the craniofacial region the Eskimo exhibits many characteristic morphological features, e.g. weakly developed brow ridges and small frontal sinuses, narrow and pinched nasal bones, narrow nasal aperture, large orbits, wide and low mandibular ramus, large bigonial width, and high frequency of gonial eversion and sagittal keel. The Eskimo face also presents pronounced midfacial flatness, indicated by large naso-malar and zygomaxillary angles (Oschinsky, '62, '64) and remarkably vertical zygomatic bones, primarily due to anteriorly prominent zygomaxillary tuberosities. Eskimos are also considered to be very long-headed (low cephalic index). However, cranial shape shows great variation with, in general, dolichocephaly among eastern Eskimos (Greenland and Labrador), while in Alaska, except in the northernmost part, cephalic index falls within the mesocephalic range. South Alaskan and Siberian Eskimos even tend to be brachycephalic.

The question of the adaptive significance of several of these features has not been adequately explained and is still a matter of considerable controversy.

This article is based on a study which describes, cephalometrically, the craniofacial skeletal morphology of the Wainwright Eskimo population. The influence of sex and age was examined to help explain the adaptive significance of some of the characteristic morphological features of the Eskimo face. Further, in order to find possible indicators of changes in functional adaptation, the contemporary Eskimo face was compared with those of two Eskimo skeletal populations, one of pre-contact origin consisting of 55 skulls (Hylander, '72), and one dated about 1860 A.D. comprising 35 skulls (Dahlberg, '68).

The village of Wainwright is located on the northwestern coast of Alaska approximately midway between Point Barrow and Point Hope. Earlier, two distinct Eskimo cultures could be distinguished within the northwestern area of Alaska (Spencer, '59; Oswalt, '67). The Tareumiut resided in permanent coastal villages and were primarily engaged in sea mammal hunting. Inland Eskimos, the Nuunamiut, on the other hand, devoted themselves to caribou hunting. However, the Nuunamiut have now virtually ceased to exist (Spencer, '59). Many inland Eskimos have been forced to move to the coast and thus change their mode of life. Before 1904, when the schoolhouse was constructed (Spencer '59), there was no village at Wainwright, although people lived nearby. Eskimos also lived along the Kuk River, and some of the Wainwright people believe them to be their ancestors. The greater part of the villagers, however, claim Nuunamiut ancestry, and many of the oldest people at Wainwright were born in inland camps (Milan, '64). Thus, the inhabitants of Wainwright have affinities with both inland and coastal Eskimos. Gene flow from other populations, e.g. Polynesians and Europeans, has had further effect on the present population. This is the result of admixture during the middle and latter part of the 1800's, when intensive commercial whaling took place in the area (Chance, '66), and the whaler crews consorted freely with the local population.

Today, the school teacher and the minister of the Presbyterian Church are usually the only non-Eskimo individuals at Wainwright, according to information given to me by Dr. Albert Dahlberg ('74). He has also informed me that the diet in the community consists of meat from whale, seal, walrus and caribou. Some items are purchased, like tea, coffee, tinned milk, fruit and flour. Fish also forms an important part of the diet. Eventhough meat is often boiled, a large amount of raw and dried meat, especially caribou, is eaten.

In 1969, the Eskimo population at Wainwright was estimated at 285 individuals by the Federal Field Committee for Development Planning in Alaska.

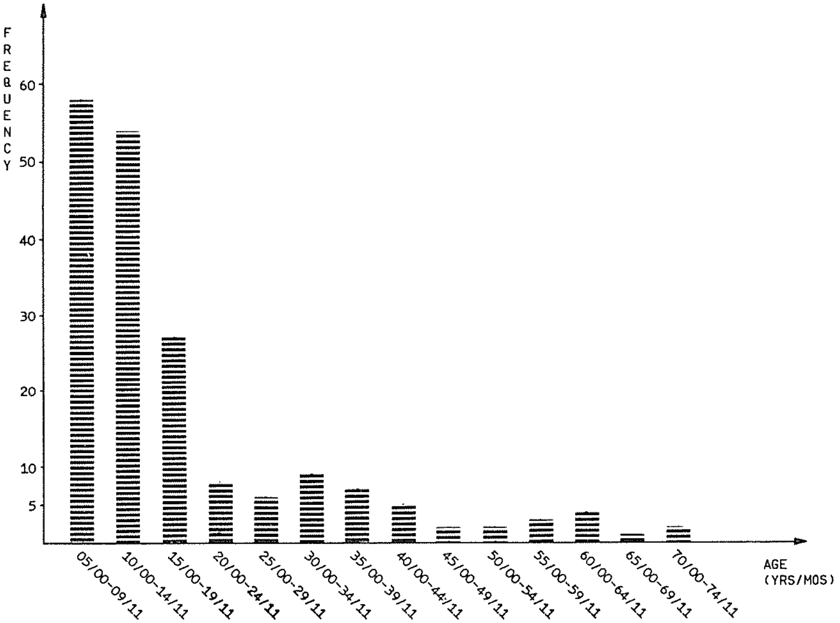


Fig. 1. Age distribution of Wainwright sample (188 individuals) at the time of the first roentgenographic cephalogram.

Materials and methods

Between 1968 and 1972, during five annual field trips to Wainwright which were directed by Dr. Albert Dahlberg, lateral roentgenographic cephalograms and other records were taken of the Eskimo population at Wainwright. The subjects were radiographed one to five times. For those who were examined more than once, the intervals between examination dates were 11 or 13 months; 11 months between 1968 and 1969 and between 1970 and 1971, 13 months between 1969 and 1970 and between 1971 and 1972. The roentgenographic cephalograms were taken with a Universal x-ray apparatus at a constant anode to midsagittal plane distance of 152.4 cm. The midsagittal plane to film distance varied for each individual.

The sample used for cephalometric analysis consisted of 188 individuals, 96 males and 92 females, of whom a total of 361 lateral skull films were available. Figure 1 illustrates the age distribution of the sample which was skewed towards the younger age groups. However, the shape of the age distribution curve for the sample was closely congruent with the one for the total population.

Thirty-one anatomical reference points (Fig. 2), as defined by Björk ('47, '60), Krogman and Sassouni ('57) and Hylander ('72) were recorded for each of the 361 roentgenographic cephalograms with a SAC Graf/Pen Model GP-2 digitizing system. The resolution of this system is 0.1778 mm. In addition three constructed reference points (Fig. 3) were used. The locations of these were calculated by a computer program. The following reference lines (Figs. 4 and 5)were used:

Axis of mandibular incisor (Björk, '60)
Axis of maxillary incisor (Björk, '60)
Balance axis of the head (Björk, '60)
Chin line (Björk, '60)
Facial line (Margolis, '47)
Functional occlusal line (Moyers, '73)

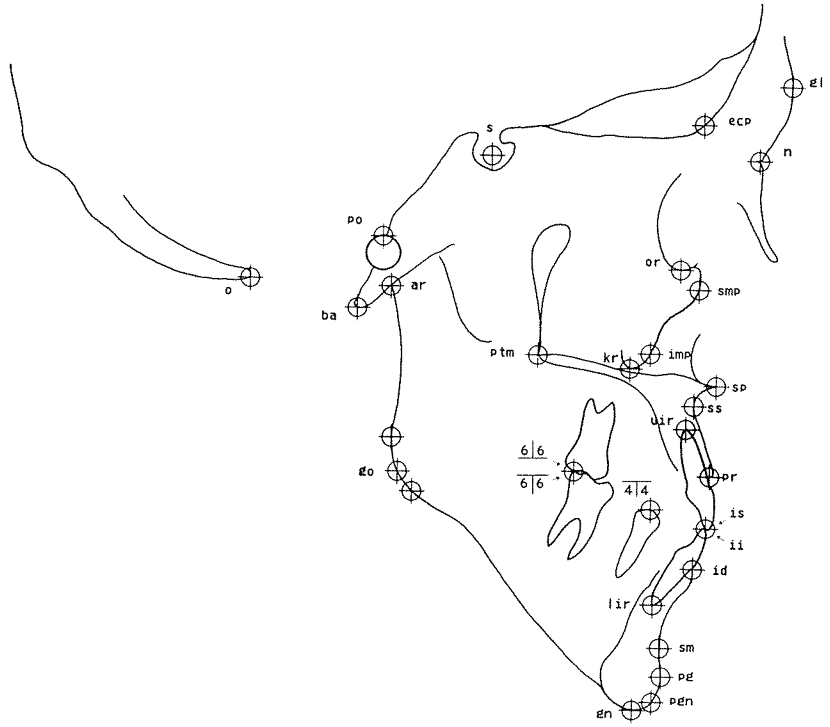


Fig. 2. Location of roentgenographic cephalometric reference points used in this study. The identification of all landmarks was made with the po/or line horisontally oriented on the digitizing tablet.

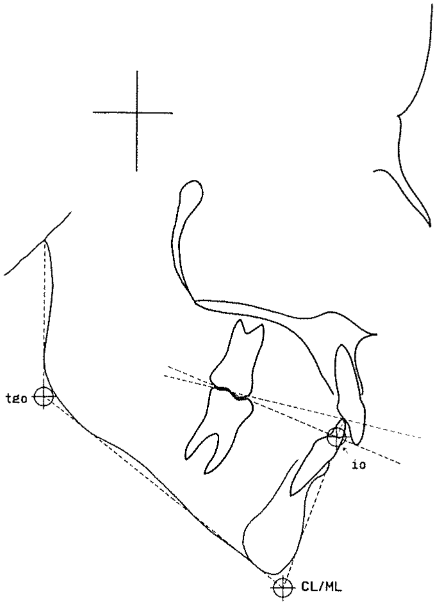


Fig. 3. Location of constructed (non-anatomical) reference points.

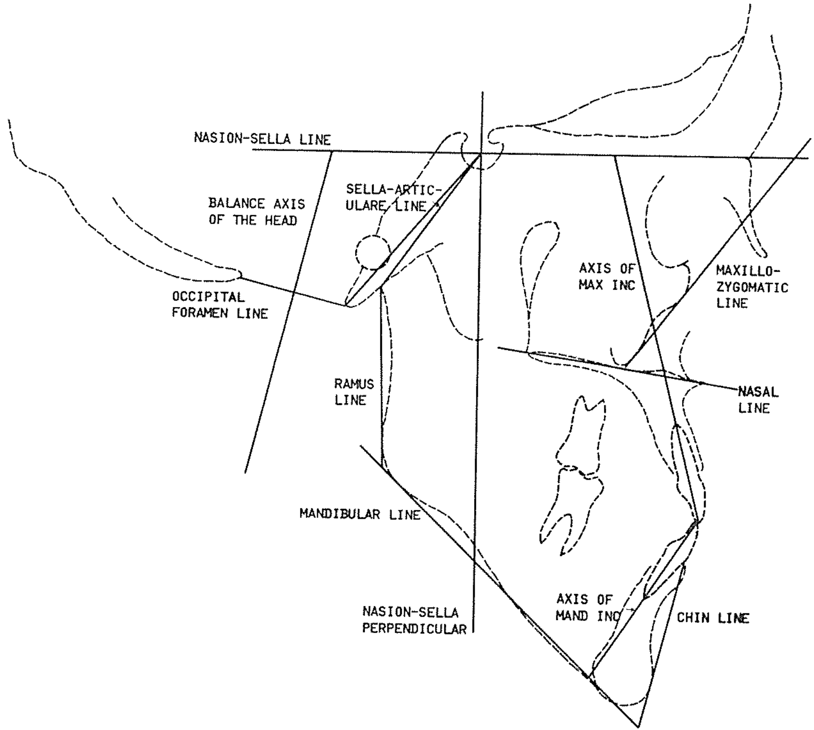


Fig. 4. Orientation of roentgenographic cephalometric reference lines used (see also fig. 5). See list in text for references to investigators whose definitions were followed in the construction of the lines.

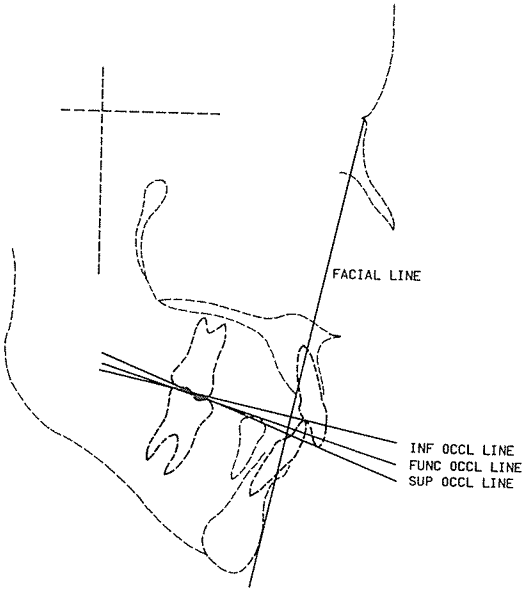


Fig. 5. Orientation of roentgenographic cephalometric reference lines used (cont. from fig. 4).

Inferior occlusal line (Björk, '60)
Mandibular line (Björk, '60)
Maxillozygomatic line (Hylander, '72)
Nasal line (Björk, '60)
Nasion-sella line (Björk, '60)
Nasion-sella perpendicular (Lindegård, '53)
Occipital foramen line (Björk, '60)
Superior occlusal line (Björk, '60)

The reference points are situated on the midsagittal plane or were projected onto this plane (Sarnäs, '59). Midpoints were used in instances of left and right images. The recordings of the reference points were made directly on the radiographs, i. e. no acetate tracings were made. The pen in the digitizing system had a dry point, thus leaving no marks on the film. The recorded x- and y-coordinates were transferred to punch cards and a FORTRAN IV program was employed for the calculation of linear and angular measurements. Sixty-three measurements, as defined by Lindegård ('57), Björk ('60), and Hylander ('72) were calculated for each radiographic cephalogram. The measurements were divided into six categories:

A. Cranial base
B. Facial vertical dimension
C. Sagittal position and shape of maxilla and mandible
D. Dental relationships
E. Midfacial flatness
F. Total facial flatness

A detailed list of the measurements is available elsewhere (Cederquist, '75). The roentgenograms were also divided into age groups, according to the age of the subject at the time of the examination. The following five groups were formed to be used for statistical evaluation and graphic representations, for males and females separately (in years/months): 05/0-09/11, 10/0-16/11, 17/0-21/11, 22/0-39/11, and 40/0-74/11. A second computer program was written to generate means, standard deviations and ranges for the linear and angular measurements within each age group. Mean coordinate values for selected reference points were also calculated in order to plot facial polygons (Cf. Björk, '47) for each group on a Calcomp Incremental Plotter. Tests of significance of differences between sample means were based on the normal curve for large samples ($n < 30$), and between means of small samples ($n \gtrsim 30$) on the Student - t distribution. The tests were one-sided for linear measurements and two-sided for angular, and the level of significance was set at 0.01.

In order to estimate the degree of inaccuracy in locating reference points with the digitizing pen, all the anatomical landmarks were recorded twice for ten randomly selected radiographs. There was a one-week interval between the two determinations. The experimental error was calculated following the technique described by Dahlberg ('40). In general, the error was greater along the y- coordinate than along the x- coordinate, i. e. the error in locating and recording an anatomical landmark was greater in the vertical dimension than in the horizontal. The range for this error in two dimensions was found to be from 0.53 mm. to 0.93 mm. The "locating-recording" error is independent of the measurement. Thus, it will affect small linear measurements more than it will larger, and it will have greater influence on angular measurements derived from points in close proximity than on angles constructed from points which are farther apart. A more detailed discussion concerning experimental errors, including calculations, has been reported elsewhere (Cederquist, '75).

When a radiographic exposure is made, the image on the film shows a certain degree of enlargement. In order to make corrections for this phenomenon a correction factor was incorporated into the computer program that generated the measurements. The correction factor varied for each individual exposure and is dependent upon the distance between the midsagittal plane and the film at each particular examination.

However, it should be noted that most measurements, both linear and angular, are projections on the midsagittal plane, and do not represent true values (Björk, '47; Sarnäs, '59; Björk and Solow, '62). For some roentgenograms the factor was not known. In those instances a mean correction factor for that specific age level was used, which will introduce an error into the linear measurements. However, these errors will be minimal and furthermore, they are, in all probability, evenly distributed in the sample and thus have little effect when the different age groups are compared.

Fairly comprehensive comparisons were performed between the results of my study and the findings of two roentgenographic cephalometric investigations on Eskimo skeletal material, one by Hylander ('72) and the other by Dahlberg ('68). Hylander's material consisted of 33 adult male and 22 adult female skulls recovered from the northwest Hudson Bay area in the Canadian Arctic. This material, which is considered pre-European contact, is associated with the Thule culture and is dated approximately 1200 A.D. to 1600 A.D. Dahlberg's material comprised 35 skulls, 15 male and 20 female, from northwest Alaska and is dated about 1860 A.D. Concerning age, no other information than "adults" was available for these samples. To allow comparison, all individuals in the Wainwright sample 30 years of age and above were pooled, males and females separately, and new means and standard deviations were calculated. Tests of significance of differences between means were based on the Student - t distribution. The level of significance was set at 0.01 and all tests were two-sided. Significant differences between means were tested for 21 variables between the Wainwright and Hudson Bay samples. Eight variables could be compared between the Wainwright group and the Alaskan skeletal material.

Results

In order to limit the volume of tabulations, only the most pertinent linear and angular measurements are presented. The comparisons between age groups are summarized in tables 1 and 2, for males and females respectively, where significant changes at the 1% level are indicated. Many angular variables were found to be significantly different between the groups. The frequency of significant changes of angular and linear measurements suggests alteration in shape as well as size (i.e. form; see Moss, '59, '62) of the craniofacial skeleton.

Significant sexual dimorphism at the different age levels within the sample is indicated in table 3. The majority of significant differences concerns linear variables which are consistently larger for males, and only a small number of significant differences were detected in angular measurements. This indicates dissimilarity in size of the craniofacial complex, but resemblance in shape. The linear measurements used in this study tend to reflect over-all size of skeletal components, while angular measurements reveal shape of individual osseous parts, as well as spatial relationships between different morphological units.

Cranial base

Linear measurements of the cranial base in females increases significantly between ten and seventeen years of age, while in males this process continues for a longer period of time as significant increases occur in linear cranial base measurements for young adult males. The angulation of the cranial base does not significantly alter with age in either males or females. This is in agreement with Björk ('55) who found no significant change of the "saddle angle" (n-s-ar) with advancing age in north European males. Both anterior and posterior cranial bases are longer in males in all age groups, and the anterior cranial base is significantly larger already before ten years of age. The posterior cranial base becomes significantly longer after that age and remains so at the subsequent age levels (i.e. even after 40 years of age). No sexual dimorphism in cranial base flexion was detected.

Facial vertical dimension

Both total anterior and posterior facial height are significantly larger in males than in females at all age levels. The lower anterior facial height (ans-gn) is 55%-58% of the total anterior facial height in all age groups, with slightly higher values for males. However, the differences are not significant. The ratio posterior/anterior facial height is not significantly different between sexes in any of the groups. For females both anterior and posterior facial height increase significantly through the younger age groups, with slightly greater increments in the posterior dimension resulting in a tendency towards an anterior rotation of the mandible. Significant changes occur in the facial vertical dimension for males as well, evident even between adult age groups. Between ten and seventeen years of age the lower anterior facial height, as a percentage of the total facial height, decreases from 58% to 56%. Significant increase in posterior/anterior facial height ratio (from 60% to 66%) is associated with a distinct anterior mandibular rotation.

Sagittal position and form of maxilla and mandible

Anteroposterior dimension of maxilla, total mandibular length, corpus lenght, and ramus height increase significantly during childhood and adolescence. There are, however, no significant differences in maxillary basal prognathism between the tested age groups for either sex. On the other hand, horizontal increments for the mandible are more pronounced, and they were seen even beyond adolescence, thereby producing a significant increase in mandibular basal prognathism and mandibular apical base position. This also results in a significant decrease in apical base relation ("ANB" angle). Further, the data revealed a significant increase in alveolar prognathism after ten years of age. The explanation for this is probably, in part, that the youngest group (5-9 years of age) included many subjects with deciduous incisors and with permanent anterior teeth still unerupted in the alveolar process. The gonial angle becomes significantly smaller with increasing age for both sexes. For females this phenomenon appears to progress over a longer period of time, as significant decreaseis seen even among adults. In contrast, the males showed a significant decrease in the mandibular plane angle (total facial angle) during adolescence, indicating a more pronounced anterior rotation of the mandible as compared to females.

Maxillary length, total mandibular length, and mandibular corpus length are, in the younger age groups. significantly greater in males than in females. Among adults, the measurements for total mandibular length and mandibular ramus height are also significantly larger for males. No significant differences between males and females were detected in maxillary and mandibular basal prognathism. The "ANB" angle, a measure of apical base relation, is significantly smaller for females up to seventeen years of age. The same tendency persists into adulthood, but it is not statistically significant.

Dental relationship

Dental overjet decreases with age for both males and females, and a significant decrease was seen earlier in males than in females. Maxillary dental protrusion increases in females during puberty. In young adult and adult males there is a definite uprighting of both maxillary and mandibular incisors, evidenced by a significant increase in the interincisal angle and decrease in maxillary and mandibular incisor inclination in relation to NSL and ML, respectively. This could not be seen in females. No significant sexual dimorphism could be detected with regard to overjet, overbite, and inclination of maxillary and mandibular incisors within the age groups. However, in the youngest group, males have significantly more mandibular dental protrusion, while later, females show more maxillary dental protrusion.

Midfacial flatness

The angulation of the anterior surface of the zygomatic process of the maxilla (MZL) in relation to NSL, n/ss line, and FL was used as measures of midfacial flatness. The results indicate that midfacial flatness increases continuously with age (i. e. the face becomes flatter) with significant increase even among young adults. There is a tendency for the male face to exhibit more midfacial flatness than the female face, and in late adolescence there is significantly less zygomatic obliquity in males than in females.

Total facial flatness

Between ten and seventeen years of age there is a significant decrease in facial convexity, i. e. the face becomes straighter, for both males and females. This change appears to continue into young adulthood for males. No sexual dimorphism with regard to total facial flatness is present within the age groups, except in the second group where males show more facial convexity than do females.

Comparison with two Eskimo skeletal populations

The angular and linear measurements of this part of the study are presented in table 4 for males and table 5 for females. Significant differences at the 1% level are indicated in these tables with an asterisk. There is a significant difference in the distance n-ecp, a measure of frontal sinus depth, between males from Wainwright and the male skulls from the Hudson Bay area. This measurement is larger for the Wainwright sample. The cranial base is flatter for the Hudson Bay sample, indicated by a significant larger n-s-ba angle. The angle n-s-ar, which is roentgenographically related to cranial base flexion, is also significantly larger for the skeletal material. For females, the cranial base angle is also different in the two samples, evidenced by significant differences in both n-s-ba and n-s-ar. The dry skulls show less flexion of the cranial base. The linear dimension of the posterior cranial base for males is significantly different, being longer in the Wainwright group. Further, females in the skeletal population show, as do males, less anteroposterior development of the frontal sinus. Significant difference was also found for the variable s-n-pg in males. The Hudson Bay material displays less mandibular basal prognathism than does the Wainwright sample. Despite some important contrasting features, great similarities in craniofacial structures exist between the two groups, and the main differences for females can be summarized as increased cranial base flexion, longer posterior cranial base, larger frontal sinuses and a more prognathic mandible in the Wainwright Eskimo sample.

The comparison between the Wainwright sample and the Alaskan skeletal material reveals no differences in maxillary and mandibular apical base position in relation to cranial base. However, the apical base relation ("ANB" angle) for males is significantly smaller in the Wainwright sample. No such difference is present between the female groups. The Wainwright males show less facial convexity than do the Alaskan male skulls, indicated by a significantly smaller n-s-pg angle. Both male and females from Wainwright have significantly more labial inclination of maxillary incisors. The tendency for increased incisor inclination is most pronounced in females, as they also show significant differences in the interincisal angle and mandibular incisor inclination. With regard to the interincisal angle, no value for females is given in Hylander's (' 72) study, and the measurement for males is based on only two skulls. Despite a 14.5 degree difference between the means, this extremely small sample size resulted in a significance where the null hypothesis could not be rejected.

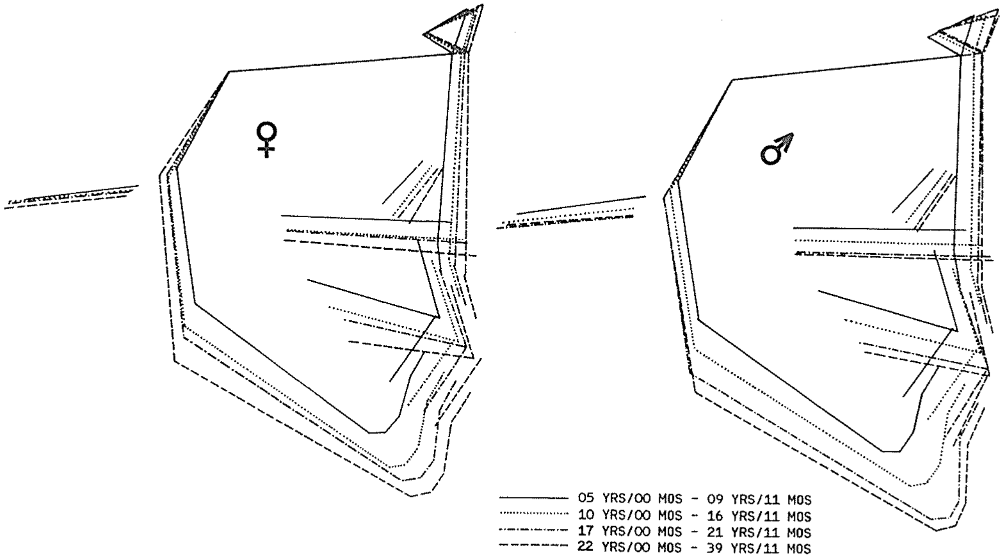


Fig. 6. Composite facial polygons for the Wainwright sample (females and males separately). Superimposition of the computer generated plots is on nasion-sella line (NSL) and registration is at sella (s). The occipital line is also included.

Discussion

Most subjects were radiographed only once or twice and thus the results are based primarily on cross-sectional data. These represent differences in craniofacial morphology associated with age within the population, and it is appreciated that individual variations in magnitude and direction of growth cannot be determined from these results. However, in order to get a general picture of the developmental sequences of the Eskimo face it is inferred that differences in mean values between two age groups are at least approximations of the changes that have taken place in the older of the two compared groups.

In the tests of significant sexual dimorphism (table 3) many of the measurement that show significant differences in the second and third age groups do not reveal similar trends in the older groups. These results may reflect a leveling out of dimensional differences between sexes with increasing age. The composite facial polygons (figure 6), however, do not support such a conclusion. They rather illustrate a consistent tendency for larger measurements in males both anteroposteriorly and vertically. The apparent inconsistencies in table 3 are likely to be caused by an inadequate number of individuals in the older age groups.

When the oldest age group (40-74 years of age) was subdivided into additional age levels it was noted that inconsistencies existed in some linear dimensions. Males between 50-74 years of age displayed, on the average, less facial prominence than did males between 40 and 49, and the older females had smaller mean vertical dimensions than did the younger. Colby and Cleall ('74), in their roentgenographic cephalometric investigation of Canadian Eskimos from the northern Foxe Basin, reported similar findings. They speculated whether this could be an effect of a secular trend within the population. However, they concluded that small sample size at the older age levels was the most likely cause. The same reasoning can be applied to the present study.

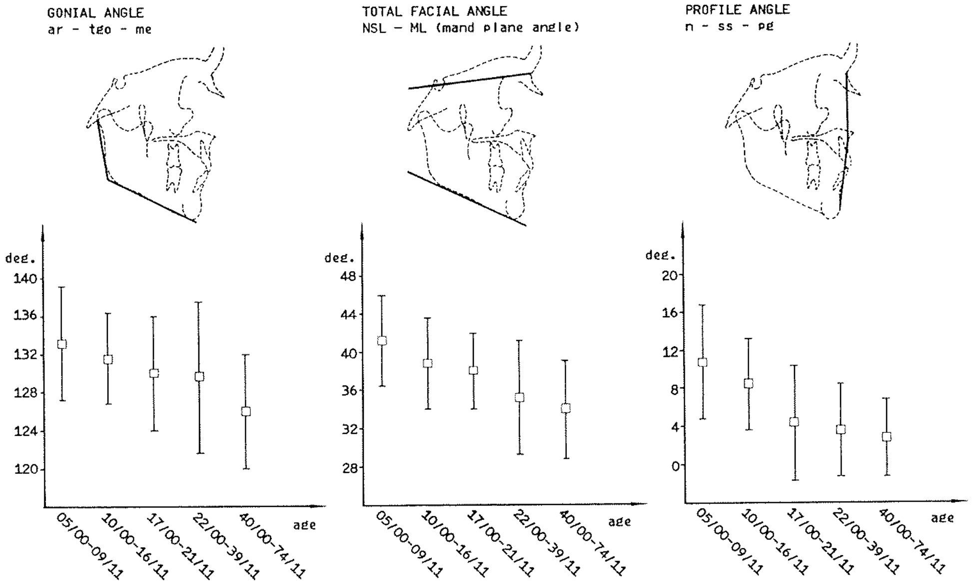


Fig. 7. Graphic representations of age changes in gonial angle, total facial angle, and profile angle for Wainwright males. The construction of the three variables is indicated above their respective graphs.

Further comparison of the Wainwright and the northern Foxe Basin samples reveals that cranial base flexion and also the degree of maxillary prognathism appear to be similar. However, the Wainwright Eskimo exhibits considerably less dental protrusion with more upright maxillary and mandibular incisors. Colby and Cleall (' 74) found the mandible in their sample to be moderately retrognathic. The Wainwright population, on the other hand, presents a well-developed and forward positioned lower jaw; a feature consistent with earlier anthropometric descriptions of Eskimo mandibular morphology (Hrdlička, ' 28; Oschinsky, ' 64). This is also in contrast with Hylander' s (' 72) Canadian Thule sample which showed definite mandibular retrognathism, indicated by a significantly smaller s-n-pg angle than for the Wainwright group. This unexpected finding is difficult to explain. In both the Wainwright and the northern Foxe Basin Eskimos the gonial angle was observed to become less obtuse with increasing age, even among adults. This is in disagreement with Hrdlicka' s (' 40) statement that in adult age, provided extensive tooth loss has not occurred, the shape of the gonial angle is stable. Nevertheless, the measurements of the gonial angle in both samples are well within the range of what earlier has been reported for Eskimo skeletal material from Alaska, both pre-contact (Cameron, ' 23; Hrdlička, ' 40) and from the middle of the last century (Dahlberg, ' 68). The continuously decreasing gonial angle for the Wainwright males is graphically illustrated in the first chart in figure 7. The total facial angle, or mandibular plane angle, also decreases with increasing age (figure 7, chart 2). There is a reduction in the profile angle as shown in the third chart in figure 7, all demonstrating the pronounced anterior facial rotation which takes place with increasing age.

Figure 8 portrays graphically the reduction in apical base relation (chart 1) with a statistically significant decrease during adolescence. Dental overjet is reduced while there is a continuous uprighting of the anterior dentition (figure 8, charts 2

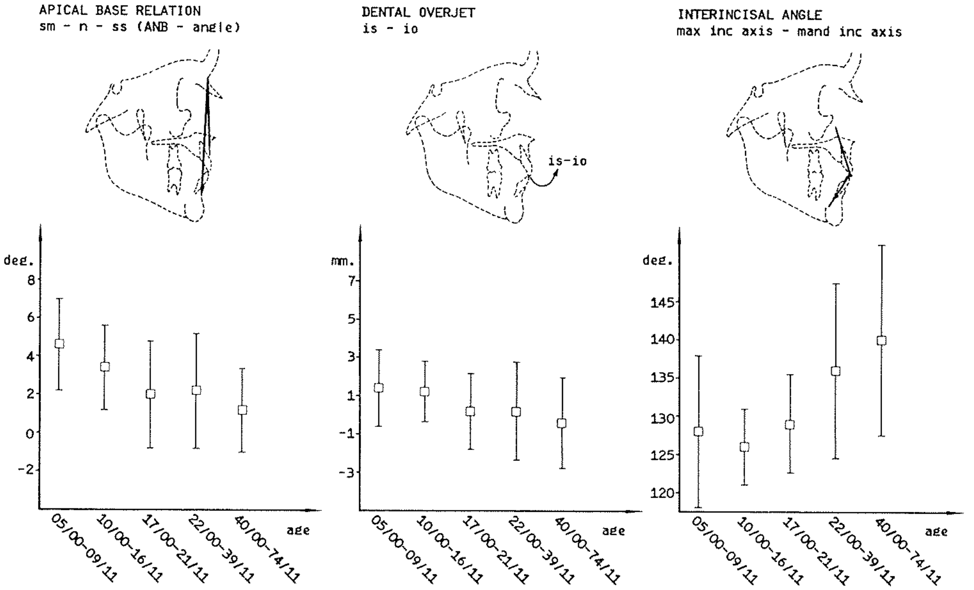


Fig. 8. Graphic representations of age changes in apical base relation, dental overjet, and interincisal angle for Wainwright males. The construction of the three variables is indicated above their respective graphs.

and 3). Some of the older individuals even had a negative dental overjet combined with severe dental wear. Association between gradual uprighting of incisors and simultaneous increase in the degree of dental wear has earlier been demonstrated (Lysell, '58). The increase in interincisal angle is most probably related to heavy masticatory function. There was also widespred radiographic evidence of apical root resorption of anterior teeth, especially among older individuals. This phenomenon has also been reported by other investigators (Pedersen, '49; Hylander, '72, '77), and it has also been linked to excessive occlusal stress. One testimony of the heavy and multitudinous use of the teeth is the fact that the dentition is among Eskimos referred to as the "third hand". The findings of the present study support earlier observations that an edge-to-edge incisor relation is associated with growth and anterior repositioning of the mandible (Moorrees, '57 ; Murphy, '58; Hylander, '77) and not with differential tooth migration in maxilla and mandible as a consequence of tooth wear (Campbell, '25; Leigh, '29; Begg, '54; Wolpoff, '71). However, attrition is necessary for anterior mandibular shift to occur and an edge-to-edge bite to be established (Moorrees, '57). Moorrees ('57) has also pointed out that an edge-to-edge relation is in part culturally conditioned.

The growth pattern of the facial region is summarized in the two facial polygons in figure 6, for males and females separately. The face emerges from beneath the cranium with advancing age. In the vertical dimension the relative changes are greatest in the posterior part of the face, while anteroposteriorly there are proportionately greater growth increments in the inferior area of the face, causing increasing prominence of the lower face. The pattern of facial change is characterized by uniformity. Growth has a distinct downward and forward rotational direction, resulting in not only flattening of total facial profile but also in increased midfacial flatness, defined as more pronounced verticality of the zygomas. Two main viewpoints have been advanced to explain the adaptive significance of midfacial flatness: (1) the morphological features of the flat or "mongoloid" face are related to cold adaptation, i. e. the flat face is adapted to withstand cold climate, and (2) midfacial flatness is related to function, i. e. there is a morphological adaptation in response to functional forces that are exerted on the craniofacial structures.

The most well-known theory concerning the adaptation of human facial form to conditions of extreme cold stress was put forward by Coon et al. ('50). They suggested facial frostbite as a selective force responsible for the characteristics of the Eskimo face. A man with thin, bony features, especially a narrow, prominent nose, would be in danger of freezing his face. From this climatic circumstance came a type of human being with a flat face, padded with fat. However, Washburn ('63) took strong exception to this climatic concept, and Steegman ('67; '70; '72) has convincingly rejected the hypothesis of Coon and coworkers after having conducted laboratory experiments on changes in surface temperature in the facial region. He found that malar temperature increased as face width decreased. Large and protrusive malars are more exposed to cold, and their surface gets colder when exposed to low temperatures. Fatty tissue paddings may protect deeper structures but they also permit surface temperature to fall. Actually, as Steegman ('70) points out, the "European" zygoma is better protected from cold than the "mongoloid."

The second, and older, theory relates the morphological features of the Eskimo face with powerful chewing (Hrdlička, '10). This is associated with voluminous muscles of mastication and with the positioning of these muscles (Washburn, '63; Hylander, '72). More specifically, Hylander ('72;'77) regards the morphological characteristics of the flat Eskimo face as particular adaptations for the generation and dissipation of heavy vertical occlusal forces. Midfacial flatness, that is the degree of verticality of the malar, was measured both to NSL and to n/ss line as illustrated in charts 1 and 2 in figure 9. The results indicate that the degree of midfacial flatness increases with advancing age, with a significant uprighting in early adulthood. This was seen in both males and females. Of interest is also that no statistically significant differences were detected in midfacial flatness between the Wainwright sample and the skeletal material. That the morphology of the Eskimo zygoma is a special adaptation for protection against facial frostbite is a doubtful theory. When midfacial flatness increases with age, as the results of the present study suggest, it is difficult to relate it to cold adaptation. They rather support the interpretation that flatness of the midface is an adaptation to biomechanical requirements.

The distance between the ecto- and endocranial surfaces of the frontal bone may be regarded as a reasonable approximation of the anteroposterior dimension of the frontal sinus. Chart 3 in figure 9 depicts the continuous separation of the external and internal tables of the frontal bone, thereby increasing the depth of the frontal sinus. When compared with the Canadian Thule Eskimo sample, the frontal sinus of the adult contemporary Eskimo at Wainwright is significantly larger.

For a functional analysis of the frontal bone, as well as the other calvarial bones, it is important to distinguish three different and functionally independent components which respond to different functional demands: (1) the outer table, (2) the diploë, and (3) the inner table (van der Klaauw, '47; Moss, '58a; '62; Moss and Young, '60; Young, '59). Size and shape of the internal table is a consequence of the form of the neural mass (Dyke et al., '33; Ross, '41; Noetzel, '49; Fischgold and Metzger, '51). The inferior part of the external part of the external table of the frontal bone makes up the roof of the orbit and is responsive to alterations of orbital soft tissue content. Other areas of the calvarial outer table (cranial superstructures) react to biomechanical forces from muscle action (Anthony, '03; Neubauer, '25; Sicher and Tandler, '28; Weidenreich, '41; Washburn, '47; Sicher, '49; Weinmann and Sicher, '55). The shape of the ectocranial surface is functionally unrelated to that of the endocranial surface (Weidenreich, '41; Moss and Young, '60). This concept is in sharp contrast to an earlier view (Anthony, '03; Hrdlička, '10) which states that muscle function influences, not only ectocranial superstructures, but also cerebral shape.

Bolk ('23) has pointed out that the development of a supraorbital ridge is closely related to the general growth phenomena of the skull during ontogeny. The size of the

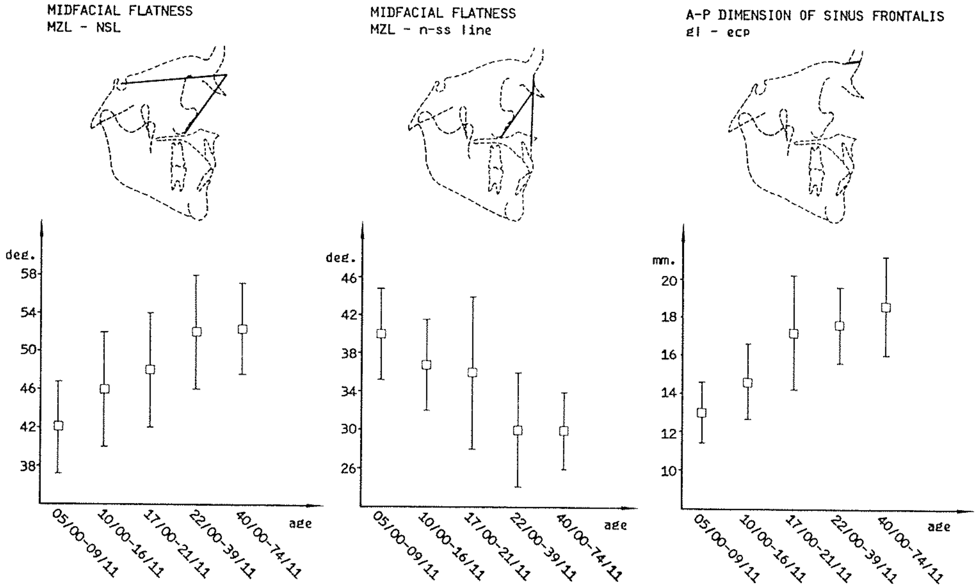


Fig. 9. Graphic representations of age changes in midfacial flatness (first two charts) and anteroposterior dimension of sinus frontalis for Wainwright males. The construction of the three variables is indicated above their respective graphs.

supraorbital ridge is a direct reflection of the amount of anterior displacement of the orbitae relative to the anterior cranial fossa. If the forward orbital shift is small, the separation in the supraorbital area of external and internal surfaces of the frontal bone is also minimal. When there is substantial spatial change of orbital content in relation to braincase, from a subcerebral to a precerebral position, considerable compensatory growth of the supraorbital bony region occurs to ensure adequate protection of the orbital content. Based on functional cranial analysis, Moss ('60a), Moss and Young ('60) have detailed the relationship between cranial functional components, including the frontal bone, and their matrices during cranial development (see also Moss, '62, '68, '72; Moss and Salentijn, '69a, '69b). They stressed that the form of the frontal bone in its anteroinferior region precisely reflects the functionally variable spatial relationship between contents of anterior cerebral fossa and orbitae. With increased spatial displacement between orbital and cerebral contents, their functional components will respond with increased separation.

Jaw size alone has been mentioned as being of importance for the presence or absence of brow ridges (Dubois, '22), but such functional relationship has been rejected with well-documented arguments (Bolk, '23; Abbie, '52; Moss and Young, '60). It has also been suggested that spatial discrepancies between braincase and orbits combined with biomechanical considerations determine supraorbital form (Thompson, '03). Recently, Moore and Lavelle ('74) have theorized about a functional correlation between brow ridging and jaw position rather than jaw size. Similar processes are most probably involved in the development of frontal sinuses and brow ridges, although this has been denied by some investigators (Zuckerkandl, 1893; Schwalbe, 1899; Ehara and Seiler, '70). Increased separation between braincase and orbits is probably of significance only during the period of cerebral, orbital, and facial translative growth which in man means until sometime during the second decade of life. However, transformative growth (remodeling) is a continuous process throughout life (cf. Garn et al., '67; Israel, '68, '73 a, b). The present study indicates that size of the frontal sinuses increases with advancing age, even during adulthood (figure 9, chart 3). Görke ('04) and Toldt ('14) were first to suggest that the biomechanics of mastication as well as the degree of inclination of the forehead (indicator of cerebral shape) are together important determinants of supraorbital development. More recently, Endo ('67; '70) has shown that the action of muscles of mastication generates intensive axial forces (compression) in the frontonasal region. Strong bending moments due to occlusal pressure are produced in the glabellar region, the medial and superior parts of the maxillae, and in the nasal buttress. With his biomechanical models Endo ('66) also established that the strong bending moments acting on the forehead tend to create almost horizontal deformation. In order to resist this a large cross-section is advantageous. A skull with a high, vertical forehead is able to withstand bending moments with its entire height. An inclined forehead, on the other hand, can only effectively resist the stress in its lower part. Thus, a sloping frontal bone compensates for strong horizontal bending moments by anterior drift of the outer table through remodeling processes. Human microcephaly serves well to demonstrate the development of frontal sinuses (cf. Cunningham and Telford-Smith, 1895; Humphry, 1895; Dru-Drury, '19-'20; Mollison, '25). Vogt (1867) conducted an extensive study on microcephaly with cases ranging from the newborn to 44 years of age and with adult cranial volumes ranging from 296 cc. to 622 cc. His data seem to indicate increased glabellar development with decreased verticality of the forehead. A relatively short anteroposterior endocranial dimension of the anterior cerebral fossa is compensated for by a large supraorbital bossing. These relationships have also been demonstrated in the canine (Weidenreich, '41) and the nonhuman primate (Schultz, '26).

The present study revealed significantly larger frontal sinuses in the Wainwright Eskimo when compared with the Canadian Thule skeletal material. The data also suggest shorter anterior cranial fossa and significantly more cranial base flexion in the Wainwright group (figure 10). A shorter anterior cranial fossa does not imply decrease in cranial volume but rather change in cerebral shape, as does the difference in cranial base kyphosis. The direction, but not magnitude, of neural mass expansion is influenced biomechanically by the dura mater. It possesses a system of fiber tracts which are related to five prominent points of the chondrocranium (for details see Beneke, '10; Bluntschli, '25; Kokott, '33; Popa, '36; Deggeler, '42; Moss, '58b, '59, '60b; Moss and Young, '60). Ehara and Tamura ('70), using breadth-length index of the brain (not cranial index!), demonstrated that with increased basal kyphosis the brain becomes increasingly brachyform. This finding suggests a higher endocranial index for the Wainwright sample than for the Hudson Bay skulls. Unfortunately, no data for these two populations are available at present to verify this. The discrepancies in the region of the anterior cranial fossa between the two samples, which is pictured in figure 10, may be explained by the processes discussed above. Sample differences in endo- and ectocranial base length are counterbalanced by anterior orbital displacement. This may initially be the primary factor for increase of the anteroposterior glabellar dimension in response to protective demands. However, increase in frontal sinus size continues even after cerebral-orbital separation has become negligible. Now mechanical requirements will be the predominant determinants. The slightly more forward maxillary positioning in the Wainwright Eskimo (figure 10) and the documented heavy use of the Eskimo anterior dentition (e.g. Waugh, '37; de Poncins, '41) may be of significance, especially when seen in the light of Endo's experiments ('66; '67; '70). Contrary to a suggestion of climatic adaptation of frontal sinuses (Koertvelyessy, '72), the significance of their form is best analyzed and explained when viewed as space-framed structures (see Badoux, '66). The principle is applicable to all facial pneumatic cavities. The static structure of the skull is reinforced since the walls of the cavities form bars along which the vectors of external and internal forces act. The bars align themselves functionally in order to establish stable frames. However, Badoux ('66) also points out that the entire structure of the skull can not be explained as an adaptation to mechanical demands only, since its form

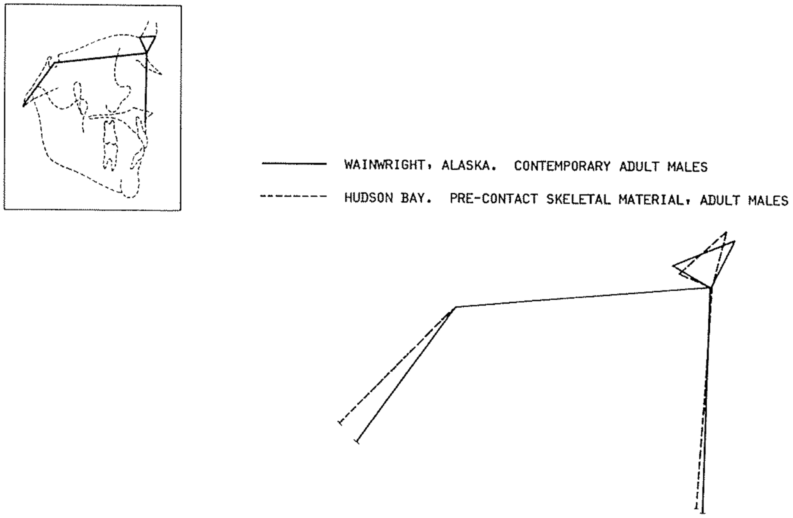


Fig. 10. "Form" (reference points n, ecp, and gl connected) of the roentgenographic image of sinus frontalis and degree of cranial base kyphosis and maxillary prognathism. Comparison between adult males from Wainwright and adult male skulls from the Canadian Thule skeletal material. Numerical data from Hylander's ('72) study were used for the construction of the outline representing the skeletal material (broken line of the main diagram). The tracings are superimposed on nasion-sella line (NSL) and registered at sella (s). The smaller framed illustration is a graphic explanation of the main diagram.

reflects both protective and mechanical funtions, which is in agreement with the bifactorial interpretation of supraorbital development outlined above.

Finally, nutritional and masticatory aspects of the Eskimo diet and its influence on skeletal development will be considered. Normal skeletal development depends on two different processes: (1) skeletal growth and (2) skeletal maturation, and it is essential to realize the distinction between these two events (cf. Krogman, '50; Acheson and Hewitt, '54). Retardation of one or the other may occur independently. An assault, such as diesease or nutritional and hormonal conditions, can affect one mechanism but not the other. The so-called Harris lines (after Harris, '26) are the sequelae of a condition where growth (e.g. increase in length of a long bone through chondrogenesis at the epiphyseal plate) is affected but not maturation (osteogenesis and calcification in the metaphyseal-epiphyseal zone). This will result in an area of hypercalcification. After recovery the two processes again become synchronized. Normal skeletal development resumes and the area of growth retardation may be discernible on a roentgenogram as a line of increased density at the metaphysis (Follis and Park, '52; Park, '54; Acheson, '59, '66; Platt and Stewart, '62; Pratt and McCance, '64).

The major portion of the native Eskimo diet is obtained from seal, walrus, whale, caribou and fish. This diet is extremely high in protein but low in carbohydrates (Krog and Krog, '13). It is also rich in vitamins A and D and in the B-complex (Høygaard, '40). The intake of calcium shows seasonal variations, usually being low in the winter (Høygaard, '40; Scott, '56). Vitamin C also varies considerably, being sufficient in the summer but very low in the winter, when the consumption of stored food is high. The native diet seems to be sufficient to satisfy the basic energy, vitamin and mineral requirements, with the possible exception of vitamin C and calcium.

In spite of the low intake of vitamin C, Høygaard ('40) has reported that severe scurvy is unknown among Eskimos, but that "sub-scurvy" may occur in the springtime. Rickets is also very rare among Eskimos (Høygaard, '40). A reason for that may be that infants commonly suckle until they are two, three years of age. Høygaard ('40) further observed that infantile cramps were not infrequent among children, and he speculated that calcium starvation was the cause. During difficult years, not only is the supply of vitamin C and calcium low, but the total caloric requirement will be difficult to satisfy. This may result in retardation of both skeletal and sexual development (Lowrey, '73). Eventhough the phenomenon of compensatory or catch-up growth after periods of retarded skeletal development is well-documented (Bauer, '54; Prader *et al.*, '63; Garrow and Pike, '67; Graham and Adrianzen, '72; Falkner, '75; Smith, '77), it has been demonstrated that deficient diet may cause, not only immediate or acute effects, but also permanent impairment of growth (Schultze, '55; Widdowson and McCance, '60). McCance *et al.* ('61) and Widdowson and McCance ('64) have shown severe retardation of the growth of the facial skeleton in the pig as an effect of malnutrition. The mandible tended to be more readily affected than the maxilla. Permanent growth arrest occurred as a result of undernutrition early in life. It did not matter in what way the diet was supplemented following this critical period; complete recovery did not take place. However, restitutio ad integrum was possible if the period of dietary deficiency occurred after the neonatal period, although the rate of growth decreased. Similar findings have also been shown experimentally for general body growth (Widdowson and McCance, '63). The developmental set-back caused by undernutrition became progressively less serious as the animal grew older.

Today, probably no Eskimos subsist exclusively on their native diet. Practically no Eskimo family is without some source of cash income and can thus rely more on imported foods, especially during the winter. This secures them from the worst consequences of famine, and the diet of modern-day Eskimos appears to have no nutritional disadvantages (Scott, '56). However, the increased dependence on imported foods has been made responsible, not only for the sharp increase in dental caries, but also for an increase in irregularities of the teeth and a decrease in jaw size (Keith, '29; Hooton, '37; Waugh, '37; Klatsky, '48). The comparison in the present study between the Wainwright and the Canadian Thule Eskimos failed to show an anteroposterior reduction in jaw size. The reduction could be limited to the alveolar process, but that can hardly be argued to be a causation for higher incidence of tooth crowding. The relationship between teeth and supporting bone is one of alveolar dependence on teeth, and not the reverse (a tooth is a functional matrix and the alveolar process is its skeletal unit, see Moss, '60c, '62, '71a, b, '72; Moss and Salentijn, '69a, b).

Occlusal and interproximal wear, as a result of gritty or coarse and unprocessed native diet, has been seen as an adjusting mechanism for proper alignment of the teeth (Begg, '54; Barrett, '57; Hunt, '59,61; Murphy, '64; Hylander, '77). However, dental arch length tends to decrease with interproximal wear (Begg, '54; Murphy, '64; Hasund, '65; Hylander, '77). Further, for interproximal wear to occur contact between the teeth has to be maintained. These conditions would *reduce* available space for erupting teeth or already malligned dental units anterior to the first molars. Thus, interproximal wear *increases* the possibility of crowding of the teeth. On the other hand, it could possibly avail the eruption of teeth posterior to the first molar. Moorrees' ('57) data do not support the hypothesis that increased dental attrition prevents or reduces dental crowding. In the Aleut population studied by him, the degree of dental wear increased sharply with age, while the amount of crowding was fairly evenly distributed in the population.

Reduction in maxillary and mandibular basal bone has been observed in animal experiments, where the experimental animals were fed a considerably softer diet than the control animals (Watt and Williams, '51; Moore, '65). Modern diet reduces the functional demands on dentition and related structures, and this could reduce size and/or alter shape of maxillary and mandibular basal bone and thus decrease available space for the developing dentition, assuming no reduction in tooth size. This circumstance (as already pointed out by Keith, '29; see also Waugh, '37; Klatsky, '48; Oppenheimer, '64), and not lack of interproximal wear, may be an important factor for an increased incidence of dental malocclusions. Bone responds with change in form more readily than the dentition to alterations in function (cf. functional matrix concept).

Acknowledgement

We want to thank Mr. Tommy P. Muller for writing the computer programs used in this study and for constructive advice in regard to methodology and statistical procedures.

Literature cited

(Serial titles are abbreviated according to BioSciences Information Service of Biological Abstracts and Index Medicus which follow the rules of the American National Standard for the Abbreviation of Titles of Periodicals.)

Abbie, A. A. 1952 A new approach to the problem of human evolution. Trans. R. Soc. S. Aust., 75: 70-88.

Acheson, R. M. 1959 The effects of starvation, septicaemia and chronic illnes on the growth cartilage plate and the metaphysis of the immature rat. J. Anat., 93: 123-130.

_____ 1966 Maturation of the skeleton. In: Human Development. F. Falkner, ed. W. B. Saunders Co., Philadelphia, pp. 465-502.

Acheson, R. M. and D. Hewitt 1954 Oxford child health survey. Stature and skeletal maturation in the pre-school child. Br. J. Prev. Soc. Med., 8: 59-65.

Anthony, R. 1903 Introduction a l' étude expérimentale de la morphogénie. Bull. Mem. Soc. Anthropol. Paris, 4 (Ser. 5): 119-145.

Badoux, D. M. 1966 Framed structures in the mammalian skull. Acta Morphol. Neerl. Scand., 6: 239-250.

Barrett, M. J. 1957 Dental observations on Australian aborigines: tooth eruption sequence. Aust. Dent. J., 2: 217-227.

Bauer, H. 1954 Nephrosesyndrom und Körperwachstum. Helv. Paediatr. Acta, 9: 127-134.

Beals, K. L. 1972 Headform and climatic stress. Am. J. Phys. Anthropol., 37: 85-92.

Begg, P. R. 1954 Stone Age man's dentition. Am. J. Orthod., 40: 298-312, 373-383, 462-475, 517-531.

Beneke, R. 1910 Ueber Tentoriumzerreissungen bei der Geburt, sowie die Bedeutung der Duraspannung für chronische Gehirnerkrankungen. Munch. Med. Wochenschr., 57: 2125-2127.

Björk, A. 1947 The face in profile. Sven. Tandläk. Tidskr., 40 (No. 5 B, Suppl.): 1-180.

_____ 1950 Some biological aspects of prognathism and occlusion of the teeth. Acta Odontol. Scand., 9: 1-40.

_____ 1955 Cranial base development. Am. J. Orthod., 41: 198-225.

_____ 1960 The relation of the jaws to the cranium. In: Introduction to Orthodontics. A. Lundström, ed. McGraw-Hill Book Co., New York, pp. 104-140.

Björk, A. and B. Solow 1962 Measurements on radiographs. J. Dent. Res., 41: 672-683.

Bluntschli, H. 1925 Zur Frage nach der funktionellen Struktur und Bedeuting der harten Hirnhaut. Wilhelm Roux' Arch. Entwicklungsmech. Org., 106: 303-319.

Bolk, L. 1923 On the significance of the supraorbital ridges in the primates. Proc. K. Akad. Wet. Amsterdam Sec. Sci., 25: 16-21.

Broadbent, B.H. 1937 The face of the normal child. Angle Orthod., 7: 183-233.

Brown, T., M.J. Barrett and K.C. Grave 1971 Facial growth and skeletal maturation at adolescence. Tandlaegebladet, 75: 1211-1222.

Cameron, J. 1923 Osteology of the Western and Central Eskimos. In: Report of the Canadian Arctic Expedition, 1913-18, 12 (Part C): 1-79. Department of the Naval Service, Ottawa.

Campbell, T.D. 1925 Dentition and palate of the Australian aboriginal. Keith Sheridan Found. Publ. No. 1. University of Adelaide, Adelaide.

Cederquist, R. 1975 Craniofacial description of Wainwright Alaskan Eskimos. Unpublished Master's thesis. University of Chicago.

Chance, N.A. 1966 The Eskimo of North Alaska. Rinehart and Winston. New York.

Colby, W.B. and J.F. Cleall 1974 Cephalometric analysis of the craniofacial region of the northern Foxe Basin Eskimo. Am. J. Phys. Anthropol., 40: 159-170.

Connolly, C.J. 1928 Growth of face in different races. Am. J. Phys. Anthropol., 12: 197-206.

Coon, C.S., S.M. Garn and J.B. Birdsell 1950 Races: a study of the problem of race formation in man. Charles C. Thomas, Springfield.

Craven, A.H. 1958 A radiographic cephalometric study of the Central Australian aboriginal. Angle Orthod., 28: 12-35.

Cunningham, D.J. and T. Telford-Smith 1895 The brain of the microcephalic idiot. Sci. Trans. R. Dublin Soc., 5: 287-360.

Dahlberg. A.A. 1968 Unpublished data.

Dahlberg, G. 1940 Statistical methods for medical and biological students. G. Allen & Unwin Ltd., London.

Deggeler, C. 1942 Beitrag zur Kenntnis der Architektur des fetalen Schädels. Z. Anat. Entwicklungsgesch., 111: 470-489.

Dru-Drury, E.G. 1919/20 An extreme case of microcephaly. Trans. R. Soc. S. Afr., 8: 149-152.

Dubois, E. 1922 On the cranial form of *Homo neandertalensis* and of *Pithecanthropus erectus*, determined by mechanical factors. Proc. K. Akad. Wet. Amsterdam Sec. Sci., 24: 313-332.

Dyke, C.G., L.M. Davidoff and C.B. Masson 1933 Cerebral hemiatrophy with homolaterial hypertrophy of the skull and sinuses. Surg. Gynecol. Obst., 57: 588-600.

Ehara, A. and R. Seiler 1970 Die Strukturen der Überaugenregion bei den Primaten, Deutungen und Definitionen. Z. Morphol. Anthropol., 62: 1-29.

Ehara, A. and H. Tamura 1970 Hirnkyphose als ein die Schädelform beeinflussender Faktor. Z. Morphol. Anthropol., 62: 50-60.

Endo, B. 1966 Experimental studies on the mechanical significance of the form of the human facial skeleton. J. Fac. Sci. Univ. Tokyo Sect. V Anthropol., 3(1): 1-106.

______ 1967 Mechanical analysis of the form of the human facial skeleton. In VII Congr. Int. Sci. Anthropol. Ethnol. V.V. Guinzburg, ed. "Hayka", Moscow, Vol. II, pp. 346-353.

______ 1970 Analysis of stresses around the orbit due to masseter and temporalis muscles respectively. J. Antrhopol. Soc. Nippon, 78: 251-266.

Falkner, F. 1975 Normal growth patterns of the newborn and the preadolescent. In: Endocrine and gentic diseases of childhood and adolescence. L.I. Gardner, ed. W.B. Saunders Co., Philadelphia, 2nd ed., pp. 8-14.

Federal Field Committee for Development Planning in Alaska 1969 Estimates of native population in villages, towns, and boroughs of Alaska. Division of Planning and Research. Office of the Governor, Juneau, Alaska.

Fischgold, H. and J. Metzger 1951 Signes radiographiques discrets et précoces des atrophies cérébrales unilatérales. J. Radiol. Electrol. Arch. Electr. Med., 32: 733-741.

Follis, R.H. and E.A. Park 1952 Some observations on bone growth, with particular respect to zones and transverse lines of increased density in the metaphysis. Am. J. Roentgenol. Radium Ther. Nucl. Med., 68: 709-724.

Garn, S.M., C. G. Rohmann, B. Wagner and W. Ascoli 1967 Continuing bone growth throughout life: a general phenomenon. Am. J. Phys. Anthropol., 26: 313-317.

Garrow, J.S. and M.C. Pike 1967 The long-term prognosis of severe infantile malnutrition. Lancet, i (No. 7480): 1-4.

Görke, O. 1904 Beitrag zur funktionellen Gestaltung des Schädels bei den Anthropomorphen und Menschen durch Untersuchung mit Röntgenstrahlen. Arch. Anthropol., 29 (NF 1): 91-108.

Graham, G.G. and T.B. Adrianzen 1972 Late "catch-up" growth after severe infantile malnutrition. John Hopkins Med. J., 131: 204-211.

Harris, H.A. 1926 The growth of the long bones in childhood with special reference to certain bony striations of the metaphysis and to the role of the vitamins. Arch. Intern. Med., 38: 785-806.

Harvold, E.P., G. Chierici and K. Vargervik 1972 Experiments on the development of dental malocclusions. Am. J. Orthod., 61: 38-44.

Harvold, E.P., K. Vargervik and G. Chierici 1973 Primate experiments on oral sensation and dental malocclusions. Am. J. Orthod., 63: 494-508.

Hasund, A.P. 1965 Attrition and dental arch space. Trans. Eur. Orthod. Soc., 41: 121-131.

Hellman, M. 1927 Changes in the human face brought about by development. Int. J. Orthod., 13: 475-515.

Hooton, E.A. 1937 Apes, Men, Morons. G.P. Putnam's Sons, New York.

Høygaard, A. 1940 Studies on the nutrition and physio-pathology of Eskimos. Skr. utgitt Nor. Vidensk.-Akad. Oslo I Mat.-Naturvidensk. Kl., No. 9, pp. 1-176.

Hrdlička, A. 1910 Contribution to the anthropology of Central and Smith Sound Eskimo. Anthropol. Pap. Am. Mus. Nat. Hist., 5: 175-285.

______ 1928 Antrhopological survey in Alaska. Annu. Rep. Bur. Am. Ethnol., 46: 19-374.

______ 1940 Lower jaw. Am. J. Phys. Anthropol., 27: 281-308.

Humphry, G. 1895 Notes on the microcephalic or idiot skull, and on the macrocephalic or hydrocephalic skull. J. Anat. Physiol., 29: 304-328.

Hunt, E.E., Jr. 1959 The continuing evolution of modern man. Cold Spring Harbor Symp. Quant. Biol., 24: 245-254.

______ 1961 Malocclusion and civilization. Am. J. Orthod., 47: 406-422.

Hylander, W. L: 1972 The adaptaive significance of Eskimo craniofacial morphology. Unpublished Ph.D. dissertation. University of Chicago.

______ 1977 The adaptive significance of Eskimo craniofacial morphology. In: Orofacial growth and development. A.A. Dahlberg and T.M. Graber, eds. Mouton Publishers, The Hague, pp. 129-169.

Israel, H. 1968 Continuing growth in the human cranial skeleton. Arch. Oral. Biol., 13: 133-138.

______ 1937 a Age factor and the pattern of change in craniofacial structures. Am. J. Phys. Anthropol., 39: 111-128.

______ 1937 b Recent knowledge concerning craniofacial aging. Angle Orthod., 43: 176-184.

Keith, A. 1929 The Antiquity of Man. 2nd ed. Williams and Norgate, London.

Klaauw, C.J. van der 1946 Cerebral skull and facial skull. Arch. Neerl. Zool., 7: 16-37

Klatsky, M. 1948 Studies in the dietaries of contemporary primitive peoples. J. Am. Dent. Assoc., 36: 385-391.

Koertvelyessy, T. 1972 Relationships between the frontal sinus and climatic conditions: a skeptical approach to cold adaptation. Am. J. Phys. Anthropol., 37: 161-172.

Kokott, W. 1933 Über den Bauplan des fötalen Hirnschädels. Gegenbaurs Morphol. Jahrb., 72: 341-361.

Krog, A. and M. Krog 1913 A study of the diet and metabolism of Eskimos undertaken in 1908 on an expedition to Greenland. Medd. Gronl., 51: 1-52.

Krogman, W.M. 1950 The concept of maturity from a morphological viewpoint. Child Develop., 21: 25-32.

Krogman, W.M. and V. Sassouni 1957 A syllabus in roentgenographic cephalometry. Philadelphia Center for Research in Child Growth, Philadelphia.

Leigh, R.W. 1929 Dental pathology of aboriginal California. Dent. Cosmos, 71: 756-767, 878-889.

Lindegård, B. 1953 Variations in human body-build. A somatometric and x-ray cephalometric investigation on Scandinavian adults. Acta Psychiatr. Neurol. (Suppl.) No. 86, pp. 1-163.

Linder-Aronson, S. 1970 Adenoids. Their effect on the mode of breathing and nasal airflow and their relationship to characteristics of the facial skeleton and the dentition. Acta Oto-Laryngol. (Suppl.), No. 265, pp. 1-132.

Lowrey, G.H. 1973 Growth and development of children. 6th ed. Year Book Medical Publishers, Chicago.

Lysell, L. 1958 Qualitative and quantitative determination of attrition and the ensuing tooth migration. Acta Odontol. Scand., 16: 267-292.

Margolis, H.I. 1947 A basic facial pattern and its application in clinical orthodontics. Am. J. Orthod. Oral Surg., 33: 631-641.

McCance, R.A., E.H.R. Ford and W.A.B. Brown 1961 Severe undernutrition in growing and adult animals. VII. Development of the skull, jaws and teeth in pigs. Br. J. Nutr., 15: 213-224.

McNamara, J.A., Jr. 1972 Neuromuscular and skeletal adaptations to altered orofacial function. Monograph No. 1, Craniofacial Growth Series. Center for Human Growth and Development, University of Michigan.

Milan, F.A. 1964 The acculturation of the contemporary Eskimo of Wainwright, Alaska. Anthropol. Pap. Univ. Alaska, 11: 1-95.

Mollison, T. 1925 Uber die Kopfform des Mikrokephalen Mesek. Z. Morphol. Anthropol., 25: 109-128.

Moore, W.J. 1965 Masticatory function and skull growth. J. Zool., 146: 123-131.

Moore, W.J. and C.L.B. Lavelle 1974 Growth of the facial skeleton in the Hominoidea. Academic Press, London and New York.

Moorrees, C.F.A. 1957 The Aleut dentition. Harvard University Press, Cambridge.

Moss, M.L. 1958a Fusion of the frontal suture in the rat. Am. J. Anatl, 102: 141-165.

______ 1958b The pathogenesis of artificial cranial deformation. Am. J. Phys. Anthropol., 16: 269-286.

______ 1959 The pathogenesis of premature cranial synostosis in man. Acta Anat., 37: 351-370

______ 1960a Functional analysis of human brow ridges. Am. J. Phys. Anthropol., 18: 357 (Abstract).

______ 1960b Inhibition and stimulation of sutural fusion in the rat calvaria. Anat. Rec., 136: 457-467

______ 1960 c Functional analysis of human mandibular growth. J. Prosthet. Dent., 10: 1149-1159.

______ 1962 The functional matrix. In: Vistas in Orthodontics. B.S. Kraus and R.A. Riedel, eds. Lea & Febiger, Philadelphia, pp. 85-98.

______ 1968 A theoretical analysis of the functional matrix. Acta Biotheor., 18: 195-202.

______ 1971a Functional cranial analysis and the functional matrix. In: Patterns of orofacial growth and development. Am. Speech Hear. Assoc. Rep. No. 6. H. L. Morris, ed. Am. Speech Hear. Assoc., Washington, DC, pp. 5-18.

______ 1971 b Facial growth: The functional matrix concept. In: Cleft Lip and Palate. W. C. Grabb, S. W. Rosenstein and K. R. Bzoch, eds. Little, Brown and Co., Boston, pp. 97-107.

______ 1972 Functional cranial analysis and the functional matrix. In: Morphology of the maxillo-mandibular apparatus. G.-H. Schumacher, ed. VEB Georg Thieme, Leipzig, pp. 160-165.

Moss, M. L. and S. N. Greenberg 1967 Functional cranial analysis of the human maxillary bone: I, basal bone. Angle Orthod., 37: 151-164.

Moss, M. L. and R. M. Rankow 1968 The role of the functional matrix in mandibular growth. Angle Orthod., 38: 95-103.

Moss, M. L. and L. Salentijn 1969a The primary role of functional matrices in facial growth. Am. J. Orthod., 55: 566-577.

______ 1969b The capsular matrix. Am. J. Orthod., 56: 474-490.

______ 1970 The logarithmic growth of the human mandible. Acta Anat., 77: 341-360.

______ 1971 Morphological attributes of the logarithmic growth of the human face: gnomonic growth. Acta Anat., 78: 185-199.

Moss, M. L. and R. W. Young 1960 A functional approach to craniology. Am. J. Phys. Anthropol., 18: 281-292.

Moyers, R. E. 1972 Handbook of Orthodontics. 3rd ed. Year Book Medical Publishers, Chicago.

Murphy, T. 1958 Mandibular adjustment to functional tooth attrition. Aust. Dent. J., 3: 171-178.

______ 1964 Reduction of the dental arch by approximal attrition. Br. Dent. J., 116: 483-488.

Neubauer, G. 1925 Experimentelle Untersuchungen über die Beeinflussung der Schädelform. Z. Morphol. Anthropol., 23: 411-441.

Noetzel, H. 1949 Über den Einfluss des Gehirns auf die Form der benachbarten Nebenhöhlen des Schädels. Dtsch. Z. Nervenheilkd., 160: 126-136.

Oppenheimer, A. 1964 Tool use and crowded teeth in Australopithecinae. Curr. Anthropol., 5: 419-421.

Oschinsky, L. 1962 Facial flatness and ceekbone morphology in Arctic Mongoloids. Anthropologica (Ottawa), 4: 349-377.

______ 1964 The most ancient Eskimos. The Canadian Research Center for Anthropology, University of Ottawa.

Oswalt, W. H. 1967 Alaskan Eskimos. Chandler Publishing Co., San Francisco.

Park, E. A. 1954 Bone growth in health and disease. Arch. Dis. Child., 29: 269-281.

Pedersen, P. O. 1949 The East Greenland Eskimo dentition. Numerical variations and anatomy. A contribution to comparative ethnic odontography. Medd. Gronl., 142 (3): 1-244.

Platt, B. S. and R. J. C. Stewart 1962 Transverse trabeculae and osteoporosis in bones in experimental protein-calorie deficiency. Br. J. Nutr., 16: 483-495.

Poncins, G. de 1941 Kabloona. Reynal and Hitchcock, New York.

Popa, G. T. 1936 Mechanostruktur und Mechanofunktion der Dura mater des Menschen. Gegenbaurs Morphol. Jahrb., 78: 85-187.

Prader, A., J. M. Tanner and G. A von Harnack 1963 Catch-up growth following illness or starvation. An example of developmental canalization in man. J. Pediatr., 62: 646-659.

Pratt, C. W. M. and R. A. McCance 1964 Severe undernutrition in growing and adult animals. XII. The extremities of the long bones in pigs. Br. J. Nutr., 18: 393-408.

Ross, A. T. 1941 Cerebral hemiatrophy with compensatory homolaterial hypertrophy of the skull and sinuses, and diminution of cranial volume. Am. J. Roentgenol. Radium Ther., 45: 332-341.

Sarnäs, K.-V. 1957 Growth changes in skulls of ancient man in North America. Acta Odontol. Scand., 15: 213-271.

______ 1959 Inter- and intra-family variations in the facial profile. Odontol. Revy, 10 (Suppl. 4): 1-116.

Schultz, A. 1926 Studies on the variability of platyrrhine monkeys. J. Mammal., 7: 286-305.

Schultze. M.O. 1955 Effects of malnutrition in early life on subsequent growth and reproduction of rats. J. Nutr., 56: 453-460.

Schwalbe, G. 1899 Studien über Pithecanthropus erectus Dubois. Z. Morphol. Anthropol., 1: 16-240.

Scott, E.M. 1956 Nutrition of Alaskan Eskimos. Nutr. Rev., 14: 1-3.

Shea, B.T. 1977 Eskimo craniofacial morphology, cold stress and the maxillary sinus. Am. J. Phys. Anthropol., 47: 289-300.

Sicher, H. 1949 Oral anatomy. The C.V. Mosby Co., Saint Louis.

Sicher, H. and J. Tandler 1928 Anatomie für Zahnärzte. Julius Springer, Wien and Berlin.

Smith, D.W. 1977 Growth and its disorders. Vol. XV in Major Probl. Clin. Pediatr. W.B. Saunders Co., Philadelphia.

Spencer, R.F. 1959 The North Alaskan Eskimo. A study in ecology and society. Smithson. Inst. Bur. Am. Ethnol. Bull., 171: 1-490.

Steegman, A.T., Jr. 1967 Frostbite of the human face as a selective force. Hum. Biol., 39: 131-144.

______ 1970 Cold adaptation and the human face. Am. J. Phys. Anthropol., 32: 243-250.

______ 1972 Cold response, body form, and craniofacial shape in two racial groups of Hawaii. Am. J. Phys. Anthropol., 37: 193-221.

Thompson, A. 1903 A consideration of some of the more important factors concerned in the production of man's cranial form. J. Anthropol. Inst. G.B. Ir., 33: 135-166.

Toldt, C. 1914 Brauenwülste, Tori superorbitales, und Brauenbögen, Arcus superciliares, und ihre mechanische Bedeutung. Mitt. Anthropol. Ges. Wien. 44: 235-315.

Vogt, C. 1867 Ueber die Mikrocephalen oder Affen-Menschen. Arch. Anthropol., 2: 129-284.

Washburn, S.L. 1947 The relation of the temporal muscle to the form of the skull. Anat. Rec., 99: 239-248.

______ 1963 The study of the race. Am. Anthropol., 65: 521-531.

Watt, D.G. and C.H.M. Williams 1951 The effects of the physical consistency of food on the growth and development of the mandible and the maxilla of the rat. Am. J. Orthod., 37: 895-928.

Waugh, L.M. 1937 Influence of diet on the jaws and face of the American Eskimo. J. Am. Dent. Assoc., 24: 1640-1647.

Weidenreich, F. 1941 The brain and its rôle in the phylogenetic transformation of the human skull. Trans. Am. Philos. Soc., 31(NS): 319-442.

Weinmann, J.P. and H. Sicher 1955 Bone and bones. Fundamentals of bone biology. 2nd ed. The C.V. Mosby Co., Saint Louis.

Widdowson, E.M. and R.A. McCance 1960 Some effects of accelerating growth. I. General somatic development. Proc. R. Soc. Lond. (Biol.), 152: 188-206.

______ 1963 The effect of finite periods of undernutrition at different ages on the composition and subsequent development of the rat. Proc. R. Soc. Lond. (Biol.), 158: 329-342.

______ 1964 Effects of nutrition and disease on growth. Br. Dent. J., 117: 326-330.

Wolpoff, M. 1968 Climatic influence on skeletal nasal aperture. Am. J. Phys. Anthropol., 29: 405-423.

______ 1971 Interstitial wear. Am. J. Phys. Anthropol., 34: 205-225.

Young, R.W. 1959 The influence of cranial contents on postnatal growth of the skull in the rat. Am. J. Anat., 105: 383-415.

Zuckerkandl, E. 1893 Normale und pathologische Anatomie der Nasenhöhle und ihrer pneumatische Anhänge. Capitel XXI. 2nd ed. Wilhelm Braumüller, Wien and Leipzig.

TABLE 1

Measurements for males in age group 1, and subsequent significant change between age groups

Variable	Age group 1		Significant difference between age groups[1]						
	M	SD	1-2	2-3	3-4	4-5	1-3	2-4	3-5
CRANIAL BASE									
med cran bse, n-ba (mm)	90.7	3.8	+	+			+	+	
ant cran bse, s-n (mm)	60.4	2.2	+	+			+	+	
post cran bse, s-ba (mm)	38.2	2.9	+	+			+	+	
sin front, n-ecp (mm)	9.7	1.7	+	+			+	+	
n-gl, proj on NSL (mm)	4.5	1.1		+			+	+	
sin front, gl-ecp (mm)	13.1	1.6	+	+			+	+	
cran bse ang, n-s-ba (deg)	132.9	4.8							
FACIAL VERTICAL DIMENSION									
ant fac ht, n-gn (mm)	105.5	6.0	+	+			+	+	
post fac ht, s-tgo (mm)	63.3	3.5	+	+			+	+	+
post/ant fac ht (%)	60.1	3.6	+				+	+	+
SAGITTAL POSITION AND FORM OF MAXILLA AND MANDIBLE									
max lth, ss-ptm (mm)	43.0	2.1	+				+	+	
mand lth, pg-ar (mm)	90.3	5.2	+	+			+	+	
mand body, pg-tgo (mm)	64.2	5.4	+	+			+	+	
ramus hgt, ar-tgo (mm)	36.3	2.8	+	+	+		+	+	+
max protr, ptm-NSP (mm)	11.7	2.6							
max bsl progn, s-n-ss (deg)	82.1	3.1							
mnd bsl progn, s-n-pg (deg)	76.9	3.7	+		+		+	+	
max alv progn. ss-n-pr (deg)	1.6	1.4	+						
mnd alv progn, sm-n-id (deg)	2.4	0.9					-		
apicl bse rel, ss-n-sm (deg)	4.6	2.5	-				-		
gonial ang, ar-tgo-gn (deg)	133.3	5.9					-	-	
total fac ang. NSL-ML (deg)	41.4	5.7	-				-	-	
DENTAL RELATIONSHIP									
overjet, is-io (mm)	1.5	2.1		-			-		
overbite, ii-io (mm)	0.5	1.2							
interinc ang (deg)	128.1	10.4			+			+	
max inc-NSL (deg)	99.8	9.3						-	
mand inc-ML (deg)	90.7	5.2						-	
MIDFACIAL FLATNESS									
MZL-NSL (deg)	42.2	5.3	+	+			+		
MZL-FL (deg)	34.6	4.9		-	-		-		
MZL-n/ss line (deg)	39.9	5.1	-	-	-	-	-		
TOTAL FACIAL FLATNESS									
profile ang, n-ss-pg (deg)	10.8	6.0		-			-	-	

---

[1] + denotes significant increase at the 1% level of confidence
- denotes significant decrease at the 1% level of confidence

TABLE 2

Measurements for females in age group 1, and subsequent significant change between age groups

Variable	Age group 1		Significant difference between age groups[1]						
	M	SD	1-2	2-3	3-4	4-5	1-3	2-4	3-5
			CRANIAL BASE						
med cran bse, n-ba (mm)	89.1	3.5	+						
ant cran bse, s-n (mm)	59.1	2.3	+				+	+	
post cran bse, s-ba (mm)	37.1	2.7	+				+		
sin front, n-ecp (mm)	8.9	1.7	+				+	+	
n-gl, proj on NSL (mm)	4.7	1.1	-					+	
sin front, gl-ecp (mm)	13.1	1.7		+	+		+	+	
cran bse ang, n-s-ba (deg)	133.0	5.1							
			FACIAL VERTICAL DIMENSION						
ant fac ht, n-gn (mm)	101.6	4.3	+				+	+	
post fac ht, s-tgo (mm)	61.2	4.7	+				+	+	
post/ant fac ht (%)	60.3	4.1							
			SAGITTAL POSITION AND FORM OF MAXILLA AND MANDIBLE						
max lth, ss-ptm (mm)	41.4	2.2	+				+	+	
mand lth, pg-ar (mm)	87.2	3.8	+	+			+	+	
mand body, pg-tgo (mm)	61.3	4.5	+	+			+	+	
ramus hgt, ar-tgo (mm)	35.7	4.6	+				+	+	
max protr, ptm-NSP (mm)	11.0	2.1							
max bsl progn, s-n-ss (deg)	80.7	2.7							
mnd bsl progn, s-n-pg (deg)	76.8	2.8	+				+	+	
max alv progn, ss-n-pr (deg)	1.6	1.2	+				+		
mnd alv progn, sm-n-id (deg)	2.0	0.8	+				+		
apicl bse rel, ss-n-sm (deg)	3.2	2.2					-		
gonial ang, ar-tgo-gn (deg)	134.3	7.7	-			-	-		-
total fac ang, NSL-ML (deg)	41.1	5.4							
			DENTAL RELATIONSHIP						
overjet, is-io (mm)	1.1	1.6			-			-	
overbite, ii-io (mm)	0.4	0.9							
interinc ang (deg)	129.9	10.8							
max inc-NSL (deg)	100.7	7.7	+						
mand inc-ML (deg)	89.9	7.5							
			MIDFACIAL FLATNESS						
MZL-NSL (deg)	42.2	5.9	+		+		+	+	
MZL-FL (deg)	34.6	5.7	-		-				
MSL-n/ss line (deg)	38.5	5.5	-		-				
			TOTAL FACIAL FLATNESS						
profile ang, n-ss-pg (deg)	8.2	5.0					-		

---

[1] + denotes significant increase at the 1% level of confidence
- denotes significant decrease at the 1% level of confidence

TABLE 3

Significant sexual dimorphism within age groups

Variable	Age groups[1]				
	1	2	3	4	5
CRANIAL BASE					
n-ba (mm)		+	+	+	+
s-n (mm)	+	+	+	+	
s-ba (mm)		+	+	+	+
n-ecp (mm)			+		
n-gl, on NSL (mm)			+		
gl-ecp (mm)		+	+		
n-s-ba (deg)					
FACIAL VERTICAL DIMENSION					
n-gn (mm)	+	+	+	+	+
s-tgo (mm)	+	+	+	+	+
s-tgo/n-gn (%)					
SAG POSITION AND FORM OF MAX AND MAND					
ss-ptm (mm)	+	+	+		
pg-ar (mm)	+	+	+	+	+
pg-tgo (mm)	+	+	+		
ar-tgo (mm)		+	+	+	+
ptm-NSP (mm)		+			
s-n-ss (deg)					
s-n-pg (deg)					
ss-n-pr (deg)		-			
sm-n-id (deg)				-	
ss-n-sm (deg)	+	+			
ar-tgo-gn (deg)					
NSL-ML (deg)					
DENTAL RELATIONSHIP					
is-io (mm)					
ii-io (mm)					
interinc ang (deg)					
max inc-NSL (deg)					
mand inc-ML (deg)					
MIDFACIAL FLATNESS					
MZL-NSL (deg)			+		
MZL-FL (deg)			-		
MZL-n/ss (deg)		-	-		
TOTAL FACIAL FLATNESS					
n-ss-pg (deg)		+			

[1] + denotes mean value for males significantly larger at the 1% level of confidence
- denotes mean value for males significantly smaller at the 1% level of confidence

TABLE 4

Measurements for Wainwright adult males (30-75 years of age) and adult males from two Eskimo skeletal populations (Dahlberg, '68; Hylander, '72)

Variable	Hudson Bay[1]			Wainwright			N-W Alaska[2]	
	M	SD	*[3]	M	SD	*[3]	M	SD
CRANIAL BASE								
n-ba (mm)	103.5	3.1		102.3	2.9			
s-n (mm)	67.2	2.2		67.0	2.4			
s-ba (mm)	43.2	1.9	*	44.8	2.4			
n-ecp (mm)	9.7	2.0	*	13.3	1.5			
n-gl, on NSL (mm)	6.0	1.3		5.8	1.4			
n-s-ba (deg)	138.7	4.7	*	131.6	4.8			
FACIAL VERTICAL DIMENSION								
n-gn (mm)	123.7	4.6		125.8	5.2			
SAG POSITION AND FORM OF MAX AND MAND								
pg-ar (mm)	111.5	3.7		112.9	5.1			
pg-tgo (mm)	81.2	3.8		78.6	4.2			
ar-tgo (mm)	48.7	4.2		51.3	4.5			
s-n-ss (deg)	82.2	3.8		83.2	3.5		84.3	3.3
s-n-sm (deg)				81.6	3.3		80.4	3.2
ss-n-sm (deg)				1.6	2.8	*	3.9	2.3
s-n-pg (deg)	78.6	3.6	*	81.7	3.1			
ar-tgo-gn (deg)	122.1	7.9		126.9	7.6		125.8	6.7
NSL-ML (deg)	35.8	5.1		34.8	5.8			
DENTAL RELATIONSHIP								
interinc ang (deg)	151.8	5.0		137.3	13.1		147.5	10.2
max inc-NSL (deg)	95.3	11.4		99.9	6.4	*	93.0	6.4
mand inc-ML (deg)	88.8	8.5		88.0	7.3		84.8	8.3
MIDFACIAL FLATNESS								
MZL-NSL (deg)	52.4	6.3		51.1	6.8			
TOTAL FACIAL FLATNESS								
n-ss-pg (deg)				3.4	5.4	*	9.6	7.1

[1] data from Hylander, '72; [2] data from Dahlberg, '68

[3] * denotes significant difference at the 1% level of confidence

TABLE 5

Measurements for Wainwright adult females (30-75 years of age) and adult females from two Eskimo skeletal populations (Dahlberg, '68; Hylander, '72)

Variable	Hudson Bay[1]			Wainwright			N-W Alaska[2]	
	M	SD	*[3]	M	SD	*[3]	M	SD
CRANIAL BASE								
n-ba (mm)	98.7	4.2		98.0	5.7			
s-n (mm)	64.4	2.9		67.4	4.1			
s-ba (mm)	41.4	2.2		41.8	3.0			
n-ecp (mm)	9.3	2.0	*	12.7	1.9			
n-gl, on NSL (mm)	5.8	1.5		5.1	1.3			
n-s-ba (deg)	137.2	4.0	*	132.8	3.6			
FACIAL VERTICAL DIMENSION								
n-gn (mm)	111.5	6.5		116.6	6.5			
SAG POSITION AND FORM OF MAX AND MAND								
pg-ar (mm)	101.0	3.9		104.9	6.2			
pg-tgo (mm)	74.3	3.5		77.1	5.1			
ar-tgo (mm)	44.6	2.9		45.6	4.6			
s-n-ss (deg)	81.6	3.2		82.8	5.0		83.4	3.3
s-n-sm (deg)				80.8	3.0		80.3	3.3
ss-n-sm (deg)				2.1	2.8		3.5	2.7
s-n-pg (deg)	78.5	2.7		80.6	3.3			
ar-tgo-gn (deg)	119.2	4.4		121.7	4.2		125.5	6.1
NSL-ML (deg)	33.5	3.7		34.6	4.0			
DENTAL RELATIONSHIP								
interinc ang (deg)				131.5	8.5	*	149.5	10.3
max inc-NSL (deg)				101.3	5.2	*	90.7	8.3
mand inc-ML (deg)	93.3	0.1		92.5	4.7	*	85.5	7.7
MIDFACIAL FLATNESS								
MZL-NSL (deg)	48.3	5.2		51.9	5.9			
TOTAL FACIAL FLATNESS								
n-ss-pg (deg)				4.7	6.2		8.8	7.3

[1] data from Hylander, '72; [2] data from Dahlberg, '68

[3] * denotes significant difference at the 1% level of confidence

A letter to Al

THELMA DAHLBERG

OSSA Vol. 6, pp. 69-74, Lund. ISSN 0345-8865.

Dear Al,

I hoped it would be, I expected it to be, a good marriage with years of companionship and contentment, the fulfillment of every American girl's dream. There would be a family of happy, healthy intelligent children, eventually a home of our own, and perhaps after a few more years, a little place in the country. Our family and home and your dental practice would be our main interests, participation in community activities and association with friends would add enrichment and satisfaction. All those hopes, expectations and dreams have been fulfilled.

What I did not anticipate on that January day in 1934 when we exchanged our vows was that you would be taking me to some far away places, at times under unusual circumstances, and we would have friends all over the globe. Your pursuit of knowledge about teeth has given us experiences seldom shared by others. There were times, I must admit, when I would ask myself, "How do you happen to be here?" I recall saying that aloud one night when I slept alone in the huge and otherwise empty barrack that was reserved for visiting women, usually entertainers, at Thule Air Base in northern Greenland. The unusual and unexpected have been thrilling at the moment, but what has given us the most happiness is our acquaintance and association with people all over the world. We could not anticipate such a large number of friends.

Our travels began when you chose the Pima Indians for your first study of a living population. You went to Washington and convinced Dr. Vern Forney, in charge of dentistry for the Bureau of Indian Affairs, that such a study would be beneficial to all concerned. At our own expense, we went to Sacaton, Arizona the next year, where we were joinedby Mickey(Dr. Mikkelson), the B.I.A. Area Supervisor for Dentistry. That was our first field trip, but it wasn't the true beginning of your study of world dentition. You had been doing extensive reading, especially W.K. Gregory's "Origin and Evolution of Human Dentition" and articles by Percy Butler on the "Field Concept". Each week, on your "day off" from clinical work, you and I went to the Field Museum, where we sequestered ourselves on the fourth floor and studied every Melanesian skull in their collection. You measured each tooth with your Boley gauge while I recorded the data. You became so excited about human dentition, you wanted to put all your information into a paper. Our home became a writing studio for you. I'll never forget my struggles in trying to keep three little children quietly occupied during the Christmas holiday while Daddy used the dining room table for a desk. "The Changing Dentition of Man" was published the following June. I like to think that the very beginning of your study of tooth morphology began in our own family. What dental characteristics would our children have? You, with a family history of peg shaped or missing lateral incisors and no third molars, and I with all thirty-two teeth and a supernumerary tooth, extracted when I was seven years old, what would our children inherit? I remember you x-rayed little Jimmie's gums to see how his secondary teeth were developing when he was only four years old.

That first visit to the Pima Indians developed into a progressive study. Year after year we returned to gather more material on tooth development and eruption patterns in children, and to develop pedigrees of family members. You also wished to make comparative observations of other tribes and our field trips included visits to the

Sioux, Sac and Fox, Utes, Navajo, Zuni and Hopi. Sometimes our field trips were family affairs wherein our children went along during spring recess of their school. Invaluable scientific data was not the only reward of our trips to "Indian country". Our lives have been enriched by the cherished friendships of some of the government workers, teachers and Indians. Field trips also gave us an opportunity to become better acquainted with your students and with visiting Japanese scholars, when our teams were enlarged.

Our involvement with Japanese dentists came about quite unexpectedly. You received a call from the American Dental Association requesting that you entertain a visiting dean of a Japanese dental school. We took Dr. Takahashi to dinner at the Quadrangle Club and you suggested that he accompany us on our next field trip to Arizona. He had time and funds to study American dentistry in any area, so he accepted. Taki, as he asked us to call him, instead of Dr. Takahashi, worked with us doing every sort of job, even "cleaning up". Later, while visiting in Japan, I learned that in his country he was held in such high esteem that he wasn't allowed to carry his own briefcase. Taki's visit with us began a fruitful and pleasant association with many Japanese dental and other biological scholars. Each year at least one young man would come from Japan to work with you and others. Their families have become part of our "family" and you and I are the American obiasan and oziisan of some wee folk. We have been treated wonderfully in visits to Japan, few Americans have seen more places of interest and beauty. In the year of your 65th birthday, we were their guests from the time we left O'Hare airport until our return and it was on this trip that you were honored and delighted by the presentation of The Order of the Rising Sun, Third Degree.

In 1960, you arranged to leave your dental practice for three months and we went to Europe and the Middle East to visit museums and study collections. We truly worked on that trip. I'm sure I am the only American woman who spent a month in Paris on her first trip to Europe and never took time to step inside a Paris shop. But I'm very familiar with the working and storage space of the Musée de l'Homme and the Institut de Paléontologie. From Paris it was Dordogne, Brussels, Göttingen, London, Stockholm, Copenhagen, anywhere tooth collections could be seen. In Zagreb there was a tense moment when a single specimen among the many pieces of the Krapina collection could not be found. It's a moment I'll never forget. The curator, the assistant curator and Dr. Kallay were quietly and politely muttering while you and I stood by, helplessly trying to show our innocence. Everyone was smiling tight little smiles, as papers and cloth coverings were gently shuffled about. At last, the invaluable missing piece was found, on a shelf far from where you and I were standing, and everyone showed relief from tension.

Egypt was fascinating, but your access to the mummy exhibits was limited. It was when we left Egypt for Iraq that adventure began for us. The plane was filled to capacity and all the passengers and crew were speaking a language we could not understand. A pleasant young man from Bulgaria sat directly in front of us and spoke to us briefly in English. We were relieved to know someone aboard could understand us. When we reached Baghdad, we found the language barrier a true handicap. Everyone else seemed able to get a taxi, but we were deliberately misunderstood, or so it appeared. After every other passenger was on his way from the airport, two young men signaled that they had a taxi available. (We had noticed that every driver had a companion.) We told them we had reservations at the Zia hotel. At last they understood the magic word Zia and nodded assent. They were very cordial and asked, "American?" We nodded and they smiled a warm welcome. But when we reached the Zia hotel they suddenly protested against our going there, "No! No!" Then, in a language we could not understand but with gestures that were clear, they indicated that they wanted to take us elsewhere. A huge banner, lettered in Arabic, was floating over the courtyard. They kept pointing toward it. We insisted on going in, we had made reservations by letter, weeks before. Reluctantly, they carried our bags to the registry desk and left with a puzzled look. We obtained the last room in the hotel, a tiny cubicle, but perhaps all the rooms were small. Immediately after our luggage was in the room, a messenger said Mr. Zia would like to see us at once in the bar. We found Mr. Zia in a large and otherwise empty room. He was a big man who spoke some English. He asked us to be seated at the bar, then summoned Jesus, the bartender, to take our drink orders. Mr. Zia's manner was polite but cool. When our drinks were before us, he turned to us and asked directly and bluntly, "Why did you come to this hotel?" "The Braidwoods recommended it," we replied. Immediately, his manner changed and he became the genial person the Braidwoods had described to us. He informed us that the hotel had been taken over by representatives from "iron curtain" countries for a conference that was beginning that day. The banner outside was a greeting to all "comrades". He assured us we were welcome as his guests, but it would be wise to keep our distance from the others. We assured him that we would be model guests. We never saw Mr. Zia again. We saw the delegates in the dining room at breakfast time in carefully chosen far corners. It amused us to hear them speaking English as their common language. And they ate Kellogg's CornFlakes! We would nod, "Good Morning" to anyone who gave us a passing glance. You were disappointed at not being able to see the Shanidar collection, which had been your main reason for going to Baghdad. The curator was "on a holiday, returning tomorrow". That tomorrow never came, even though we returned two succeeding days. On the day of our departure, all the boulevards were decorated with bunting and plants. We pretended it was for our departure, but we knew it was for Sukarno, who was arriving the next day to visit with his good friend Kassem. Our plane to Tehran was to leave at two o'clock, but there was so much excitement about Sukarno's visit, we decided to leave the heart of the city in the morning and wait for our plane at the airport. The hours dragged by, there was nothing to do and little to eat or drink. We anticipated some delay, but when the time approached midnight, we began to wonder where we could hide when Sukarno arrived the next day. A little after 11 P.M., our plane arrived and we could board. It was an Iranian plane with an American pilot, a sandy haired young man with a southern accent. We couldn't believe it was the right plane, for all the seats had been removed from one side and cargo, big awkward boxes, had been tied in. "Are you sure those boxes are secure?" I heard you ask. You even tried to push one a bit. The pilot's family was in the tail end of the plane. You and I had to sit opposite the cargo. There was a plump Iranian stewardess, whose only service was to check our seat belts. We were glad to be on our way at last, and we relaxed. After a while, I didn't know how long after we had started, for I had closed my eyes, I felt extremely cold, as though ice water were flowing through my veins. I told you how cold I felt, then a sweet drowsiness came over me, and I didn't care about anything. I remember hearing you say, "Give me one of those" in a demanding voice, then, "well, get one for me." It was so peaceful, I didn't even wonder what you wanted. Later, after the pilot had given you an oxygen mask, I learned what had happened. We had been flying over the mountains between the two countries and the plane's cabin was not pressurized. The pilot had been bringing oxygen masks to his family when you asked for one. You had looked for the stewardess, but she was sprawled on a seat using a mask, too.

In Tehran you went to the University Dental School and asked for a young dentist who could assist us and also be an interpreter and guide. It was our good fortune to have Ezat Khamessi chosen to fill this need. He has been a close friend ever since. Ezat went with us to Kermanshah, where we joined the Braidwoods and their staff, who where on an archeological dig. They had taken over part of the compound of a former Presbyterian hospital; two large homes that had once been doctors' residences were the housing quarters. In one, the Braidwoods and some of the staff had sleeping rooms, an office was set up, and in the kitchen all meals were prepared. In the other house, identical to the first, the remainder of the staff and visitors had sleeping rooms. The kitchen was in use as well, not for preparing food, but for cooking the flesh from bones, so that Charlie Reed, the biologist for the group, could increase his collection of animal bones. What a picture that kitchen presented! Large cauldrons were bubbling on the huge stove, one pot had the horns of a mountain sheep curled out and over the rim. The smells were hauntingly pungent, for specimens were brought in wherever found, some not very fresh. I never saw the rest of the first floor, I was always in a hurry to get to my room, away from the smells. You did a wonderful service for the Iranians in the mud villages around Kermanshah. The traveling dentists would come only at intervals and there were many aching teeth. You and Dr. Khamessi would set up a "tailgate clinic" in the back of a car, and then we would wait. Usually we were ready to leave in frustration before anyone would be willing to have a tooth extracted. I remained nearby, notebook in hand, ready to record data as you dictated. There was always a pause after the first extraction while the patient spread the news, "no pain"-- oh, how carefully you worked! Then there would be a flood of patients.

You always were cautious about not offending others, even if you had to be offensive to yourself. In one rural area some men wanted to give us the treat of a drink of cold buttermilk. You've never liked buttermilk, and being told it was from the rich milk of a sheep, didn't make it sound more appetizing. Two glasses were produced, a large one for you and a small one for me. When the buttermilk was brought from the cooling stream, it was in a bag made from an animal skin, with all the extremities tied tightly. I knew I couldn't drink any, and you very chivalrously came to my rescue, explaining that I had stomach trouble and couldn't drink anything with acidity. Your big glass was filled, even though you kept protesting it was too much. I had never seen you drink anything so fast. You told me later it was the only way you could get it down. The men thought you liked the buttermilk so much, they wanted to fill your glass again. You were noble and good and everyone was pleased. I was pleased that you managed to keep it down.

After we returned to Tehran, you wanted to go to north eastern Iran to look at the teeth of natives who had some Mongoloid features. We informed the American Embassy in Tehran that we were going to Bandershah and Ezat got our train tickets. On the morning of our departure, we left so early, we had breakfast served in our room. There were huge stacks of coarse bread toast and two fried eggs apiece. We ate what we wished, then, "pack rat" that I am, I made sandwiches of the remaining toast and eggs, and put them in my big purse. The ride through northern Iran was spectacularly beautiful. Frequently we could look from one mountain to another and see where our train would be winding its way. By late afternoon we reached Bandershah, the end of the line for the train. We were surprised to see soldiers at the station, who kept us from getting a taxi. A man in uniform approached Dr. Khamessi and some excited conversation which we couldn't understand took place. We learned we couldn't come to Bandershah. There had been some border incidents in which foreigners had been killed. We had to leave. When? The next train was at ten o'clock in the morning, the train we had arrived on and the one we had expected to use in return. What were we to do? We couldn't stay and it was impossible to leave. Dr. Khamessi asked the rank of the man speaking to us and when he learned he was a sergeant he refused to communicate any further with him. Dr. Khamessi had the rank of a captain and he would speak only with a captain. The sergeant's captain, unfortunately, was at some distance, at a camp on the shore of the Caspian sea. A jeep was brought to the station and the three of us were taken out to the camp where the two captains could converse. While they talked I looked out over the sea and watched the sun setting into the water. It was a beautiful sight, but I couldn't help thinking "Where are we and how did we ever get to this lonely spot at this time of day?" The captain decided to return to town with us. He would help us in our study, then we must go to our hotel and not leave until he called for us the next morning. "House arrest," we quietly agreed between us. The captain insisted on driving the jeep back to town. Dr. Khamessi sat beside him and you were to sit by Dr. Khamessi. I started to get in the back seat, where the sergeant was sitting alone, but Dr. Khamessi would not allow that. I was told I could not share a seat with someone so far below my status, so I had to sit in front on your lap. The front seat of a jeep holds two comfortably, but four -- it was misery for us, but quite proper. By request or command from the captain, a dentist who had patients waiting in his outer room and a patient in the chair, gave up his premises to you and Dr. Khamessi. Soldiers were sent out to bring anyone they found who looked the least bit mongoloid: epicanthic fold in the eyelids, wide zygomatic arch. Frightened but obedient people looked relieved when they learned they were brought in so that we could look at their teeth. I took notes while you dictated your observations. Shortly after ten o'clock, you let the dentist resume his work and we were escorted to our hotel. By this time, the lunch we had eaten on the train was long digested. Our cold, fried egg sandwiches tasted like a banquet. We had been warned not to drink the water, but I had sealed cans of water that had been given to us on Air France some time ago, so our thirst was quenched. It was a night of giggling and jests, and the paper-thin walls allowed us to hear Dr. Khamessi laughing in the next room. The following morning, the captain called for us and took us for a brief visit to a boarding school. Standing near the station, just before train time, he asked if you would examine his teeth. You were very obliging, even though curious spectators came closing in, trying to see what your were trying to find in the gentleman's mouth.

In 1961, Bill Laughlin opened a new study area to us, the Arctic. There have been many subsequent trips to Alaska with Bill and Fred Milan, but neither of us will forget an experience we had the first summer, off Kodiak Island. We had been using open skiffs, fitted with army surplus outboard motors, to travel short distances from our headquarters at Old Harbor. You seemed to have the most luck in making the old motors behave (if only we had known, we were supposed to use white gasoline). Bill wanted to go to Three Saints Bay to make a survey for possible digging sites the following summer. He and Carter Denniston went in one boat, you and I in another. We camped at beautiful Three Saints Bay for a couple of days, explored caves and did some digging. On the morning of our planned departure, a storm was threatening. We were concerned about getting beyond some rocks at the mouth of the bay and into the open water. Just as we were congratulating ourselves on our success, I looked ahead and saw the dorsal fin and tail of a killer whale diving into the water, coming our way. I called to you and almost immediately we felt a jolt and our motor stopped. Our shaft had been hit and the shearing pin was broken. You struggled with the motor, trying to get it into the boat, I started rowing, trying to keep the waves from carrying us back into the rocks we had just escaped. Finally, we attracted the attention of Bill and Carter. You needed Carter's help in getting the shaft into the boat, but first we should be towed farther away from the boulders. While the rest of us held the two boats side by side, Carter eased himself over the edges and into our boat. It was a dangerous act and took much courage and caution. The two of you got the shaft into the boat and a new pin was inserted. We were feeling "safe and sound", the boat was working and we had seen no more of the whale. Just as we were heading again toward Old Harbor, you saw Bill reach down to pick up something from the bottom of his boat. In doing so, he momentarily took his hand from the control. Like a helicopter, his motor shizzed up into the air, off the mooring, then fell into the ocean. It was not lost, for it was secured by a rope, but it was utterly useless until cleaned and dried.

By this time the storm was getting strong. We had no choice but to anchor our boats at the nearest shoreline. There were four feet of gravel beach between the edge of the water and the perpendicular face of a rock cliff. You managed to start a little fire by shaving away the damp coating from driftwood. I suggested eating some lunch and you said with all sincerity, "I don't think you should prepare a big lunch." We had the finest lunch that one can serve of damp sea biscuits and soggy cheese. After some consultation, you and I started out for Old Harbour in our boat, while Bill and Carter would wait for rescue. As soon as we had gone far enough to be out of sight, I became concerned for our welfare. They had the only gun, and if our motor failed we would have to beach our boat wherever the waves carried us. We would have no protection against the huge Kodiak bears, and bear tracks were obvious everywhere, in the high, dense vegetation. So we returned to Bill and Carter and told them we wanted to stay together. The rain was heavy by now. We unloaded everything expendable and the four of us got into our boat and started once again for Old Harbor. We'd scarcely started when the motor quit. Bill and Carter began rowing in unison, you held up a plastic sheet for a sail, and I bailed out water. Bill wisely decided that we were taking too many risks; if we were swamped by a wave or overturned, survival time in the icy water was only seven minutes, in spite of our rubber suits and the tight rope belts we all wore. We headed for a spit of land that marked Barling Bay. Across the mouth of the bay, Old Harbor was less than two miles away, but if we had to walk along the shoreline it would be an eighteen mile trek. While you and the others secured the boat, I walked through the short grass on the spit of land, to look at the other side. There I saw the most beautiful sight that could greet my eyes. Anchored in the bay was a fisherman's boat! I called to him, and in doing so awakened a little dog sleeping on the deck. Our shouts from the shore and the barking of the dog finally awakened the owner from his nap. He had been getting all the rest he could before government regulations let him return to fishing on Sunday night. The rain had stopped, and the fisherman got in his dinghy and came to us. Where had we come from? What were we doing there? "Now I've seen everything," he said when he observed one was a woman. He took us aboard, served us hot coffee, then lifted anchor and steered his boat into the open waters to pick up our skiffs. How nicely he treated you. With your white beard, he thought you too elderly to do manual labor, so he had Bill and Carter help him with the rescue proceedings. You winked at me to keep quiet, you didn't want to hurt his feelings, and it was very nice to be compelled to sit still. It was dark by the time we reached Old Harbor, and the storm had come up again. The fishing boat had to remain quite some distance from shore and we had to go the remainder of the distance rowing our skiffs. The waves and wind were getting violent and the light from the fishing boat was our only illumination. The villagers were there to meet us, forming a chain to grasp the bow of our boat and give us support. As I stepped from the skiff, a wave nearly swept me from my feet, but the Baptist Missionary grabbed my rope belt and helped me to firm ground. "You sure look good to me," I told him, "You look like a drowned rat to me," he replied.

We stayed away from the skiffs in succeeding visits to Kodiak, our children demanded that of us. Some people may think we should curb all our activities, for according to statistics we are past the age of retirement. But please don't let your enthusiasm and interest wane. You never look happier than when you are describing the evolution of human dentition from the single cone or are tracing the development of a tooth from the anlage to eruption.

I need not tell you I have enjoyed being a "toothsome twosome" with you. It's been an interesting and fun dividend to our marriage.

Thelma

A note on sexual dimorphism in the early hominid dentition

JEAN KITAHARA - FRISCH

OSSA

One of the clearest characteristics of the modern human dentition among that of other primates is the nearly complete absence of sexual dimorphism in tooth size and shape. Terrestrial habits and increasingly large body size is associated in primates with increased sexual dimorphism. In the course of human evolution, however there has been a decrease in sexual dimorphism.

Recent discoveries of numerous new fossil hominids further complicate the problem since they show sexual dimorphism in canines and molars to have evolved independently.

In order to account for these data, a model has recently been presented by Wolpoff (1976a) where tool making by early hominids is assumed to have played a major role. Tool use and tool making account, in this view, both for the reduction of the canines in males and for the increase in size of the molars.

The present paper attempts to show how the accumulating fossil evidence makes Wolpoff' s model highly questionable. Recent observations on chimpanzee tool behavior also fail to support Wolpoff' s views. Following this criticism, an alternative model is proposed where the use of tools and the influence it had on the reduction of sexual dimorphism is considered to have occurred in two successive stages. It is concluded that the reduction of sexual dimorphism in hominids resulted from a wide array of cultural activities (such as intensive hunting, division of labor, social organisation, etc.). Of these, tool making was perhaps one of the earliest manifestations. By itself, however, tool making appears to have been insufficient to bring about the reduction of sexual dimorphism seen in modern hominids.

Keywords: Early Hominid, Dentition - Sexual dimorphism

Одной из наиболее отчетливых характеристик современных человеческих зубов по сравнению с зубами приматов является почти полное отсутствие полового диморфизма в размере и форме зубов. Сухопутный образ жизни и возрастающий крупный размер тела связаны у приматов с возрастающим половым диморфизмом. В процессе человеческой эволюции происходило, однако, уменьшение полового диморфизма.

Недавние открытия многих новых ископаемых гоминидов усложняют далее проблему, поскольку они обнаруживают наличие развивавшегося независимо полового диморфизма у клыков больших коренных зубов.

Для того, чтобы объяснить эти данные, Вольпофф /1976а/ предложил недавно модель, где предполагается, что созданные ранними гоминидами орудия труда играли главную роль. Производимые и используемые орудия труда послужили, в свою очередь, причиной уменьшения клыков у мужских особей и возрастания размера больших коренных зубов.

Настоящая статья пытается показать, как накопление ископаемого материала подвергает сомнению модель Вольпоффа. Недавние наблюдения за поведением шимпанзе при использовании ими орудий также ставит под сомнение вышеприведенную гипотезу. Учитывая эти критические замечания, была предложена альтернативная модель, где использование орудий и их воздействие на уменьшение полового диморфизма рассматриваются как встречающиеся в двух последовательных стадиях. Было сделано заключение, что уменьшение полового диморфизма у гоминидов является результатом разнообразной деятельности /такой, как интенсивная охота, разделение труда, социальная организация и т.д./. Среди этой деятельности производство орудий труда принадлежало, возможно, к одному из ранних ее проявлений. Само же по себе производство орудий труда, как кажется, было недостаточным для того, чтобы вызвать уменьшение полового диморфизма, наблюдаемого у современных гоминидов.

Ключевые слова: ранний гоминид, зубы, половой диморфизм.

Jean Kitahara-Frisch, Life Science Institute, Sophia University, Kioicho, Chiyoda-ku, Tokyo 102, Japan.

Vol. 6, pp. 75-82, Lund. ISSN 0345-8865.

The Problem

In order to better understand the peculiar pattern of sexual dimorphism characteristic of Homo it is helpful to first view human sexual dimorphism among primates in general and hominoids in particular.

Table 1, based on data provided by Schultz ('69) and Napier & Napier ('67), reveals that the most pronounced examples of sexual dimorphism in living primates occur either in predominantly terrestrial species (e.g. Papio) or in species with large body size (e.g. Pongo and Gorilla). The two arboreal forms showing unexpected marked sexual dimorphism (Pongo and Nasalis) are, it will be noticed, larger than related forms (e.g. Pan and Presbytis respectively). Among South American monkeys it is also the largest species, Alouatta, that shows the greatest amount of dimorphism.

In comparison with these observations, the outstanding characteristic of Homo is found to be the coexistence of terrestrial living habits and large body size with a sexual dimorphism more reduced than in nearly all hominoid primates, with the exception of the gibbon (Frisch, '73). Moreover, if man is considered not only in his present condition but also in his evolutionary history, human evolution appears to be characterized jointly by an increase in body size in both males and females and by a progressive reduction of sexual dimorphism.

Such are the characteristics that need to be explained since they run counter to what the rest of primate evolution would have led one to expect.

When trying to account for the peculiar type of sexual dimorphism characteristic of Homo, the increasing number of early hominid fossil finds may be expected to provide valuable evidence for tracing the development of this unusual trait. However, as the fossil record becomes more complete, a number of new difficulties also appear that make the solution of the problem more complex. As can be seen in table 2, early hominids show much more dimorphism in molar size than the chimpanzees or even the gorillas, although the latter are two to three times heavier than estimates for early hominids (Robinson, 1972). Simultaneously, however, the canines of the early hominids show much less dimorphism than in either of these two great apes.

A comparison of early hominids from East and South Africa reveals an additional anomaly: East African hominids are found to be conspicuously more dimorphic than South African hominds for molar size but to be practically identical with them as far as the canines are concerned.

Such anomalies must be explained in any attempt to interpret the significance of sexual dimorphism in early hominids. More specifically, one must account for the fact that molar size remained apparently dimorphic much longer than in the case of the canines. The possiblity must also be considered that in some hominid species the molars became even more dimorphic as time went by (Wallace, '75).

A model for Hominid Sexual Dimorphism

The nature of the difficulties mentioned above seems to call for a separate consideration of canine and molar sizes. This is because of the possibility that canines and molars were submitted, during early hominid evolution, to different selective pressures. This is what Wolpoff attempts to do in a series of recent publications (Wolpoff, '75, '76 a. b). Dahlberg's observation, fifteen years ago (Dahlberg, '62), that developments in the evolution of the hominid dentition may occur within some tooth groups independently or in combination with other groups may apply to the evolution of sexual dimorphism in distinct tooth groups.

As far as the canines are concerned, Wolpoff suggests that emerging tool use and developing cultural behavior brought about a reduction in size of the canines in both males and females, as these teeth were replaced or supplemented by tools. On the other hand, the process thought to have led to increased molar size and increased sexual dimorphism in these teeth is seen by him as more complex. It is believed to reflect the use of clubs and rocks as weapons. The efficient use of these weapons would have put a premium on physical strength and would have thus favored an increase in body size, particularly in males engaged in the defense of the group. Increased body size would have called in turn for a higher caloric intake, more processing of food and, ultimately, larger molar grinding surfaces. Thus, in Wolpoff's view, the emergence of culture, under the form of tools and/or weapons, had a differential effect on canines and molars.

Wolpoff's hypothesis shows concern for the evolutionary processes involved in the development of the hominid dentition. He thus certainly stands to be commended for heeding the warning given by Dahlberg ('62) that only a consideration of the biological principles involved would succeed in illuminating points in tooth morphology which until then had been mere subjects for statistical data recording. Nevertheless, the hypothesis he formulates raises a number of serious difficulties. Some of these will be considered in the following paragraphs and an alternative model suggesting how sexual dimorphism may have evolved in early hominids will be briefly outlined.

The first difficulty with Wolpoff's model originates in the fossil record. For instance, the canine was already reduced in a number of Pliocene hominoid genera that are not known to have been using tools. Such is the case with Oreopithecus (Huerzeler, '58) and Ramapithecus (Simons, '61). More recent finds from Hungary (Kretzoi, '75) confirm that forms with small canines were no exceptions but were part of a wide-spread radiation covering the three continents of the Old World.

As a matter of fact, as more finds of early fossil hominids are made, the orthodox view of deriving Homo from an ancestor possessing large canines becomes increasingly questionable. Kinzey's ('71) suggestion that man's immediate ancestors had small canines is therefore strengthened. However, even if this is not the case it is already clear that the link between canine reduction and tool use is far from being as close as previously suggested. Such may also have been the case for sexual dimorphism as a whole.

Another difficulty in accepting Wolpoff's hypothesis resides in the fact that canines are considerably less reduced in Homo erectus than they are in the robust australopithecines. According to Tobias ('67), the mean labiolingual diameter of the canines in Homo erectus (10.5 mm) is surpassed by only one out of 13 Paranthropus (= Australopithecus robustus) canines and by none of the known Australopithecus canines. Brace et al. ('73) report the maxillary canine area to average 84.88 mm^2 in 23 South African australopithecines as opposed to an average area of 96.50 mm^2 in the canines of Homo erectus.

Likewise, sexual dimorphism in canine area is reported by Wolpoff ('76b) to be larger in Homo erectus than for the combined South African australopithecine sample. As for Australopithecus robustus, the smaller average size of the canine suggests that sexual dimorphism would probably be even smaller in that form and the difference with Homo erectus even larger. Stone tools, however, as is well known, were frequently used by Homo erectus with considerable skill in stone tool manufacture. Stone tools have so far never been found in definite association with robust australopithecine remains (Tobias, '71). The combined fossil and archeological evidence thus speaks strongly against associating tool making and reduction of canine size.

A different type of difficulty in the model here considered stems from the newly acquired knowledge of chimpanzee behavior under natural conditions. The consideration of that behavior is helpful in that it gives some idea of the kind of behavioral basis that may be assumed to have been present in the common hominoid heritage.

Chimpanzees are known to use tools chiefly in food producing activities and displays (Nishida, '73; Beck, '75). It is important in this context to observe that most objects used by chimpanzees for procuring food do not and could not replace or supplement canines. A possible exception would be the crushing of nuts with stones (Struhsaker and Hunkeler, '71), but this behavior is still most imperfectly known.

On the other hand, objects are also used by chimpanzees in displays or, rarely, for offensive and defensive purposes. But, in this case also, the objects used do not appear to replace the canines any more than in food procuring activities. As early as fifty years ago Koehler remarked that displays in chimpanzees contained an important element of play and that sticks were thrown away as soon as the game became serious, the apes "falling on one another with hands, feet and teeth" (Koehler, '25:83).

Behavioral evidence thus indicates that, where tools are used by chimpanzees, they seldom, if ever, replace canines. That they did replace them in early hominids and were thus responsible for canine reduction in males is a claim that remains unsupported by all available evidence of hominoid behavior.

Finally, if tool use and tool making had been sufficiently developed to account for a reduction of the canines, it is hard to understand why these same tools did not take care of the needs for processing larger amounts of food and why, instead, the grinding surfaces of the molars had to be increased. In this context, it may be significant that the grinding surfaces of the molars are most enlarged in the robust australopithecine type which is the one not known for certain to have manufactured stone tools. This fact led Wallace (' 75) to suggest that some early hominids became specialized for crushing and grinding food within the mouth while others took to grinding food with tools outside the mouth. If this suggestion is correct, the existence of large molars with small canines in robust australopithecines constitutes additional evidence that tools cannot be held responsible for canine reduction, at least not in this hominid species.

An alternative model

As an alternative to Wolpoff' s model, it is suggested in the following paragraphs that the use of tools and the influence it had on the reduction of sexual dimorphism is best considered as having occurred in two successive stages.

During the first stage, conceived to have been that characteristic of early hominids, stone tools, it is argued, were of a very simple make and were used chiefly for collecting purposes. As such, they were without effect on the size of the male canines. Reduction of the canines in males, and consequent decrease in sexual dimorphism, are best attributed, it is suggested, at this stage, to other factors, such as pressure for greater sociability (Holloway, '67) or the fact that smaller canines, as proposed by Jolly (' 70), facilitated chewing on small hard objects. Such an explanation of canine reduction would account for the reduction of the canine in species of early hominids, such as Australopithecus robustus, that are not known to have made or used stone tools to any large extent.[1]

On the other hand, considerable sexual dimorphism in molar size may reflect terrestrial habits and the larger body size of males, a common feature in terrestrial primates. The apparent dimorphism may also be, to an extent, an artifact produced by the unwarranted lumping of specimens belonging to different species, particularly where the East African sample is concerned. It is certainly not hard to visualize the coexistence of two or more species or early hominids characterized by different degrees of reliance on molars for the grinding of hard seeds. Some populations may in fact have started using stone tools for grinding purposes, thereby replacing the molar dentition, as suggested by Wallace (' 75). The point should be clarified by a more accurate analysis of the distribution of dental variability in early hominids by geological age and geographical site.[2]

The second stage proposed here concerns later (middle Pleistocene) hominids: division of labor by sexes. More complex stone tools were used in hunting activities (as weapons, knifes for skinning game, etc.), chiefly by males. Collecting, on the other hand, became the more exclusive role of females and, as such, may have contributed in part to increasing selective pressure for larger body size in females, thereby reducing the amount of overall sexual dimorphism.

Increase in body size in females, however, may be more easily accounted for in terms of the selective pressures prompted by an increased reliance on hunting in the subsistence pattern of middle Pleistocene hominids. Increased hunting perhaps re-

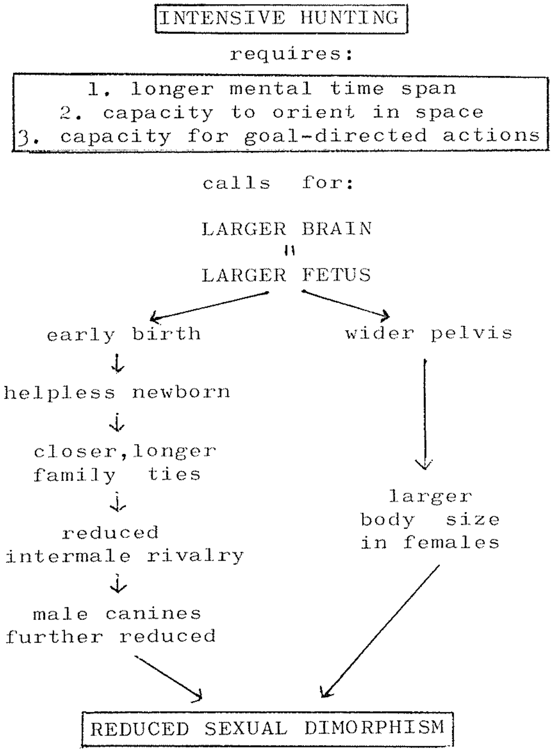


Fig. 1. Flow chart showing hypothesized impact of intensive hunting on the reduction of sexual dimorphism.

flected the deteriorating climate in the Northern latitudes. The link between hunting and larger female body size may be visualized in the following fashion. Successful hunting is thought to have required a considerable increase in mental time span (Krantz, '68) and also an increased capacity for orientation in space and goal directed actions (Brown and Lahren, '73). These requirements eventually brought about, it has been hypothesized, the doubling and tripling of hominid brain size from Australopithecus to Homo erectus and H. sapiens. The rapid increase in brain size would, in turn, have favored a larger body size in females so as to provide a wider birth canal for delivering the larger brained fetus (Campbell, '66).

The obstetric problem, however, may also have been solved, at least partly, by hastening the time of birth of the fetus and causing the delivery to occur before term. This would account for the remarkable immaturity of modern man's newborn when compared to that of other primates (Portmann, '51). Such an early delivery would have entailed a greater helplessness in the newborn and have favored, as suggested by Campbell ('66), the development of more permanent family ties.

Opportunities for male rivalry would thereby have become fewer and the role of canines in sexual intermale competition would have been considerably diminished. Canine reduction, a process that had already begun in the first stage outlined above, would have thus proceeded further and resulted eventually in the extremely reduced sexual dimorphism characteristic of the canine in modern Homo sapiens.

Thus, as seen in figure 1, intensive hunting, by calling for a rapid increase in brain size, can readily be visualized to have set in motion a series of processes, such as increase in female body size, accelerated delivery of the fetus and reduction in male rivalry. The global outcome of these processes amounted, it is suggested, to a considerable reduction of sexual dimorphism reached principally through the increase in size of the female body and the decrease in size of the male canines.

The model here proposed considers separately the processes responsible for the reduction of sexual dimorphism in the canines and in the molars. It is consistent with the evidence recently presented by Leutenegger and Kelly (1977) to the effect that the factors determining canine size dimorphism and body size dimorphism in primates differ in magnitude and origin. The key factor controling canine dimorphism, these authors argue, is male intrasexual selection which, in turn, is related to the social structure of the reproductive unit. Body size dimorphism, on the other hand, they show to be determined by a multitude of factors interrelated in a complex manner.

The model presented in this article outlines briefly what this complex interrelationship may have been in the case of early hominids. It also concurs with the views of Leutenegger and Kelly on the importance of the social factors involved in determining dimorphism in both canines and molars.

The model proposed is also seen to agree with that of Wolpoff in considering culture as the principal agent responsible for the overall reduction of sexual dimorphism in the hominid lineage. It avoids, however, to postulate a direct causal relationship between the use of tools and the reduction of canines.

The influence of culture was mediated, it is suggested, by an array of activities, such as hunting, division of labor, tool making and social organization. Of these activities tool making may well have been one of the earliest manifestations, but simple tool making appears, on the strength of the evidence considered above, to have been insufficient to bring about the unique pattern characteristic of human sexual dimorphism.

Literature cited

Andrews, P. and J. A. H. Van Couvering 1975 Palaeoenvironments in the East African Miocene. In: Approaches to Primate Paleobiology. F. S. Szalay, ed. Contrib. Primat. Vol. 5: pp. 62-103. Karger, Basel.

Beck, B. 1975 Primate tool behavior. In: Socioecology and Psychology of Primates. R. H. Tuttle, ed. Mouton, The Hague, pp. 413-447.

Brace, C. L., P. E. Mahler and R. B. Rosen 1973 Tooth measurements and the rejection of the taxon "Homo habilis". Yearbk. of Phys. Anthrop., 16: 50-68.

Brown, C. and S. L. Lahren 1973 More on hunting ability and increased brain size. Curr. Antrhop., 14: 309-310.

Campbell, B. G. 1966 Human Evolution. Aldine, Chicago.

Dahlberg, A. 1962 On the teeth of early Sapiens. In: Evolution und Hominisation. G. Kurth, ed. Fischer, Stuttgart, pp. 205-211.

Frisch, J. 1973 The hylobatid dentition. In: Gibbon and Siamang. D. Rumbaugh, ed. Karger, Basel, vol. 2, pp. 56-95.

Gingerich, P. D. and M. Schoeninger 1977 The fossil record and primate phylogeny. Hum. Evol, 6: 483-505.

Holloway, R. 1967 Tools and teeth: some speculations regarding canine reduction. Am. Anthrop., 69: 63-67.

Huerzeler, J. 1958 Oreopithecus bambolii Gervais. A preliminary report. Verh. Naturf. Gesellsch. Basel, 69: 1-48.

Jolly, C.J. 1970 The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man, 5: 5-26.

Kinzey, W.G. 1971 Evolution of the human canine tooth. Am. Anthrop., 73: 680-694.

Koehler, W. 1925 The Mentality of Apes. Routledge and Kegan, London.

Krantz, G.S. 1968 Brain size and hunting ability in earliest man. Curr. Anthrop., 9: 450-451.

Kretzoi, M. 1975 New Ramapithecines and Pliopithecus from the lower Pliocene of Rudabaya in north-eastern Hungary. Nature, 257: 578-581.

Leutenegger, W. and J.T. Kelly 1977 Relationship of sexual dimorphism in canine size and body size to social, behavioral and ecological correlates in anthropoid primates. Primates, 18: 117-136.

Napier, J.R. and P.H. Napier 1967 A Handbook of Living Primates. Academic Press, New York.

Nishida, T. 1973 The ant-gathering behavior by the use of tools by wild chimpanzees. J. Hum. Evol., 2: 357-370.

Portmann, A. 1951 Biologische Fragmente zu einer Lehre des Menschen. Schwalbe, Basel.

Robinson, J.T. 1972 Early Hominid Posture and Locomotion. Univ. of Chicago Press, Chicago.

Schultz, A.H. 1969 The Life of Primates. Universe Books, New York.

Simons, E.L. 1961 The phyletic position of Ramapithecus. Postilla (Yale Peabody Museum) 57.

Struhsaker, T.T. and P. Hunkeler 1971 Evidence for tool-using by chimpanzees in the Ivory Coast. Folia Primat., 15: 212-219.

Tattersall, I. 1969 Ecology of North Indian Ramapithecus. Nature, 221: 451-452.

Tobias, P.T. 1967 Olduvai Gorge, vol. 2. The Skull and Maxillary Dentition of Australopithecus (Zinj.) boisei. Cambridge University Press, Cambridge.

______ 1971 The Brain in Hominid Evolution. Columbia Univ. Press, New York.

Wallace, J.A. 1975 Dietary adaptations of Australopithecus and early Homo. In: Paleoanthropology, Morphology and Ecology. R.H. Tuttle, ed. Mouton, The Hague, pp. 203-224.

Wolpoff, M.H. 1975 Sexual dimorphism in the australopithecines. In: Paleoanthropology, Morhpology and Ecology. R.H. Tuttle, ed. Mouton, The Hague, pp. 245-284.

______ 1976a Primate models for australopithecine sexual dimorphism. Am. J. Phys. Anthrop., 45: 497-510.

______ 1976b Some aspects of the evolution of early hominid sexual dimorphism. Curr. Anthrop., 17: 579-606.

Notes

1 Jolly's proposal is consistent with what is known of the environments in which Middle Miocene hominoids with small canines lived, both in India and in East Africa. These environments appear to have included open woodland areas where seed-like hard objects are likely to have formed part of the diet and where, consequently, reduced canines would have become advantageous (Tattersall, '69; Andrews and Van Couvering, '75)

2 Confirmation of the coexistence of distinct species of early hominids in East Africa depends on a more accurate analysis of the distribution of fossil remains by geographical site and stratigraphic layer, a point recently well brought out by Gingerich and Schoeninger (1977).

TABLE 1

SEXUAL DIMORPHISM IN PRIMATES

(Body Weight)

Species	Habitat[2]	Index[1]	Male Body Weight (in Kg.)
Homo sapiens	T	89	60 - 80
Gorilla gorilla	T	48	140 - 180
Pan troglodytes	M	89	aver. 48.9
Pongo pygmaeus	A	49	aver. 69
Erythrocebus	T	54	7.5 - 12.6
Macaca mulatta	M	69	5.6 - 10.9
Nasalis larvatus	A	48	11.7 - 23.6
Presbytis entellus	A	68	9.5 - 20.9
Papio papio	T	43	22 - 30[3]
Alouatta palliata	A	81	aver. 7.4

1: weight of female in percent of weight of male
2: T = terrestrial, M = mixed, A = arboreal habitat
3: weight range in males of *Papio anubis.*

(Data from Schultz, 1969 and Napier & Napier, 1967)

TABLE 2

SEXUAL DIMORPHISM IN MANDIBULAR MOLARS AND CANINES OF EARLY HOMINIDS AND APES

(Tooth area of females in % of area in males)

	M_1	M_2	M_3	C,
South African samples combined	87.7	84.9	81.7	79.1[n.1]
East African samples combined	71.9	66.7	64.4	81.3
Pan	95.4	95.8	92.7	66.0
Gorilla	89.1	86.7	82.8	48.6

n.1 The value for C of the South African samples refers to the maxillary canine.

(Data from Wolpoff, 1976b)

Postmature development of supernumerary premolars

TATSUO FUKUHARA

OSSA

Two cases of postmature development of supernumerary premolars are presented in regard to the reversion theory of the human dentition. Garn's concept of third molar agnesis ('61-'64) which may be related to reduction of tooth size and/or number of the remaining teeth is viewed as an extreme degree of expression of the factor delaying the tooth formation over a long period of development. A presumption in line with this concept may be raised that postmature formation of so-called supernumerary teeth formerly normal in ancestral form inclines toward complete reduction in modern man through a long process of evolution.

Keywords: Development - Postmature - Supernumerary Premolars.

Отмечаются два случая развития дополнительных малых коренных зубов после наступления половой зрелости, относящиеся к атавистической теории формирования человеческих зубов. Концепция Гарна рассматривает агенезию третьего большого коренного зуба /'61 -'64/ которая может быть связана с уменьшением размера зуба и /или/ числа остальных зубов. Она оценивается как крайняя степень проявления фактора, задерживающего формирование зуба на протяжении длительного периода развития. В соответствии с этой концепцией может возникнуть предположение, что, благодаря длительному процессу эволюции, формирование так называемых дополнительных зубов после наступления половой зрелости, ранее нормальное в унаследованной форме, имеет тенденцию к полному исчезновению у современного человека.

Ключевые слова: развитие, период после наступления половой зрелости, дополнительные малые коренные зубы.

Tatsuo Fukuhara, Department of Orthodontics, Showa University Dental School, Ohta-ku, Kitasezoku 2-1-1, Tokyo 145. Japan.

Vol. 6, pp. 83-88, Lund. ISSN 0345-8865.

Prevailing trend toward complete panoramic roentgenograms in oral diagnosis has made it possible to disclose almost true incidence of supernumerary and congenital missing teeth in the dentition. Stafne ('32) stated that definite determination of the frequency of the supernumerary teeth can be made by observation of many subjects from the time the deciduous dentition is completed until the last teeth of the permanent dentition have become fully calcified. Morphogenetic reductions in the tooth number and size which occur in the third molars, second premolars of the the four quadrants, maxillary lateral incisors and mandibular central and lateral incisors are accepted as evolutionary changes which prophesy a future dental formula of fewer teeth. Garn et al. ('61-'64) made extensive studies on agenesis of third molars and found a correlation between the congenital absence of this tooth and polymorphism in tooth size and delayed timing of the formation of remaining teeth. Concerning supernumerary teeth, on the other hand, various hypotheses have been advanced in relation to the evolution of dentition. These hypotheses can be classified into three major groups (Stafne, '32): (1) all supernumerary teeth are attributed to reversion; (2) reversion may be accepted in some instances and rejected in others, and (3) reversion is rejected entirely. Based on the examination of 48,550 consecutive patients from whom complete dental roentgenograms were made, Stafne ('32) indicated that ancestral tooth number would be 56 if one assumed that all supernumerary teeth which occur fall under the reversion hypothesis. Hanihara et al. ('65) studied a possible relationship of the tooth number anomaly to the normal characters as presented by crown diameters in regard to the evolutionary significance of the supernumerary teeth. This statistical survey demonstrated that the supernumerary teeth, or at least

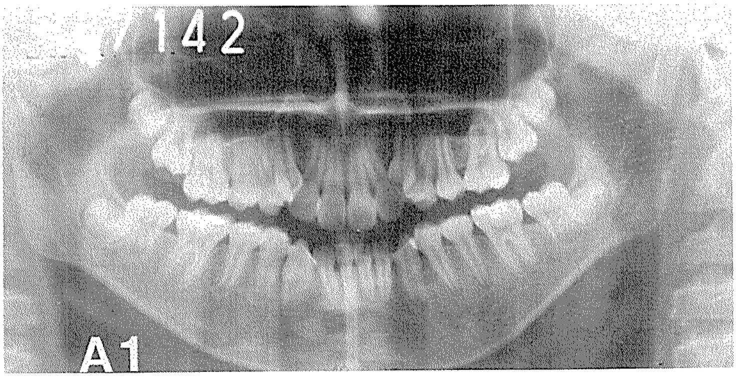


Fig. 1. Case 1. Boy, 11 years old. Panoramic view of the dentition. No specific finding in tooth number and shapes (A 1).

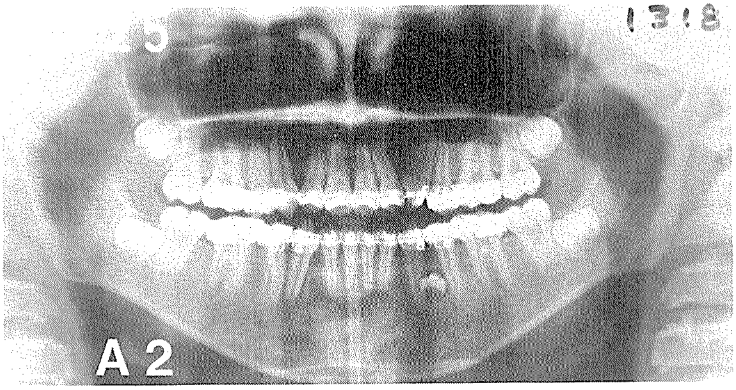


Fig. 2. Panoramic roentgenogram taken 2 years and 1 month later than that in Figure 1. Clear image of extra premolar in the left of the mandible (A 2).

the mesiodentes which were used for the materials, have no evolutionary importance. It was also concluded that this result might support the theory of accidental variation in tooth germs for the origin of the supernumerary teeth and the reversion theory was rejected. The following two cases concern supernumerary mandibular premolars which were not found on the initial examination during the early stage of orthodontic treatment and during which time the normal premolars were fully calcified.

Case 1. An eleven year old boy who was referred to us by a general practitioner in August, 1974. Routine intraoral and facial examination, panoramic and cephalometric roentgenograms were taken. Tooth number and shapes were normal (Fig. 1). Treatment planning was made and maxillary and mandibular first premolars were removed. Two years and one month later, in September, 1975, another panoramic roentgenogram was taken which revealed an unusually developing extra premolar on the left side of the mandible (Fig. 2). In the magnifying picture from the original film, it is possible to compare with the dental film taken six months later (Fig. 3). The obscured image of the early stage of the uncalcified tooth germ is illustrated in the white circle.

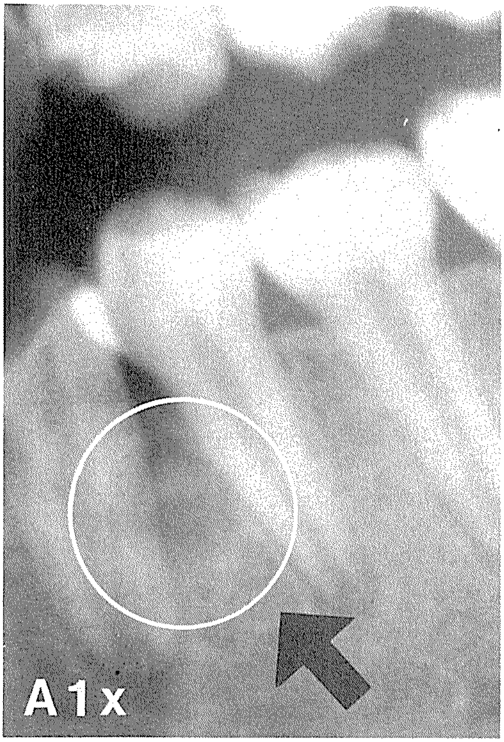


Fig. 3a. (A 1 X)
Magnifying picture of premolar region of Fig. 1. Obscured image of uncalcified tooth germ is revealed in white circle.

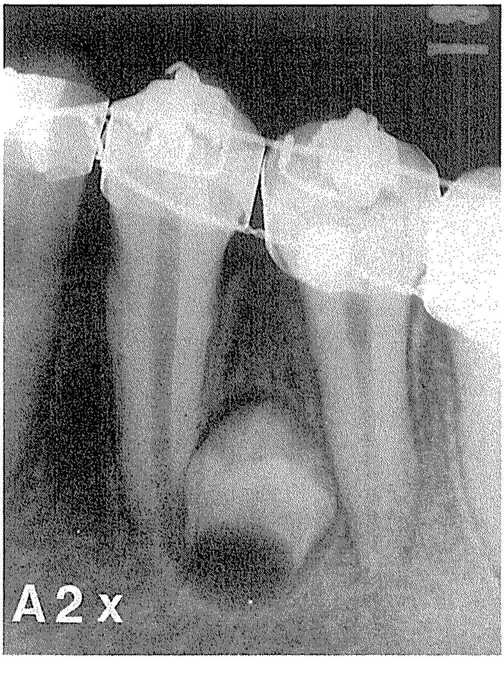


Fig. 3b. (A 2 X)
Magnifying picture of premolar region of Fig. 2. Postmature development of supernumerary premolar.

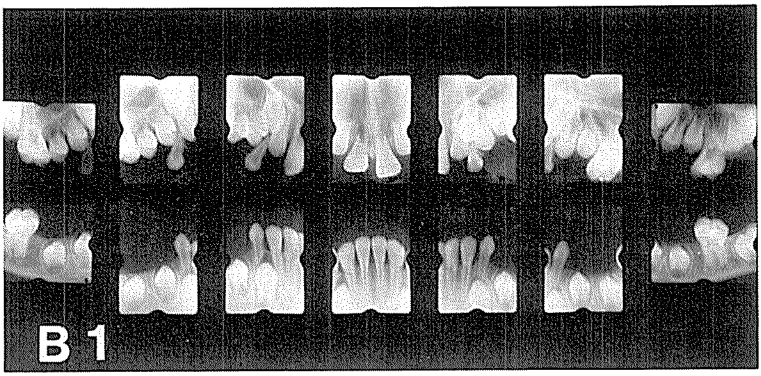


Fig. 4. Case 2. Dental roentgenograms. Individual seems to be normal in tooth number and shapes (B 1).

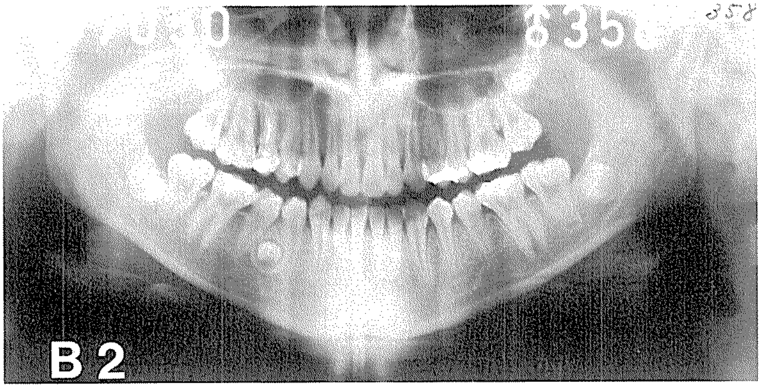


Fig. 5. Panoramic film taken 6 years and 7 months later than that in Fig. 4. A postmature development of supernumerary premolar is now clearly illustrated (B 2).

Case 2. A boy aged eight years and eleven months with anterior crossbite. Dental roentgenogram as well as the cephalogram were taken in October, 1970, soon after the consultation. However, no variation was found in tooth number and shapes (Fig. 4). An additional panoramic roentgenogram was taken in May, 1977, when the patient was 15 years and six months old, and revealed a right supernumerary premolar in the mandible with its crown about 70% calcified (Fig. 5).

Comment:

Supernumerary premolars are not infrequently found in dental patients. However, postmature calcification of the tooth germs, like the present cases, is very unique and enables a consideration from the viewpoint of the evolutionary process of diminution in tooth number or reversion nature probably persistent in the human dentition. Poyton et al. ('60) reported a most unusual case of recurring supernumerary premolars although they were removed five years ago. As Garn et al. ('61-'64) have described, agenesis of the third molar is viewed as the extreme degree of expression of factors delaying the tooth formation over a long developmental period ranging from the first month of life (for the first molar) to the eighth year or beyond (for the third molar). A presumption along the line of Garn's concept is that postmature calcification of the supernumerary premolars during the period of normal premolar formation in modern man indicates that so-called supernumerary premolars are the manifestation of the reversion of tooth number and indicative of the process of evolutionary reduction.

Literature cited

Garn, S.M., A.B. Lewis and B. Bonne 1961 Third molar polymorphism and the timing of tooth formation. Nature, 192:989.

Garn, S.M., A.B. Lewis and J. H. Vicinus 1963a Third molar polymorphism and its significance to dental genetics. J. Dent. Res., 42. Suppl. to No. 6:1344-1363.

Garn, S.M., A.B. Lewis and R.S. Kerewsky 1963b Third molar agenesis and size reduction of the remaining teeth. Nature, 200: 488-489.

Garn, S.M., A.B. Lewis and R.S. Kerewsky 1964 Third molar agenesis and variation in size of the remaining teeth. Nature, 201: 839.

Hanihara, K., T. Masuda and T. Tanaka 1965 Evolutionary significance of reduction and supernumerary teeth in the dentition. J. Anthrop. Soc. Nippon, 73: 72-81.

Poyton, G.H., G.A. Morgan and S.A. Crouch 1960 Recurring supernumerary mandibular premolars. Report of a case of postmature development. Oral Surg. Oral Med. and Oral Pathol., 13: 964-966.

Stafne, E.C. 1932 Supernumerary teeth. Dent. Cosmos, 74: 653-659.

Tissue culture of the development of teeth and jaws

SHIRLEY GLASSTONE

OSSA

Tissue culture has been used for the study of the morphogenetic field within the tooth itself and within the jaw including the squamo-mandibular joint. In studies using a culture medium of chicken embryo extract and fowl plasma and later a chemically defined medium, normal histological and morphological differentiation occurred. Normal cusps formed as well as the differentiation of odontoblasts and ameloblasts and the formation of dentine and enamel.

In tooth germs cut into two before cusps were present and grown in tissue culture regulative changes took place and each part formed a whole tooth. In pieces of jaw explanted at a very early stage of development when no teeth were present, whole teeth developed. The portion from the anterior part formed incisors and those from the posterior region molars. These findings illustrate the presence of a morphogenetic field within the jaw and within the tooth itself.

Combined mandibular and maxillary segments before differentiation of the mesenchyme was present were grown as tissue cultures. From the undifferentiated mesenchyme Meckel's cartilage developed as well as the body of the mandible, the mandibular ramus and the squamo-mandibular joint.

The formation of the joint in organ culture indicates that the joint formation does not depend on muscular, nervous or vascular factors but that the factors are intrinsic to particular regions of the mandibular and maxillary mesenchyme.

Keywords: Development - Teeth and Jaws - Tissue cultures.

Культура ткани была использована для изучения морфогенетической области внутри самого зуба и в нижней челюсти, а также в чешуйчато-мандибулярном суставе. Применяли питательную среду, содержавшую экстракт из куриного эмбриона и птичью плазму, а также среду определенного химического состава. Отмечены нормальные гистологическая и морфологическая дифференциации. Формируются нормальные эмалевые органы, происходит дифференциация одонтобластов и амелобластов, а также образуются дентин и эмаль.

Зачаток зуба, разрезанный на две части перед появлением эмалевого органа и росший в культуре ткани, обнаруживал регулятивные изменения, причем каждая из частей сформировала полный зуб.

В частях челюсти, культивированных вне организма на очень ранней стадии развития, когда еще не обнаруживалось никаких зубов, развивались полные зубы. Участок передней области формировал резцы, а часть задней области - большие коренные зубы. Эти наблюдения иллюстрируют наличие морфогенетической области внутри челюсти и внутри самого зуба.

Комбинированные нижнечелюстные и верхнечелюстные сегменты перед дифференциацией мезенхимы росли в виде культуры ткани. Меккелев хрящ развивался из недифференцированной мезенхимы, так же как и тело нижней челюсти, ее альвеолярный отросток и чешуйчато-челюстной сустав.

Формирование сустава в культуре ткани показывает, что этот процесс не зависит от факторов, связанных с мышцами, нервами или сосудами, но что эти факторы внутренне сопряжены со специфическими участками верхнечелюстной и нижнечелюстной мезенхимы.

Ключевые слова: развитие, культура ткани, зубы и нижняя челюсть.

Shirley Glasstone, 34 Porson Road, Cambridge C2 2EU, England.

Vol. 6, pp. 89-104, Lund. ISSN 0345-8865.

Introduction

Probably the first experiment on the transplantation of teeth on record was that of Cadmus, who, it may be remembered, explanted into the soil dragons' teeth which grew into armed men (Stesichorus, 6 B.C.). Apart from this legendary experiment which had such a singular result, very little work has been done on the self-differentiating capacity of dental tissues outside the mouth.

Legros and Magitot (1874) made homologous and heterologous transplants of whole tooth germs and the component parts of tooth germs, into the subcutaneous tissues of guinea pigs and dogs. As these grafts were made in the days when aseptic precautions were not taken, the results were remarkably satisfactory. Seven of the twenty-six transplants of whole teeth developed dentine and enamel. In the grafts of the pulp alone, dentine sometimes formed, but those of the isolated enamel organ were absorbed. The authors drew no conclusions from their results.

No further work of value on the embryology of grafted tooth germs was done until that of Huggins, McCarroll and Dahlberg (1934). They showed that the soft tissues of tooth germs taken from dogs were able to differentiate readily when transplanted into the abdominal wall of the same dog.

From their results they were able to formulate some interesting embryological facts. They found that only when the ameloblasts were in contact with the odontoblasts did these cells maintain their columnar shape, and form enamel. In grafts of the isolated enamel organ the ameloblasts lost their cylindrical shape, and this layer of cells formed a stratified squamous epithelium. No cysts formed, whereas they did so in grafts of the gingival tissue. They also found that the enamel organ induced the formation of the odontoblasts, but once these latter cells were present they were able to form dentine, in an irregular fashion, in its absence. But the presence of the enamel organ was essential for the normal morphology of the tooth. This result confirmed experimentally the view of Turner (1872), Tomes (1874) and Von Brunn (1887, 1891) who described teeth with enamel organs but with no enamel. Von Brunn held the view that no odontoblasts, and consequently no dentine formed in the absence of the epithelial sheath. The epithelial sheath was the enamel organ in its reduced form. The external and internal epithelia were in apposition and there was no stellate reticulum present.

Huggins, McCarroll and Dahlberg were able to modify this view on experimental grounds and said (p. 207): "... odontoblasts, which have arisen as a result of epithelial influence on connective tissue, do not further need for their function the presence of epithelium".

A certain amount of work has been done on the development of tooth germs in tissue culture but not much has emerged so far from these studies.

Glasstone (1936, 1938, 1952, 1967) studied the growth and differentiation of isolated rudiments as well as whole incisor and molar tooth germs. Tissues from the embryonic rat, mouse, rabbit, golden hamster and human were cultivated in a medium of fowl plasma and chick-embryo extract. The cultures were grown in watch glasses or as hanging drops, and incubated at 37°C.

The following experiments and observations were made.

Growth and differentiation of isolated rudiments of the tooth germs

A. Enamel Organ

The enamel organ was stripped off from molar tooth germs just before calcification. This tissue, when cultivated alone at this early stage of development, survived for a few days and there was no histological change.

B. Dental Papilla

In some of the incisors a calcified cap of dentine was present; this cap was stripped off with the enamel organ, leaving the dental papilla. During this process some odontoblasts were stripped off whilst others remained behind on the papilla. Where there was no enamel organ present, these odontoblasts formed an irregular band of dentine instead of a sheet of dentine. In a number of the cultures part of the enamel organ remained behind. When this happened the internal cells of the enamel organ, that is the pre-ameloblasts, differentiated into functional ameloblasts; the cells became cylindrical in shape with the nucleus at the end of the cell furthest away from the dental papilla. At this stage the adjacent cells of the pulp differentiated into odontoblasts and formed regular bands of dentine.

In another set of experiments, the cells of the periphery of the papilla were cut away, leaving a central portion consisting of fibroblasts and mesenchyme cells. When such a part of the dental papilla was grown as a tissue culture the cells remained healthy but no further differentiation occurred.

Of particular interest is the question of the influence of the enamel organ on dentine development. It had previously been shown that the enamel organ, which is present even in teeth where no enamel forms, is necessary for the formation of dentine. Turner (1872) had observed that the teeth in the narwhal had an enamel organ but no enamel, and a similar observation was made by Tomes (1874) in the armadillo. Hertwig (1874) in his work on amphibian teeth described the presence of the enamel organ in a reduced form, in the region of root formation where no enamel is formed. Von Brunn (1891) observed its presence on the tips of the cusps of rat molars and on the palatal surface of the rodent incisors, all of which are enamel-free areas. Von Brunn came to the conclusion that the epithelial sheath, the enamel organ in a reduced form, is responsible for the development of odontoblasts and dentine and that its primary function is that of determining the form of the future tooth.

In the tissue cultures of the dental papilla alone, the odontoblasts present at the time of explantation produced convoluted bands of dentine. Wherever dentine was formed in contact with the epithelium it was deposited as a regular sheet. This result clearly showed that one of the functions of the enamel epithelium is to determine the morphological structure of the tooth. This confirmed, experimentally, the views based on the morphological deductions of the investigators of the 19th century. Therefore the enamel organ, even in its reduced form, has an organizing effect on the dental papilla, inducing odontoblast formation. Once the connective-tissue cells have reacted to this influence, the presence of the enamel epithelium is not necessary for the deposition of dentine.

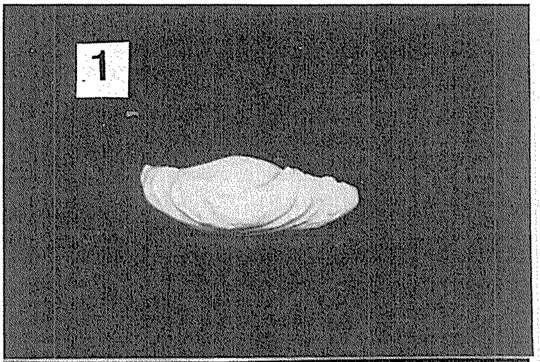
The results of this study fully confirm the conclusions of Huggins, McCarroll and Dahlberg (1934). Their evidence was derived from the transplantation of tooth-germ elements into the abdomen of the dog, whereas the results of the present study were obtained from the cultivation of tooth germs in vitro. By this experimental method, all vascular and nervous connexions were eliminated; this produced a more complete isolation than grafting.

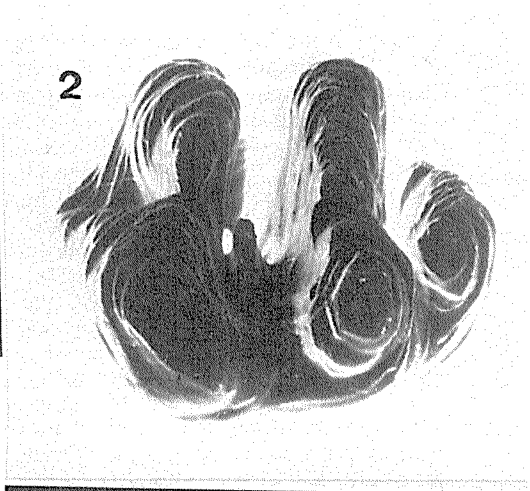
Whole tooth germs

A. Incisors

Incisor tooth germs of the rat, mouse, and golden hamster were removed at the cap stage and grown in a medium of fowl plasma and chick-embryo extract.

As the incisors increased in size they changed from the cap stage and became bell-shaped. They gradually elongated and had a pointed incisive edge, the buccal surface became convex and the palatal or lingual surface concave. The cells on the periphery of the dental papilla, that is adjacent to the enamel epithelium differentiated into odontoblasts which formed normal tubular dentine. The cells of the internal





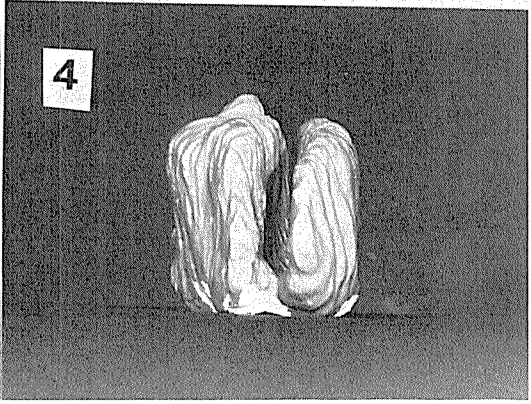


Fig. 1. Wax reconstruction of the dental papilla of the first lower molar of a 17-day rat embryo. Cusps have not yet formed. x 45.

Fig. 2. Wax reconstruction of the dental papilla of the first lower molar of a 17-day rat embryo grown in vitro for 6 days. Note the three groups of cusps formed during this period. x 80.

Fig. 3. Wax reconstruction of the dental papilla of the first lower molar of a 20-day rabbit embryo grown in vitro for 6 days. (No cusps are present at 20 days.) Note that the cusps formed during the period in vitro are similar to those of the normal tooth (see Fig. 4). x 120.

Fig. 4. Wax reconstruction of the dental papilla of the first lower molar of a 26-day rabbit embryo. x 20.

enamel epithelium on the labial surface of the tooth differentiated into typical ameloblasts, but only in a few cultures did these cells form enamel; the enamel was prismatic in structure (Fig. 5).

B. Molars

Molar tooth germs of several rodents besides the rabbit were cultured in a medium similar to that used in the previous experiments. The teeth were explanted at various stages of development and, during the period of cultivation, growth and differentiation continued.

Teeth, explanted at a stage before cusp formation, developed cusps. The teeth increased in size, but in the end they only grew to be less than one-third the size of the normal tooth of the same age. There was a remarkable similarity of cusp development in the tissue cultures to that in normal teeth in situ. The number, shape and arrangement of cusps were almost identical (Figs. 1, 2, 3, 4).

The histological development was like that seen in the normal tooth; odontoblasts differentiated and formed normal tubular dentine. Histologically normal ameloblasts, with their Tomes processes, were present, but only in a few instances was enamel formed (Figs. 6 and 7).

The rabbit molar is a persistently growing tooth. During normal development this tooth is divided into two portions, a single distal cusp and a large mesial cusp. In the mesial cusp a very small extra cusp can be observed which is later covered by a layer of enamel. In the cultivated rabbit tooth germs the development of this extra small cusp in the mesial group was frequently noticed; the form and position of this cusp showed very little variation.

An extra cusp known as the paramolar tubercle is often seen in the molars of New Britain Melanesians and New Hebrides Melanesians; it has been observed in the teeth of other races. Also the cusp of Carabelli is a further example of an extra cusp found in the molars of man. The fact that extra cusps appeared quite regularly in the rabbit tooth explants, and were always in the same position, suggests that possibly a genetic influence may be operating.

The mechanism of cusp formation is an obscure and interesting problem. In the growth of whole tooth germs isolated from their normal surroundings by the Tissue Culture method, it has been shown that the development of the shape of the tooth, and of the cusps, is self-differentiating. From these results it can be concluded that there is a morphogenetic field within the tooth which is independent of the influence of the surrounding tissue.

Development of divided tooth germs

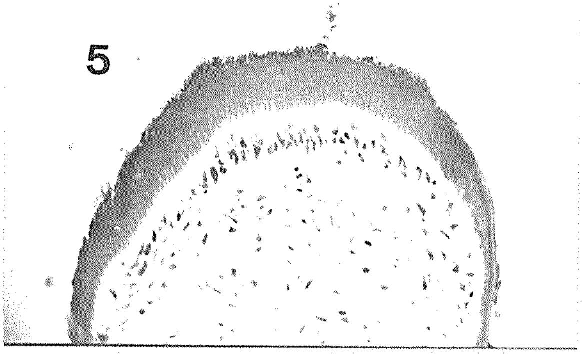
Molar tooth germs of 20-22-day-old rabbit embryos were cut into two in a buccal-lingual direction. They were grown in a medium as described above.

When the two portions were approximately equal, each portion formed a whole tooth (Figs. 8 and 9).

Divided tooth germs from 22-day-old embryos did not form whole teeth but each portion formed its own cusps.

Cusp-forming regions are not morphologically determined in the tooth germs at an early stage of development, since half tooth germs can form complete tooth germs when grown as tissue cultures. These half-tooth rudiments, although smaller than the explants of whole tooth germs, follow the same developmental pattern even to the extent of sometimes forming additional cusps in the mesial group. Odontoblasts, dentine and ameloblasts differentiated in the cultures.

This capacity for morphological regulation in explanted halves in the rabbit molar persists up to the twenty-second day of foetal life, that is until just before the odontoblasts have begun to form. After this stage, regulative changes can no longer take place in the cultures, and each half forms its own cusps.



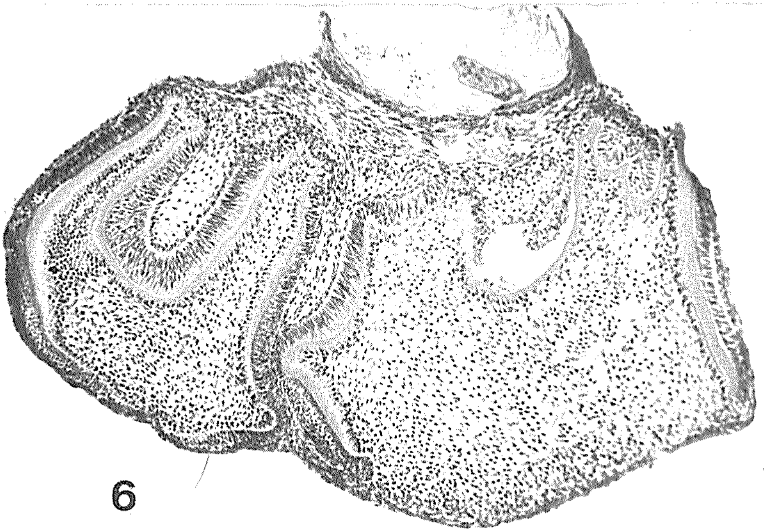
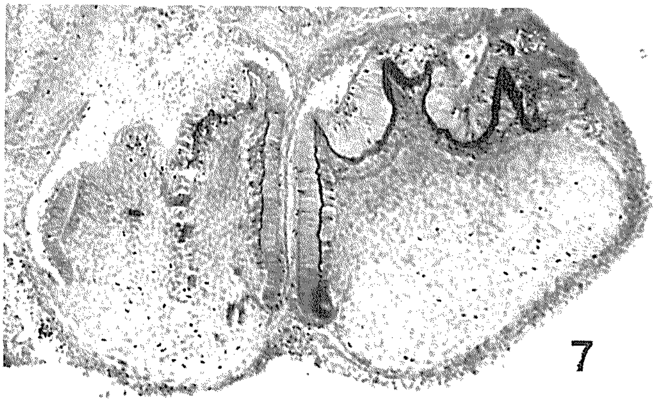
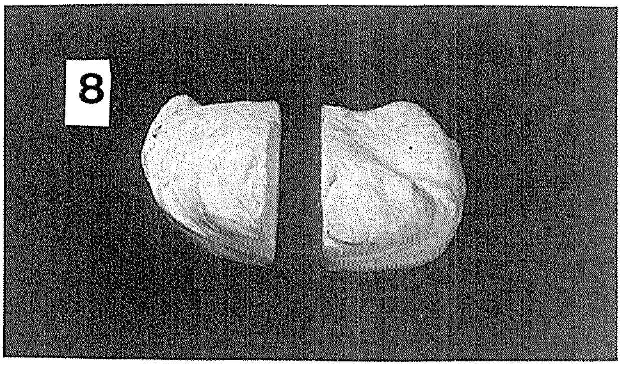


Fig. 5. Part of a longitudinal section of an incisor after 14 days in vitro. Note the dentine and enamel formed during this period. Haematoxylin and eosin. x 406.

Fig. 6. Longitudinal section of molars one and two from a 17-day mouse embryo after 12 days in vitro. Note that the cusps have formed. A layer of dentine is also present. Haematoxylin eosin. x 114.





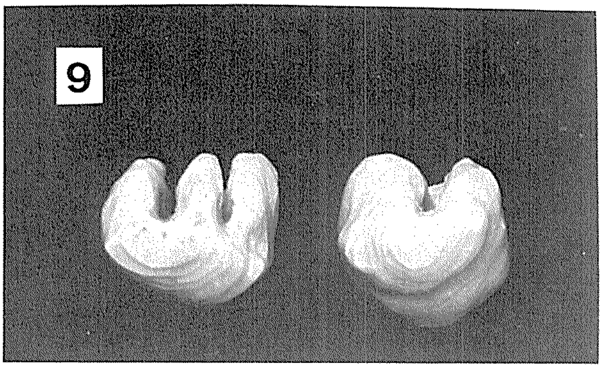


Fig. 7. Longitudinal section through the first and second molars of a 17-day mouse embryo after 7 days in a chemically defined medium *in vitro*. Note that the cusps have formed in both molars. Also there is a layer of dentine. Azan. x100.

Fig. 8. Wax reconstruction of the dental papilla of the first lower molar of a 20-day rabbit embryo cut into 2 parts. (Orig. mag. x 90).

Fig. 9. Wax reconstruction of the dental papilla of a halved molar tooth germ from a 20-day rabbit grown *in vitro* for 5 days. Each half has formed a complete set of cusps. The tooth on the left has an extra cusp. (Orig. mag. x 100).

Jaws

Segments of the upper and lower jaws of the 11-12-day-old mouse-embryo have been cultivated in fowl plasma and chick-embryo extract (Glasstone, 1967). The stage of development between litters is variable (Fig. 10). During the culture period Meckel's cartilage, bone and teeth, differentiated. In portions taken from the anterior part of the jaw a normal rodent incisor developed (Fig. 11). The labial surface of the tooth was convex, the lingual side was concave and the incisive edge was chisel-shaped. Both the first and second molars were present and their morphological differentiation was as in the normal. Furthermore there was histological differentiation of ameloblasts and odontoblasts as well as the formation of dentine. From these experiments it can be seen that the morphological field is already mapped out for the development of the individual tooth (Figs. 12. 13).

Huxley and de Beer (1934) wrote "The determination and localization of organ rudiments is revealed sooner or later by the presence of chemo-differentiated material or morphogenetic substances in certain places which may be called fields or areas of differentiation of organs." These authors based their conclusions on much experimental work with lower animals. With a view to applying this principle to the dentition as a whole, as well as to individual teeth, Butler (1939) studied the teeth of Cenozoic mammals and concluded that "... the teeth are repeated organs that occupy different positions in a continuous morphogenetic field." He thought that, as yet, there was no experimental evidence to indicate these factors involved in the determination of dental form. Neither grafting experiments nor the growth of teeth in vitro had demonstrated existing field gradients.

This may be partly true, but Glasstone has shown that, in isolated molar tooth germs cultivated in vitro, there is a morphogenetic field within the tooth itself and that a morphogenetic field potential difference of tooth development is present in the mandible as well. She also has demonstrated that, although the cusp-forming regions are morphologically determined in the tooth germ, regulative changes can take place at an early stage of development.

Differentiation of the mouse embryonic mandible and squamo-mandibular joint in organ culture

At one time it was suggested that movement in the embryo was responsible for the development of joint formation, a conclusion reached without experimental evidence.

As tissue culture is an experimental method for the study of the development of tissues and organs, Fell and Canti (1935) used this method for a detailed analysis of the developmental mechanics of the knee-joint in the embryonic chick. In their experiments, normal knee-joints differentiated in the explants but, if the explants were cultivated for a long period, there was fusion of the rudiments and the joint disappeared. They were able to show that joint formation does not depend on muscular nervous and vascular factors but on factors intrinsic in the presumptive knee-joint area. However, for the maintenance of the joint, extrinsic factors such as muscular acitivty are necessary. That muscular activity is only necessary for maintenace of the joint was also demonstrated by Chalmers (1965) who made grafts of whole joints from new-born mice to the spleen of adult mice; after a month, he also found that there was fusion of the transplanted joint.

The normal development of the mandible and squamo-mandibular joint in man, and in many other animals, has been described by many investigators but no experimental work has been done in tissue culture.

Fell and Jacobson (1941), in their analysis of the development of the chick mandible, said (p. 581) "The results have shown that the chondrogenic proliferation centre fulfils not only a histogenic but also a morphogenic function". They also said (p. 582) "It was demonstrated experimentally that elongation of the mandibular arch to form the jaw is mainly due to apical growth caused by proliferation from the paired chondrogenic centres.

10

Fig. 10.
Longitudinal section of the jaws of an 11-day mouse embryo. (H & E stain; orig. max. x 52).

11

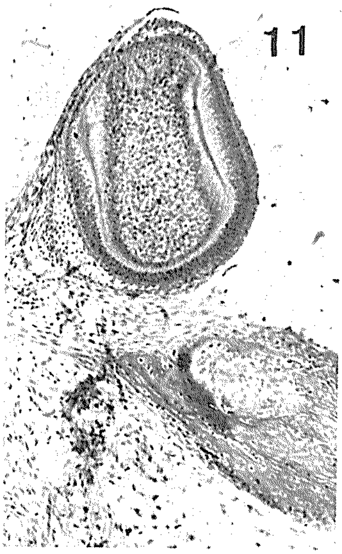


Fig. 11.
Section of an incisor formed from the anterior portion of the mandible after 12 days in vitro. Ameloblasts, odontoblasts, and dentin are present. Cartilage and bone have developed. (Azan stain; orig. mag. x 130).

12

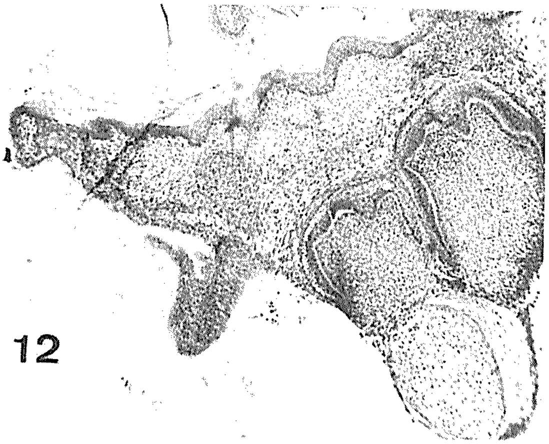


Fig. 12.
Section of the posterior part of the mandible after 12 days in vitro. First and second molars have appeared, and cusps have developed. Meckel's cartilage is present. (Azan stain; orig. mag. x 52).

Thus the mechanism of its growth produces a long rod of cartilage which stretches the branchial arch into the form of a primitive jaw and at the same time exerts a tension on the ossification centres, causing the bones to assume their characteristic, elongated shape".

It has also been shown that segments of jaws from 11-day embryonic mice continue to develop when grown in tissue culture (Glasstone, 1967). Incisors and molars of normal shape developed. Odontoblasts and ameloblasts also differentiated and both dentine and enamel were formed; there was also differentiation of bone, cartilage and salivary gland. In these experiments, a biological medium of chick embryo extract and fowl plasma was used although isolated tooth germs have been shown to survive equally well in a chemically defined medium (Glasstone, 1964). More recently Melcher and Hodges (1968), using a chemically defined medium, explanted segments of mandibles from older animals, 18-day-old mouse embryos, 7 days older than those used by Glasstone (1967). Under these conditions, the tissues survived as in the biological medium used by Glasstone (1967).

The aim of the present work was to analyse the developmental potentials in tissue culture of mouse mandibular and maxillary segments of 13-day-old embryos (Glasstone, 1971).

The maxilla and the mandible of 13-day-old mice embryos were divided through the mid-line leaving the two half jaws of the maxilla and mandible attached to each other in the region of the presumptive squamo-mandibular joint. These were cultured in a chemically defined medium for a period of up to 13 days.

At 13 days, a condensation of mesenchyme forming the pre-chondrocytes was seen in the middle of the previously undifferentiated mesenchyme of the mandibular arch (Fig. 14). It is from this centre that Meckel's cartilage differentiated and grew forward and backwards. After 2 days in culture, Meckel's cartilage had grown in a forward direction to the anterior part of the mandible to form half of the rostral process.

Meckel's cartilage had also grown in a backward direction and, at its posterior end, the anlagen of malleus and incus were present. Thus the cartilaginous skeleton of Meckel's cartilage extended from the mid-line to the distal ear region. Lateral to the area where the anlage of Meckel's cartilage first formed was an area of membranous ossification, the early stage of mandibular bone differentiation. After 3 days in culture, membranous bone of the mandibular ramus had formed with a crescentic area of condensed mesenchyme at its end; this developed laterally to Meckel's cartilage which appeared to guide its directional growth. The condensed mesenchyme is the future vertical ramus. Malleus and incus could be seen with the former joined to Meckel's cartilage (Fig. 15).

One day later, after 4 days in culture, there was an increase in the ossification of the mandible and its ramus which grew close to Meckel's cartilage. There was now a joint between malleus and incus. The squamosal bone had appeared as an area of membranous ossification in the region of the joint. The auditory capsule could be seen as well as the early ossification of the tympanic bone (Fig. 16).

After 5 days in culture, separate angular and condylar cartilages had differentiated in the mandibular ramus; each cartilage was surrounded by a thick layer of mesoderm. A day later, the cartilaginous areas were enveloped in a thin layer of membranous bone except for the tip of the condylar cartilage; these cartilages were also joined together by a thin strip of similar bone (Fig. 17). In both the angular and condylar cartilages, the zones of progressively enlarging cartilage cells developed as they do in vivo. The presence of osteoclasts indicated that remodelling of bone was in progress. The process of chondrification and ossification in vitro in the mouse has been described before by Crellin and Koch (1967), (Fig. 18).

By the seventh day in culture, there was further ossification of the squamosal bone and a slit appeared between the bones of the skull and the condylar process of the mandibular ramus (Fig. 19).

Bhaskar et al. (1953) and Bhaskar (1953), in their histological studies of the relationship of Meckel's cartilage to the developing mandible, stated that the cartilage in the rat had two functions to perform; namely that it supports and directs the growth of the mandibular process as well as controlling the development of the mandibular articular surface. Therefore, these authors, by their histological studies of the rat mandible, came to the same conclusions that Fell and Jacobson reached earlier from their in vitro experimental work on the chick mandible.

The timing of the morphological and histological differentiation approximated, in many of the cultures, very closely to the description given by Frommer (1964) but there was delayed development in some of the cultures.

Meckel's cartilage grew and differentiated as in the normal and, after 2 days in vitro, the anlagen of malleus and incus appeared; in normal development the anlagen are present in the 15-day-embryo. Malleus and incus continued to develop and a joint formed between these bones as in the timing of normal development.

In these experiments, there was no difference in the histological and morphological development of the tissues in the different media and different gas phases.

The formation of the squamo-mandibular joint in organ culture indicates that joint formation does not depend on muscular, nervous or vascular factors but that the factors promoting the joint formation in the embryonic mouse are intrinsic to a particular region of the maxillary and mandibular mesenchyme explanted in a virtually undifferentiated state from a 13-day-old embryo. This implies that determination of this zone of mesenchyme had in fact occurred prior to the 13th day; hence determination of these tissues precedes histological and morphological differentiation.

References

Bhaskar, S. N. 1953 Growth pattern of the rat mandible from 13 days insemination age to 30 days after birth. Am. J. Anat. 92: 1-54.

Bhaskar, S. N., Weinmann, J. P. and Schour 1953 Role of Meckel's cartilage in the development and growth of the rat mandible. J. dent. Res. 32: 398-410.

Biggers, J. D., Gwatkin, R. B. L. and Heyner, S. 1961 Growth of embryonic avian and mammalian tibiae on a relatively simple chemically defined medium. Exp. cell Res. 41: 58.

Butler, P. M. 1939 Studies of the mammalian dentition - Differentiation of the post-canine dentition. Proc. Zoo. Soc. Lond., B, 109: 1-36.

Chalmers, J. 1965 A study of some of the factors controlling growth of transplanted skeletal tissue. Calcif. Tiss. 31: 177-184.

Crelin, E. S. and Koch, W. E. 1967 An autoradiographic study of chondrocyte transformation into chondroclasts and osteocytes during bone formation in vitro. Anat. Rec. 158: 473-484.

Fell, H. B. and Canti, R. G. 1935 Experiments on the development in vitro of the avian knee joint. Proc. R. Soc. B. 116: 316-351.

Frommer, J. 1964 Prenatal development of the mandibular joint in mice. Anat. Rec. 150: 449-461.

Glasstone, S. 1936 The development of tooth germs in vitro. J. Anat. Lond. 70: 260-266.

______ 1938 A comparative study of the development in vivo and in vitro of rat and rabbit molars. Proc. Roy. Soc. B. 126: 315-330.

______ 1952 The development of halved tooth germs in tissue culture. J. Anat. Lond. 86: 12-15.

______ 1964 Cultivation of mouse tooth germs in a chemically defined protein-free medium. Archs oral Biol. 9: 27-30.

______ 1967 Morphodifferentiation of teeth in embryonic mandicular segments in tissue culture. J. dent. Res. 46: 611-614.

______ 1968 Tissue culture of the mandible and mandibular joint of mouse embryos. Nature, Lond. 220: 705-706.

——— 1971 Differentiation of the mouse embryonic mandible and squamo-mandibular joint in organ culture. Archs and Biol. 16: 723-729.

Hertwig, O. 1874 Ueber das Zahnsystem der Amphibien und seine Bedeutung für die Genesse des Skelets der Mundhöhle. Arch. mikr. Anat. 11: Supplement 77.

Huggins, C.B., McCarroll, H.R. and Dahlberg, A.A. 1934 The transplantation of tooth germ elements and the experimental heterotopic formation of dentine and enamel. J. exp. Med. 60: 199-210.

Huxley, J.S. and DeBeer, G.R. 1934 *The Elements of Experimental Embryology*, pp. 221, 352. Cambridge: Cambridge University Press.

Jacobson, W. and Fell, H.B. 1941 The developmental mechanics and potencies of the undifferentiated mesenchyme of the mandible. Quart. J. microscl. Sci. 82: 563-586.

Legros, C. and Magitot, E. 1874 Greffes de follicules dentaires et de leur organes constitutif isolement. C.R. Acad. Sci., Paris 78: 357.

Melcher, A.H. and Hodges, G.M. 1968 *In vitro* culture of an organ containing mixed epithelial and connective tissues on a chemically defined medium. Nature, Lond. 219: 301-302.

Stesichorus 6 B.C. Europa.

Tomes, C. 1874 On the existence of an enamel organ in an armadillo. Quart. J. micr. Sci. 114: 44.

Turner, W. 1872 Some observations on the dentition of the narwhal. J. Anat. Phys. 7: 75.

Von Brunn, A. 1887 Ueber die Ausdehnung des Schmelzorganes und seine Bedeutung für die Zahnbildung. Arch. mikr. Anat. 29: 367.

——— 1891 Beitrage zur Kenntniss der Zahnenentwicklung. Arch. mikr. Anat. 38: 142.

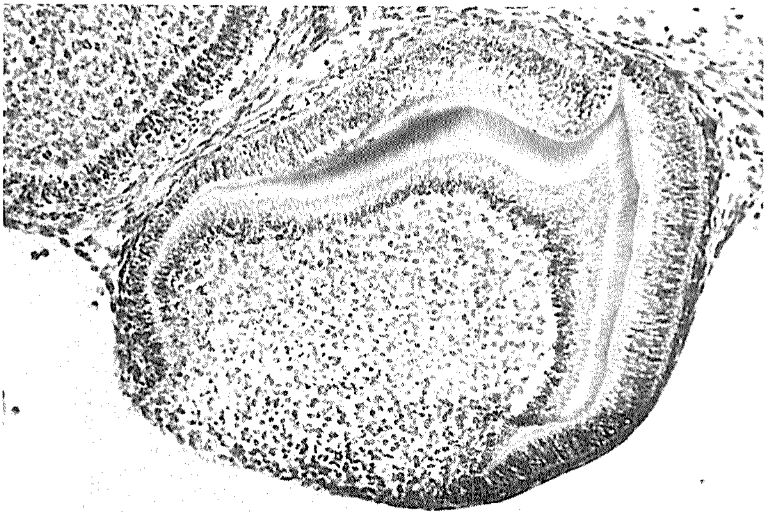


Fig. 13. Section through another region of first molar shown in Fig. 12, both dentin and enamel matrix are present. (Azan stain; orig. mag. x 160).

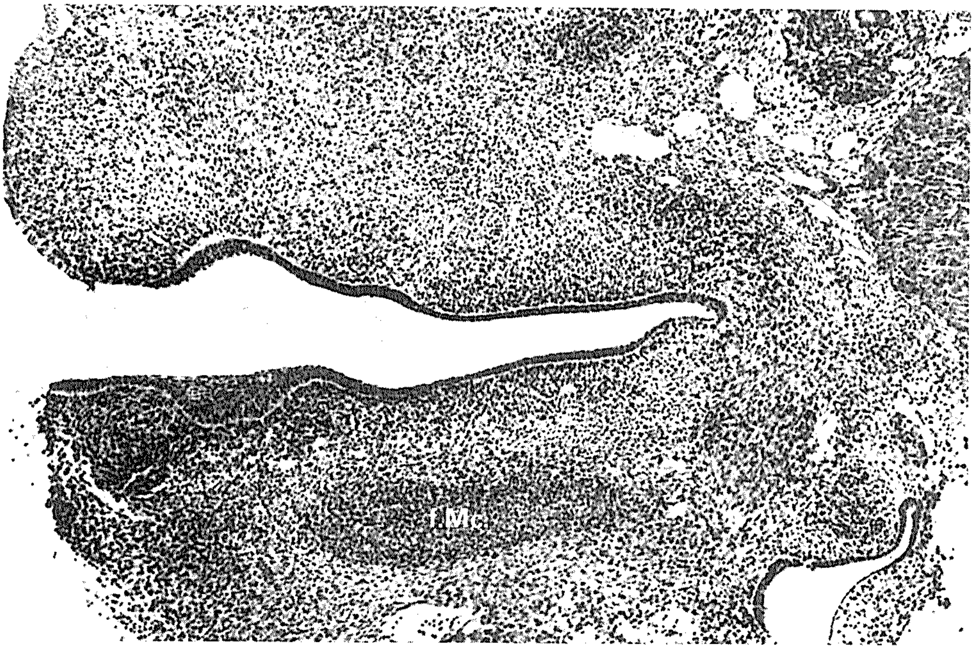


Fig. 14. The upper and lower jaws of a 13-day-old mouse embryo. The anlage of the incisor tooth can be seen and the mesenchymal condensation of the future Meckel's cartilage. (fM.c.). Haematoxylin and eosin. x 92.

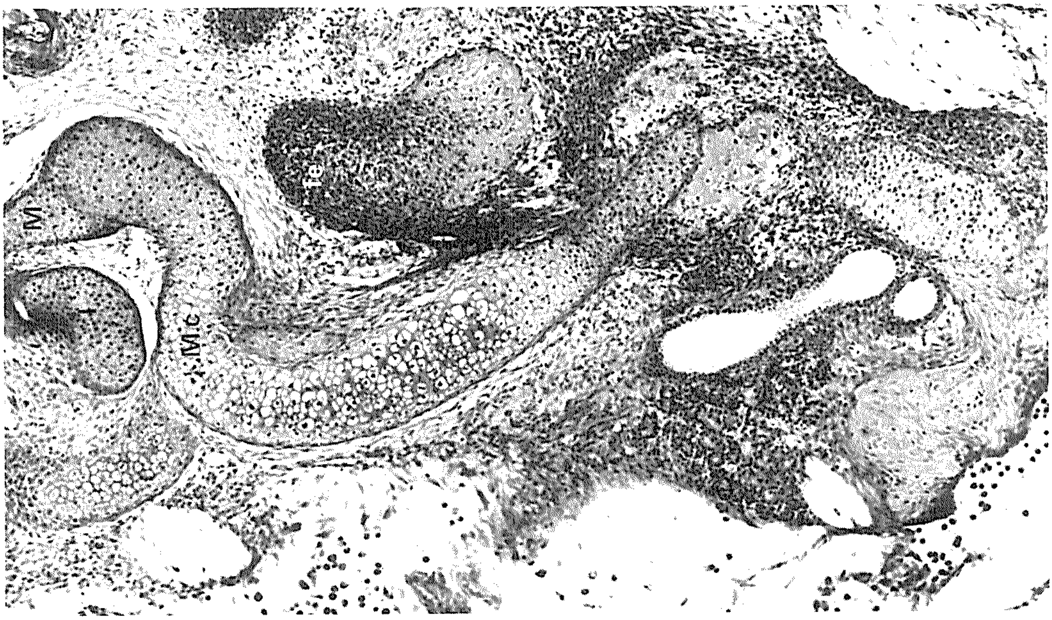


Fig. 15. Explant of 3 days showing Meckel's cartilage (M.c.), malleus (M) and incus (I) and the mesenchymal condensation of the future condyle (f.c.). Haematoxylin and eosin. x 94.

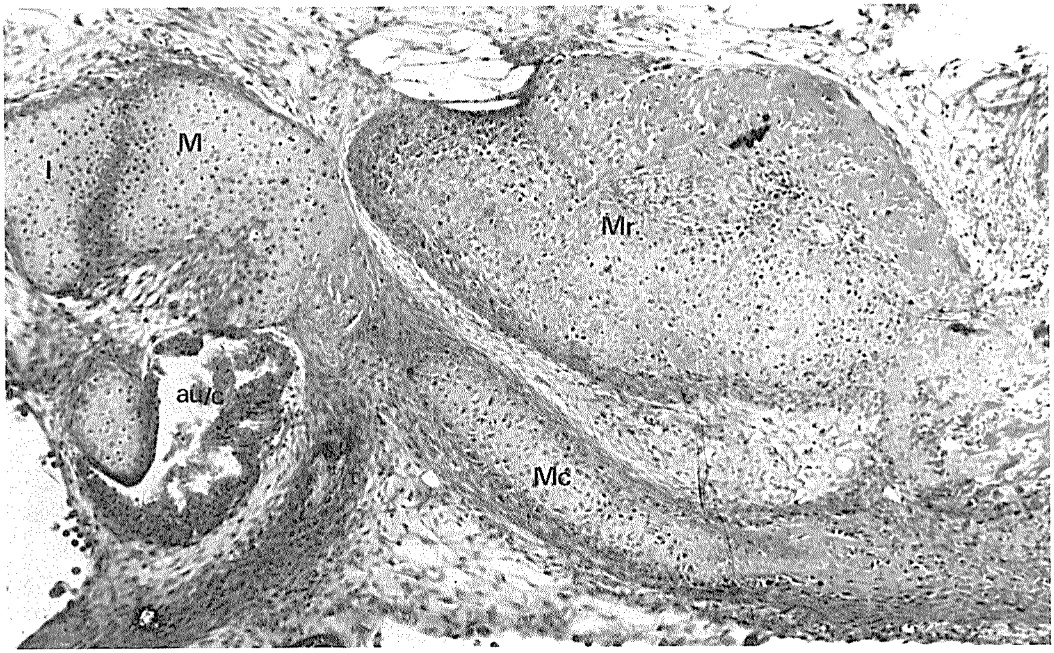


Fig. 16. Explant of 4 days showing further development of the mandible and the mandibular ramus (M.r) where perichondral ossification is progressing. Meckel's cartilage (M.c), malleus (M) and incus (I) are present. The auditory capsule (aud.c) and the tympanic bone (t) can be seen. Haematoxylin and eosin. x 104.

Fig. 17. Explant of 5 days showing the ramus with the angular (A. c) and condylar cartilages (C. c) and the body of the mandible (Ma). The submaxillary gland is present. There is ossification in the squamosal bones (S). Meckel's cartilage (M. c) and malleus (M) and incus (I) are present. Haematoxylin and eosin. x 97.

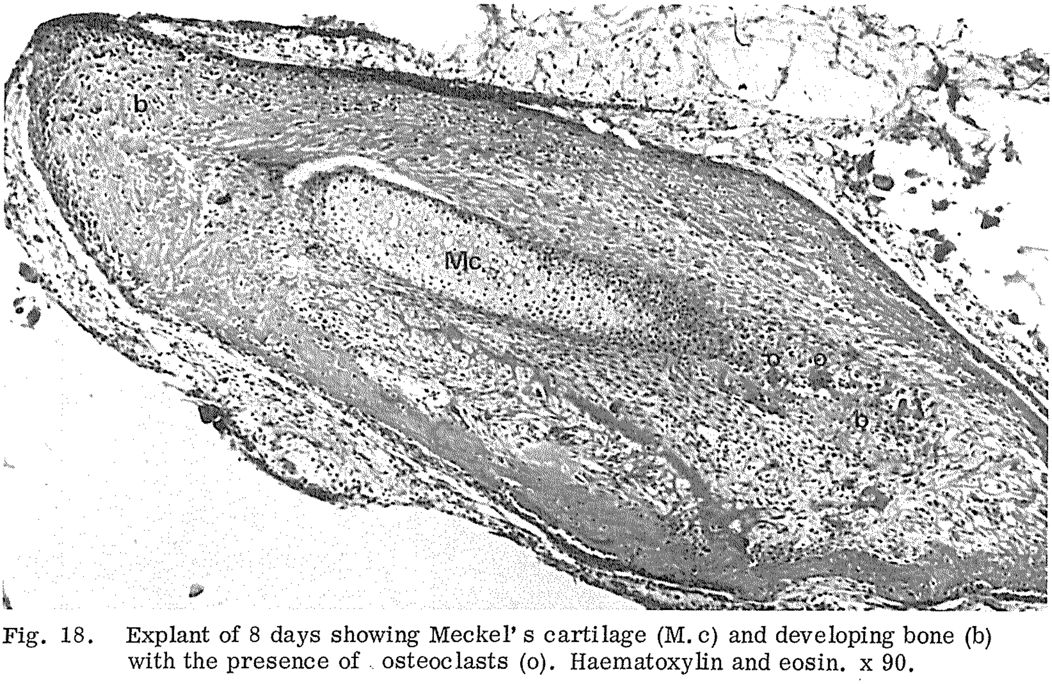


Fig. 18. Explant of 8 days showing Meckel's cartilage (M. c) and developing bone (b) with the presence of osteoclasts (o). Haematoxylin and eosin. x 90.

Fig. 19. Explant of 13 days showing ossification of the squamosal bone (S) the mandibular condylar process (C) and the squamo-mandibular joint (arrow) can be seen. Malleus (M) and incus (I) are present but Meckel' s cartilage is not shown in this section. Haematoxylin and eosin. x 131.

Crown diameters in Japanese – American F_1 hybrids

KAZURO HANIHARA AND HIROSHI UEDA

OSSA

The dentitions of 170 Japanese-American hybrid children are examined in an attempt to assess the degree of similarity in mesiodistal permanent tooth crown diameters to the parental populations. Several methods of analysis demonstrate that crown size in hybrid populations are equally affected by both parental populations in size and shape factors. These results support the hypothesis of non-linked polygenic inheritance of tooth crown diameters.

Были изучены зубы 170 японо-американских детей-метисов в попытке установить степень сходства диаметров коронок мезодистальных постоянных зубов с теми же характеристиками у популяций родителей. Различные методы анализа показали, что размер и форма коронки в гибридных популяциях одинаково подвергаются влиянию популяций обоих родителей. Эти результаты поддерживают гипотезу о несвязанном полигенном наследовании диаметров зубной коронки.

Ключевые слова: японо-американские F_1 гибриды, зубы, диаметр коронки.

Kazuro Hanihara, Hiroshi Ueda, The University of Tokyo, Department of Anthropology, Faculty of Science, Hongo, Bunkyo-ku, Tokyo 113, Japan.

Vol. 6, pp. 105-114, Lund. ISSN 0345-8865.

Introduction

A fairly large number of children were born of mixed parentage between Japanese women and American servicemen immediately after the World War II. Part of the children were accommodated in Elizabeth Sanders Home at Oiso, Kanagawa Prefecture, which was established by Mrs. Mika Sawada for the welfare of these children whose mothers were unable to bring them up for some reasons.

Members of Department of Anthropology, the University of Tokyo, started anthropological studies of these children in 1951, under the direction of Professor Akiyoshi Suda who retired from the University of Tokyo in 1961, and the studies were continued for nearly twenty years.

In this research project, Hanihara, one of the present authors, was concerned with investigation of dental characteristics, and made plaster casts of both deciduous and permanent dentitions. Since all the children were F_1 hybrids between Japanese and Americans, both Caucasians and American Negroes, this set of dental casts is a unique collection to analyse the dental characteristics in hybrid populations.

As regards the dentition of hybrid populations, Abel (1933) reported dental characteristics in Bushmen, Hottentots, Negroes and their hybrids. In this case, however, the magnitude of hybridization was unknown. In this respect, the F_1 hybrids presented here may provide some important findings which have so far been not necessarily evident in the field of dental anthropology.

Since 1954, Hanihara has reported morphology of their deciduous dentition, but detailed studies of the permanent dentition still remained unpublished. The present report is concerned with comparative studies on crown diameters of the permanent dentition, and the hybrid populations are compared with their parental populations.

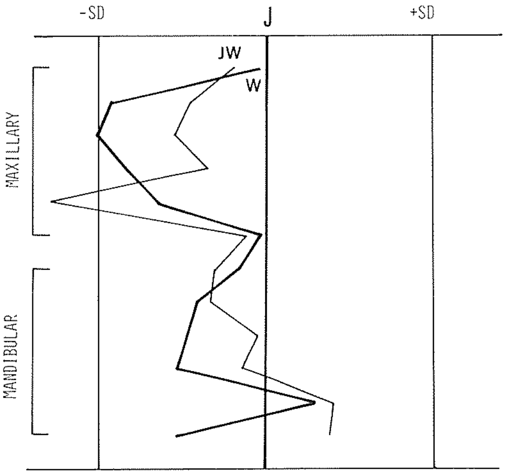


Fig. 1. Deviation Diagram for JW and W.

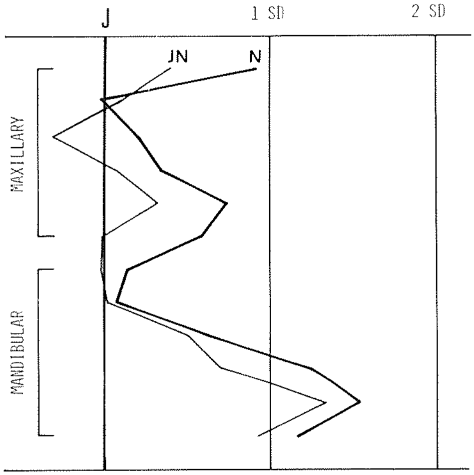


Fig. 2. Deviation Diagram for JN and N.

Materials and Methods

The materials used in this study were plaster casts from male Japanese (J), American Caucasians (W), American Negroes (N), Japanese-Caucasian hybrids (JW) and Japanese-Negro hybrids (JN), among whom the hybrid children were in their early teens.

Plaster casts of Japanese were from boys living in the Tokyo metropolitan area; those of Caucasians were selected from a collection of the Department of Anthropology, the University of Chicago; and those of American Negroes were from a collection of the Department of Orthodontics, Howard University.

The raw data consisted of mesiodistal crown diameters in the permanent teeth from which the second and third molars were excluded, since most of the materials were from young individuals. All the measurements were made by the present authors. The analyses were performed on the basis of descriptive as well as multivariate statistical methods, for which the computation was processed by HITAC OS-7 system of the University of Tokyo Computer Centre.

Comparison of the Crown Diameters in Individual Teeth

Table 1 shows numbers of samples, means and standard deviations of the mesiodistal crown diameters in each population. Among the parental populations, W represents, in general, the smallest teeth and N the largest, J being in between. The hybrid populations tend to fall between the parental populations in most of the teeth measured.

Such a finding may be more evidently observed on the deviation diagrams in which the thick perpendicular line represents the mean values in Japanese, and the thin perpendicular lines represent a standard deviation (figures 1 and 2). In both cases of JW and JN, the pattern of deviation from Japanese is quite similar to the paternal populations. This shows probably that the tooth diameters of the hybrid populations are strongly affected by that of the parental populations. At the same time, the majority of the teeth in hybrid populations show intermediate crown diameters between the parental populations.

To measure the variability of the mesiodistal crown diameters, coefficients of variation were calculated (table 2). If the parental populations are largely different from each other in tooth crown diameters, the variabilities of this trait may be expected to be greater in the hybrid populations than in the parental populations. However, as shown by table 2, this is not the case. When the variabilities are examined in each tooth, the largest variabilities among the five populations are recognized in only a few cases of the hybrids. In fact, most of the coefficients of variation in JW and JN are exceeded by those of Tristanites (Thomsen, 1955) who are hybrids between Europeans and Colored races. This fact may be due to the relatively small differences in the crown diameters between the parental populations.

The maxillary lateral incisors show the largest variabilities in most of the populations. The same trend can be observed in several other populations so far reported. Among the five populations under consideration, only JN presents a relatively small variation for this tooth. This possibly results from the small number of samples, because the reduced type of incisors is also found in N.

Distance Analysis

In order to analyse the overall differences in the tooth crown diameters, Mahalanobis' and Penrose's distance coefficients were computed. Figure 3 was drawn on the basis of canonical variates of Mahalanobis' generalized distances. The three parental populations, J, W and N, are well separated from each other and the hybrid populations are located intermediate between respective parental populations. In particular, JW occupies the point which is almost the same distance from J and W, while JN is closer to N than to J.

Almost the same pattern is recognized in figure 4, which was drawn on the basis of Penrose's shape distances using the technique of Hayashi's quantification theory model IV (Hayashi, 1952, 54). Here again JW is located almost in the midst between J and JW, but JN is very close to N.

Principal Component Analysis

For the purpose of summarizing the mesiodistal crown diameters in the twelve teeth under consideration, the principal component analysis was employed. The computation was based on the correlation matrix obtained from all the individuals (170 individuals) used in this study.

As shown in table 3, the first two eigenvalues are greater than 1.0, but their cumulative proportion is only about 67% of total variance. If the first three eigenvalues are taken into account, about 74% of total variance can be explained.

The factor loadings for the first component show all positive and relatively large values (table 4). This fact shows that the first component is possibly interpreted as the size factor as can be seen from most of the cases in morphological analyses.

The factor loadings for the second component represent positive values for the front teeth (incisors and canines), negative values for the back teeth (premolars and molars), and the absolute values are all alike. This means probably that this component contrasts the size of the front and the back teeth. Therefore, those individuals who carry larger front teeth and smaller back teeth may represent larger principal component scores, and vice versa.

The third factor loadings show either positive or negative values, and their absolute values are not so large, excluding the maxillary lateral incisor. The value for the latter tooth is 0.5136, but those for the remaining teeth range from 0.3837 to -0.3148. The third component, therefore, may be interpreted as having a close correlation with the size of the maxillary lateral incisor.

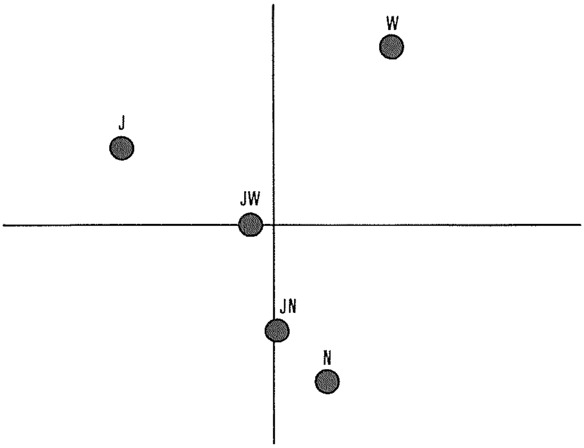


Fig. 3. Two-Dimensional Expression Based on Mahalanobis' Generalized Distances.

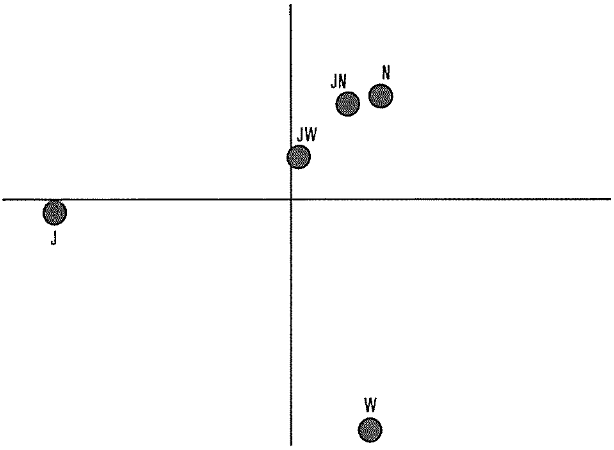


Fig. 4. Two-Dimensional Expression Based on Penrose's Shape Distances.

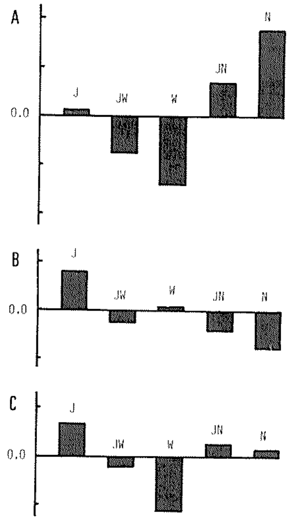


Fig. 5.
Mean PC Scores: A - PC1
B - PC2
C - PC3

In the next step of the analysis, principal component score (PC scores) were computed individually, and their means for each population were compared (table 5).

Figure 5A compares mean values for the first PC scores which represent the overall size of the tooth crowns. As already pointed out, the overall crown size is largest in N, smallest in W, and J in between. The mean PC scores in the hybrid populations, both JW and JN, are almost in between those of the parental populations. As far as judged from the PC scores, therefore, no particular affinity of the hybrid populations to one of the parental populations is observed, but affinities of the hybrid populations are almost equal to both parental populations.

In regard to the second component, J represents a positive and fairly large mean score. This means that, in this population, the front teeth are relatively large in comparison with the back teeth. On the other hand, the mean score for N is negative and the absolute value is relatively large. This is the reverse of the condition in J, and is interpreted as N having relatively small front teeth and large back teeth (figure 5B).

Although the mean scores for the hybrid populations are not necessarily intermediate between those of the parental populations, they are close to W and N, respectively. This fact apparently shows that the proportion of the front and back teeth are genetically affected by the parental populations.

The third component largely concerns the size of the maxillary lateral incisor which shows a unique behavior among the permanent dentition. Among the parental populations, J represents the largest score, W the smallest, and N in between. In this case, mean scores for the hybrid populations are again intermediate between the respective parental populations (figure 5C).

As regards the three principal components presented here, the first apparently concerns the size factor, and the second and the third the shape factors. It may be of importance that the hybrid populations represent intermediate mean PC scores between those of the parental populations with a minor exception, and, in general, the former are almost in the midst of the latter in PC scores. This fact shows that the crown size of the hybrid populations is almost equally affected by the parental populations in both the size and shape factors.

Discussion

Perhaps the most important finding in the present study may be the fact that the crown diameters in the hybrid populations are, as already mentioned, almost equally affected by those of the parental populations. In other words, at least as far as the present materials are concerned, the hybrid populations do not show any particular affinity to anyone of the parental populations in particular, but show almost the same degree of affinity to each.

Garn, Lewis and Kerewsky (1963, '64) suggested an X-linked inheritance of tooth crown size. In contrast to this view, Townsend (1976) analysed family data from Australian Aborigines and came to a conclusion that the crown diameters involved a polygenic mechanism, and "neither the X nor Y chromosomes appeared to be directly implicated in the determination of tooth size" (p. 200).

Since, the present study, Japanese correspond to the maternal population and Caucasians and American Negroes to the paternal populations, in the view of Garn et al. is correct, the crown diameters of the hybrid populations may be expected to show a closer affinity to that of Japanese. As shown above, however, the results do not agree with this expectation, but rather with the hypothesis of polygenic inheritance without implication of the sex chromosomes.

In the shape factors of the crown diameters, the hybrids occasionally represent a closer affinity in the PC scores to the paternal populations than to the maternal population. This fact also opposes the view of an X-linked inheritance of the tooth crown diameters.

Acknowledgements

We are deeply indebted to Mrs. Miki Sawada, Head of Elizabeth Sanders Home, who kindly allowed us to investigate the hybrid children, and to Professor A. Suda who warmly encouraged us to continue this investigation. Thanks are due to Dr. S. Shimizu, Dr. T. Minamidate, Dr. T. Masuda and Dr. T. Tanaka for their generous cooperation in making plaster casts. Also we are deeply grateful to Dr. A. A. Dahlberg and Dr. L. A. Altemus for permission to study valuable dental casts from Caucasians and American Negroes.

Literature cited

Abel, W. 1933 Zähne und Kiefer in ihren Wechselbeziehungen bei Buschmännern, Hottentotten, Negern und deren Bastarden. Z. Morph. Anthrop., 31: 314-361.

Garn, S. M., A. B. Lewis and R. S. Kerewsky, 1963 Sex differences in tooth size. J. Dent. Res., 43: 306.

______ 1964 X-linked inheritance of tooth size. J. Dent. Res., 44: 439-441.

Hanihara, K. 1954-57 Studies on the deciduous dentition of the Japanese and the the Japanese-American hybrids.
I. Deciduous inciors,
II. Deciduous canines,
III. Deciduous lower molars,
IV. Deciduous upper molars,
V. General conclusion.
J. Anthrop. Soc. Nippon, 63: 168-185; 64: 63-82, 95-116; 65: 67-87, 151-164. (In Japanese with English summary.)

______ 1963 Crown characters of the deciduous dentition of the Japanese-American hybrids. In Brothwell (ed.): Dental Anthropology, pp. 105-124, Pergamon Press.

______ 1968 Morphological pattern of the deciduous dentition in the Japanese-American hybrids. J. Anthrop. Soc. Nippon, 76: 114-121.

Hayashi, C. 1952 On the prediction of phenomena from qualitative data and the quantification of qualitative data from the mathematico-statistical point of view. Ann. Inst. Mathem. Statis., 3: 69-98.

______ 1954 Multidimensional quantification with applications to analysis of social phenomena. Ann. Inst. Mathem. Statis., 5: 121-143.

Thomsen, S. 1955 Dental morphology and occlusion in the people of Tristan da Cunha: Results of the Norwegian Scientific Expedition to Tristan da Cunha, 1937-1938, No. 25. Det Norske Videnskaps-Akademi. (Cited by Barrett et al. appeared in Aust. Dent. J., Vol. 8, 1963.)

Townsend, G. C. 1976 Tooth size variability in Australian Aboriginals. Doctoral Dissertation, the University of Adelaide.

Table 1. Mesiodistal Crown Diameters in the Permanent Dentition (in mm.)

	J			JW			W			JN			N		
	N	M	SD	N	M	SD	N	M	SD	N	M	SD	N	M	SD
I^1	48	8.64	.4627	36	8.51	.4797	38	8.64	.6118	13	8.75	.4371	37	9.07	.5564
I^2	48	7.12	.5314	36	6.88	.5533	38	6.56	.5698	13	7.06	.4234	37	7.13	.6689
C	48	8.18	.3688	36	7.97	.4467	37	7.81	.4563	13	8.08	.4357	37	8.25	.4416
P^1	48	7.46	.4325	36	7.31	.4573	38	7.09	.3979	13	7.46	.4331	37	7.63	.4614
P^2	48	6.95	.3457	36	6.89	.3322	38	6.78	.5060	13	7.08	.3395	37	7.21	.5371
M^1	48	10.70	.5058	36	10.62	.4356	38	10.72	.6356	13	10.70	.5051	37	11.03	.6224
I_1	48	5.54	.3305	36	5.41	.2892	38	5.46	.4189	13	5.52	.2620	37	5.59	.3332
I_2	48	6.16	.3488	36	6.03	.4266	38	5.97	.4473	13	6.14	.2931	37	6.20	.4011
C	48	7.09	.3816	36	7.02	.4614	38	6.85	.4210	13	7.25	.4196	37	7.31	.5286
P_1	48	7.30	.3815	36	7.24	.3247	38	7.09	.4076	13	7.49	.5008	37	7.78	.4896
P_2	48	7.19	.3707	36	7.40	.3799	38	7.30	.4947	13	7.66	.5576	37	7.77	.6037
M_1	48	11.50	.4602	35	11.64	.5209	38	11.22	.6834	13	11.87	.5423	37	12.00	.6592

Table 2. Coefficients of Variation

Tooth	J	JW	W	JN	N	Tristanite*
I^1	5.36	5.64	7.08	5.00	6.13	6.9
I^2	7.46	8.04	8.69	6.00	9.38	9.5
C	4.51	5.60	5.84	5.39	5.35	6.2
P^1	5.80	6.26	5.61	5.81	6.05	6.5
P^2	4.97	4.02	7.46	4.80	7.45	6.9
M^1	4.73	4.10	5.93	4.72	5.64	5.4
I_1	5.97	5.35	7.67	4.75	5.96	9.7
I_2	5.66	7.07	7.41	4.77	6.47	9.4
C	5.38	6.57	6.15	5.79	7.23	6.9
P_1	5.23	4.48	5.75	6.69	6.29	9.9
P_2	5.16	5.13	6.78	7.28	7.77	7.4
M_1	4.00	4.48	6.09	4.57	5.49	5.3

Underlined shows the largest C.V. in each tooth.

*Thomsen, 1955.

TABLE 3.

First three eigenvalues and cumulative proportions in total variance.

No.	Eigenvalue	Cumulative proportion
1	6.7720	0.5643
2	1.2513	0.6686
3	0.8478	0.7393

TABLE 4.

Factor loadings for the first three components (without rotation)

Tooth \ Component	1	2	3
I^1	0.7626	0.3068	-0.1553
I^2	0.5592	0.4401	0.5136
C	0.7642	0.2750	0.2179
P^1	0.7671	-0.2766	0.3837
P^2	0.7778	-0.3908	0.1323
M^1	0.7116	-0.2219	-0.3148
I_1	0.7469	0.3680	-0.3110
I_2	0.7777	0.3577	-0.2279
C	0.8101	0.1905	0.0445
P_1	0.7929	-0.3433	0.1656
P_2	0.7749	-0.3870	-0.1166
M_1	0.7386	-0.2052	-0.2384

TABLE 5.

Mean PC scores in each population

Population	PC1	PC2	PC3
J	0.0262	0.4227	0.3431
JW	-0.7426	-0.1106	-0.0063
W	-1.4178	0.0203	-0.5616
JN	0.6846	-0.2069	0.1100
N	1.7732	-0.3735	0.0846

Morphology of the Wainwright Eskimo dentition: Carabelli's structures

STEPHEN E. HERSHEY

OSSA

Carabelli's structures were examined and classified using the system developed by A. A. Dahlberg. The Zoller Dental Laboratory plaques were used for reference. The presence of an actual cusp was very rare, however, the total absence of Carabelli's structures was equally rare. Most frequently observed were the negative structures (furrows, pits, and grooves). The population was found to exhibit a high frequency of bilateral asymmetry in the occurence of these features and there was no evidence of sexual dimorphism.

Keywords: Dentition - Eskimos - Carabelli's Structures.

Структуры Карабелли были изучены и классифицированы на основании системы, разработанной А.А. Дальбергом. В качестве стандартов применяли бляшки Зубной лаборатории Цоллер. Наличие подлинного выступа, как и полное отсутствие структур Карабелли, оказались одинаково крайне редкими. Наиболее часто наблюдались негативные структуры /борозды, ямки и углубления/. У населения была обнаружена высокая частота билатеральной асимметрии в распространении этих черт. Данных, свидетельствующих о половом диморфизме, не получено.

Ключевые слова: зубы, эскимос, структуры Карабелли.

Stephen E. Hershey, Department of Orthodontics, The University of Michigan, Ann Arbor, Michigan, 48109 U.S.A.

Vol. 6, pp. 115-124, Lund. ISSN 0345-8865.

Dental structures play an important role in evolutionary studies. The preservation of teeth in the fossil record in disproportion to their skeletal tissues requires that their form and function be intensely investigated. The use of dental morphology as an aid in the interpretation of hominoid phylogentic relationships must be based on a thorough understanding of the ranges of variation in modern, as well as early hominoid dentitions.

The excessive number of diagnoses of fossil species and genera that rely solely or substantially on dental evidence demonstrates a lack of such understanding and supports the observation that paleontologists have tended to underestimate the variability of fossil species (Butler, '63). Just criticism has also been made of the use of dental structures to distinguish modern populations and determine interindividual distances by single comparisons (Le Gros Clark, '50; Goose, '63).

When commencing a comparative dental study it is well to proceed cautiously remembering that, "Just as resemblances do not necessarily prove relationship. so differences do not prove the lack of relationship" (Butler, '63). The dentition then must be used only as supportive evidence when the entire biological structure and activity of the species has been considered in determining an individual's and/or population's affinities to other individuals or groups.

A number of other problems, particularly the lag in genetic explanation of dental variation behind the collection of data, are associated with any study of dental variation (Brothwell, '67; Osborne, '67). However recent admixture among formerly isolated populations has resulted in an urgency to continue such work and to present such odontological information in easily comparable form. To wait for a more complete understanding of the mode of inheritance of dental characteristics would be to lose the opportunity to gain information about human variation from the remaining and rapidly disappearing number of local and isolated groups.

It is the purpose of this paper to describe the variation of a number of dental traits among one such group. the Wainwright Eskimos of Alaska, and to show how this information may be analyzed and presented in a standardized method resulting in easily comparable data.

Materials and General Methodological Aspects

The village of Wainwright is located on latitude 70°38' N and longitude 160°01' W on the northwestern coast of Alaska between Point Hope and Barrow. In 1969 the Eskimo population of Wainwright was estimated at 285 individuals. The historical background of this population has been presented elsewhere (Cederquist, '76).

The materials used in this study were collected as a part of the International Biological Programs' investigation of Eskimo populations. The dental casts are housed in the Department of Anthropology at the University of Chicago.

Under the direction of Dr. Albert A. Dahlberg of the University of Chicago, dental studies of the Wainwright Eskimos were conducted for five consecutive years beginning in 1968. The data collected included dental casts, lateral roentgenographic cephalograms, posterior periapical radiographs, saliva samples, and clinical records.

This information revealed a large number of decayed, missing or filled posterior teeth, particularly in the mandible. These results and the availability of comparative data were used to select the morphological traits which would be examined for the present study.

All measurements and morphological observations were made on the casts under laboratory conditions. Dr. A. A. Dahlberg instructed the author in techniques of measurement, proper use of the Zoller dental plaques, and made a substantial number of random duplicate measurements and morphological classifications as a check for accuracy. During the classification work, the casts were identified only by number; neither sex nor the geneology of the individual was known to the author.

The dimensional accuracy of the alginate impression technique and of dental stone casts have been shown to be satisfactory for odontometric and morphological studies (Lundström, '54; Hunter and Priest, '60; Richardson, et al., '63).

Classification of morphological traits requires careful examination from various angles, with and without magnification. Two sources of light, direct and indirect, were used to create shadows, making the traits easier to observe.

Although the classification of dental traits is more or less subjective, the development of the Zoller laboratory plaques by A. A. Dahlberg has helped to standardize what was a very arbitrary process. These three-dimensional models were used throughout the study.

Carabelli's Structures

Various terms have been used to describe the structures that may occur on the mesiolingual surface of the protocone of maxillary molars. The often used "Carabelli's cusp" or "trait" does not indicate the range of features which may be expressed, and "Carabelli's anomaly" (preferred by Kraus, '50) has been objected to on the grounds that structures which occur so frequently cannot be considered an abnormality (Kotzchke, '53). Descriptions such as Carabelli's structures or Carabelli's polymorphism seem to be the most adequate, for they may include all positive (protuberances and cusps) or negative (pits, grooves, and furrows) structures. It has been suggested that Carabelli's cusp be restricted to those instances where a protuberance or cusp is actually present (Korenhof, '60).

The occurrence of Carabelli's structures is not restricted to man, but may appear in other Hominoidea (Korenhof, '60), some prosimians (Remane, '60), and has been described rarely in Dryopithecus and Gigantopithecus (Korenhof, '60), and more frequently in Australopithecus (Robinson, '56) and Neanderthal (Korenhof, '60).

The frequency of Carabelli's traits in modern populations of man are summarized in Table 4.

The cingular origin of the structures has been generally accepted (Osborn, '88; Cope, '89; Adolff, '08; Schwalbe, '16; Gregory, '22; Hrdlicka, '24; Dahlberg, '49; Keller, '54; Vallois, '55; Robinson, '56; Dietrich, '58; Korenhof, '60).

The phylogenetic significance of Carabelli's structures is unclear. Early studies found the occurrence of these traits to be rare in fossil hominoids with a tendency to increase in frequency and size in recent man (Sprawson, '22; Gregory, '22; Weidenreich, '37). Based on this trend, these structures were thought by many to be of a recent evolutionary origin (Weidenreich, '37; Dahlberg, '49; von Koenigswald, '57).

It may be argued, however, that there are too few teeth representing most fossil hominoids to draw these conclusions, and that in some prehistoric populations such as Krapina, Carabelli's structures appear at a frequency well within the range of variation in recent man (Korenhof, '60). One feature, the pit, appears to be a structure that is common to the evolutionary development of all primates, including the anthropoids (Weidenreich, '37)

A multifactorial mode of inheritance of Carabelli's structures is the most widely accepted hypothesis (Dietz, '44; Oschinsky and Smithurst, '60; Goodman, '65; Garn et al., '66 a,b; Dahlberg, '71; Goose and Lee, '71). The association between these and other hereditary traits can be found in a previous report by Kirveskari ('74).

A negative association exists between Carabelli's structures and a reduction in molar size and congenital absence of third molars in a study of white American military inductees (Keene, '65, '68). This evidence rejects the theory of De Terra's that Carabelli's cusps is a functional adaptation to increase the occlusal surface in a buccal-lingual direction while the molar series is reduced in mesial-distal width, thus maintaining approximately the same masticatory area (De Terra, '05). In modern populations, only the Melanesians have a high incidence of large, Carabelli's cusps which actually function during mastication (Dahlberg, '76).

Methods

Classification of Carabelli's structures was done according to the eight categories developed by Dahlberg ('63). This system offers the most thorough and complete analysis of the structures and is useful for comparative purposes. The data can be easily grouped into three larger categories: (1) smooth, (2) pitted or grooved, and (3) presence of a protuberance or cusp, which allows further comparison with studies using different classifications.

The Zoller Laboratory plaques (12A and B) were used as references in determining the classification of the Carabelli's structures. Each cast was examined in natural and artificial light, with and without magnification. As a test for consistency, many of the casts were examined by two workers, and the classifications assigned were found to be in nearly 100 per cent agreement. Care was taken to exclude the protoconule groove originating from the occlusal surface and thought to be associated with the mesial and not the protoconule cingulum (Korenhof, '60).

Results

The generally low manifestation of Carabelli's structures in the Wainwright population is presented in Table 3. For comparative purposes the data from other studies was recalculated and grouped according to the three categories previously mentioned and listed in Table 4.

The presence of an actual cusp was very rare in the Wainwright Eskimos, occurring on only 6 per cent of the first molars, and was completely absent on the second molars. The greatest size was in the form of a "small cusp" with no instances of moderate or large cusps. The total absence of Carabelli's structures was equally rare on the first molars, occurring in 8 per cent of the cases, but increased significantly in the second molars with the smooth condition being present on 56 per cent of these teeth.

More frequently observed were the negative structures (furrows, pits, and grooves) which occurred on 66 per cent of the first molars and on 40 per cent of the second molars.

Discussion

It is clear, therefore, that the high frequency of intermediate expressions of Carabelli's structures, rather than their absence (Pedersen, '49), should be considered characteristic of mongoloids (Kraus, '59; Hanihara, '68; Kirveskari, '74). The reverse condition is found among caucasoids, who frequently demonstrate a smooth surface or cusp, and rarely the intermediate structures (Table 4). Considering the amount of racial admixture which is thought to have taken place among the Wainwright Eskimos with the influx of Europeans, Chinese, and other groups of whalers and hunters, the frequency of Carabelli's cusp was unexpectedly low (Dahlberg, '76).

Occurrence of the pit was exceedingly rare. This low frequency (less than 1 per cent) is a common finding in other populations such as the Apaches (Kraus, '59) and the Skolt Lapps (Kirveskari, '74), and raises questions concerning the significance of the pit and its relation to the other expressions (Kirveskari, '74).

The frequency of bilateral symmetry of Carabelli's structures in Wainwright Eskimos is recorded in Table 1.

TABLE 1

Frequency of bilateral symmetry in the expression of Carabelli's structures

	First Molar		Second Molar	
	Symmetrical %	Asymmetrical %	Symmetrical %	Asymmetrical %
Male	62	38	54	46
Female	58	42	64	36
Total	60	40	59	41

The degree of bilateral symmetry is known to vary between populations but has generally been thought to be high (Dietz, '44). The frequency of assymetrical expression of the structure has been reported as ranging from 0 to 44 per cent (Meredith and Hixon, '54). Thus the results of this study place the population near the maximum reported frequency of bilateral asymmetry. When the classification system is lumped into three categories, smooth, pitted, or grooved, and protuberance or cusp, the frequency of bilateral asymmetry drops sharply. It is apparent, therefore, that should the more detailed classification system be applied to other studies, an increased frequency of asymmetrical expression would be expected.

Although a male preponderance in the frequency of positive expressions has been reported in many studies (Meredith and Hixon, '54; Tsuji, '58; Hanulik, et al., '66; Barnes, '69; Snyder, et al., '69; Goose and Lee, '71; Joshi, et al., '72; Kirveskari, '74), there was no evidence of sexual dimorphism among the Wainwright Eskimos (Table 2). This finding is in agreement with other studies which also showed Carabelli's structures to be without sexual dimorphism (Garn, et al., '66 a,b).

TABLE 2

Extent of sex influence on Carabelli's structures

	First Molar			Second Molar		
	s (%)	p/g (%)	p/c (%)	s (%)	p/g (%)	p/c (%)
Male	7	67	26	57	38	4
Female	9	65	26	55	41	4

s = smooth p/g = pitted or grooved p/c = protuberance or cusp

Acknowledgement

I would like to thank Dr. Albert A. Dahlberg for his guidance in the preparation of this paper. His sincere interest in this work as a teacher and friend will always be remembered and appreciated.

Literature cited

Adloff, P. 1908 Das Gebiss des Menschen und der Anthropomorphen.Vergleichende - Anatomische Untersuchungen. Zugleich ein Beitrag zur menschlichen Stammesgeschichte. Julius Springer, Berling. (As reported in Korenhof, 1960).

Bailit, H. L., S. J. DeWitt, and R. A. Leigh. 1968 The size and morphology of the Nasioi dentition. Am. J. Phys. Anthrop., 28: 271-288.

Bang, G., and A. Hasund. 1973 Morhpologic characteristics of the Alaskan Eskimo dentition. III. Number of cusps on the upper permanent molars. Am. J. Phys. Anthrop. 38: 721-725.

Barnes, D. S. 1969 Tooth morphology and other aspects of the Teso dentition. Am. J. Phys. Anthrop., 30: 183-194.

Brothwell, D. R. 1967 Some problems and objectives related to the study of dental variation in human populations. J. Dent. Res., 46: 938-941.

Butler, P. M. 1963 Tooth morphology and primate evolution. In: Dental Anthropology. D. R. Brothwell, ed. Pergamon Press, New York.

Cederquist, R. K. 1976 Craniofacial description of Wainwright Alaskan Eskimos. Master's Thesis, University of Chicago.

Cope, E. D. 1889 On the tritubercular molar in human dentition. J. Morphol., 2: 7-26.

Dahlberg, A. A. 1949 The dentition of the American Indian. In: Papers on the Physical Anthropology of the American Indian. Fourth Viking Fund Summer Seminar. W. S. Laughlin, ed. The Viking Fund, Inc., New York. Printed by Edwards Brothers, Inc., Ann Arbor, 1951, pp. 138-176.

______ 1963 Analysis of the American Indian Dentition. In: Dental Anthropology. D. R. Brothwell, ed. Pergamon Press, New York, pp. 149-177.

______ 1971 Penetrance and expressivity of dental traits. In: Dental Morphology and Evolution. A. A. Dahlberg, ed. University of Chicago Press, Chicago, pp. 257-262.

______ 1976 Personal Communication.

De Terra, M. 1905 Beiträge zu einer Odontographie der Menschenrasses. Berlinische Verlagsanstalt, Berlin.

Dietrich, W. O. 1958 Die Australopithecinen. Forschung und Fortschritte, 32: 263-268, 1958.

Dietz, V. H. 1944 A common dental morphotropic factor, the Carabelli cusp. Am. Dent. A. J., 31: 784-789.

Garn, S. M., R. S. Kerewsky, and A. B. Lewis. 1966a Extent of sex influence on Carabelli's polymorphism. J. Dent. Res., 45:1823.

Garn, S. M., A. B. Lewis, and R. S. Kerewsky. 1966b Genetic independence of Carabelli's trait from tooth size or crown morphology. Arch. Oral. Biol., 11: 745-747.

Goodman, H.O. 1965. Genetic parameters of dentofacial development. Am. J. Phys. Anthrop., 6: 63-84.

Goose, D.H. 1963. Dental Measurement: An assessment of its value in anthropological studies. In: Dental Anthropology. D.R. Brothwell, ed. Pergamon Press, New York, pp. 125-148.

Goose, D.H. and G.T.R. Lee. 1971 The mode of inheritance of Carabelli's trait. Hum. Biol., 43: 64-69.

Gregory, W.K. 1922 The origin and evolution of the human dentition. Williams and Wilkins Co., Baltimore.

Hanihara, K. 1968 Mongoloid dental complex in the permanent dentition. Proceedings of the VII International Congress of Anthropological and Ethnological Sciences, S-2, Vol. 1, pp. 298-300.

Hanulik, M., A. Bachraty, and P. Andrik. 1966 Bemerkungen zum Vorkommen des Tuberculum anomale Carabelli. Z. Morph. u. Anthrop., 57: 168-172.

Hrdlicka, A. 1924 New data on the teeth of early man and certain fossil European apes. Am. J. Phys. Anthrop., 7: 109-132.

Hunter, W.S., and W.R. Priest. 1960 Errors and discrepancies in measurement of tooth size. J. Dent. Res., 39: 405-414.

Joshi, M.R., R.N. Godiawala, and A. Dutia. 1972 Carabelli's trait in Hindu children from Gujarat. J. Dent. Res., 51: 706-711.

Keene, H.J. 1965 The relationship between third molar agenesis and the morphology variability of the molar teeth. Angle Orthodont., 35: 289-298.

Keene, H.J. 1968 The relationship between Carabelli's trait and the size, number, and morphology of the maxillary molars. Arch. Oral Biol., 13: 1023-1025.

Keller, I. 1954 Der Zahnbau der Prosimien. Thesis, University of Greifswald, 1954. (As reported by Korenhof, 1960).

Kirveskari, P. 1974 Morphological traits in the permanent dentition of living Skolt Lapps. Finnish Dent. Soc. Proc., 70: Suppl. II.

Korenhof, C.A.W. 1960 Morphogenetical aspects of the human upper molar. A comparative study of its enamel and dentine surfaces and their relationship to the crown pattern of fossil and recent primates. Uitgeversmaatschappi, Weerlandia, Utrecht.

Kotzschke, G. 1953 Das Carabellische Hoerkerchen. Zahnartztl. Reform. Heidelberg, 54: 263-265.

Kraus, B.S. 1959 Occurrence of the Carabelli Trait in Southwest ethnic groups. Am. J. Phys. Anthrop., 17: 117-123.

Le Gros Clark, W.E. 1950 Hominoid characters of the Australopithecine dentition. Roy. Anthrop. Inst. J., 80: 37.

Lundström, A. 1954 Intermaxillary tooth width ratio and tooth alignment and occlusion. Acta Odont. Scand., 12: 265-292.

Meredith, H.V. and E.H. Hixon. 1954 Frequency, size,and bilateralism of Carabelli's tubercule. J. Dent. Res., 33: 435-440.

Moorrees, C.F.A. 1957 The Aleut Dentition. Harvard University Press, Cambridge.

Osborn, H.F. 1888 The evolution of mammalian molars to and from the tritubercular type. Am. Naturalist, 22: 1067-1079.

Osborne, R.H. 1967 Some genetic problems in interpreting the evolution of the human dentition. J. Dent. Res., 46: 945-948.

Oschinsky, L. and R. Smithurst. 1960 On certain dental characters of the Eskimo of the Eastern Canadian Artic. Anthropologica, 2: 105-112.

Pedersen, P.O. 1949 The east Greenland Eskimo dentition. Numerical variations and anatomy. Re-issue, 1965. C.A. Reitzels Forlag, Kobenhavn.

Pinto-Cisternas, J. and H. Figueroa. 1968 Genetic structure of a population of Valparaiso. II. Distribution of two dental traits with anthropological importance. Am. J. Phys. Anthrop., 29: 339-348.

Remane, A. 1960 Zähne und Gebiss. In: Primatologia, Handbuch der Primatenkunde III, Teil 2. H. Hofer, A. H. Schultz, and D. Starck, eds. S. Korger and Basel, New York.

Richardson, M. E., and P. C. Admans, and T. P. G. McCartney. 1963 An analysis of tooth measuring methods on dental casts. Europ. Orthodont. Soc. Tr., 39: 285-301.

Robinson, J. T. 1956 The dentition of Australopithecines. Transvaal Museum Memoir, No. 9, Pretoria, South Africa.

Rosenzweig, K. A., and Y. Silberman. 1967 Dental morphology of Jews from Yemen and Cochin. Am. J. Phys. Anthrop., 26: 15-22.

Schwalbe, G. 1916 Über der fossilen Affen Oreopithecus bambolii. Ausgleich ein Beitrag zur Morphologie der Zähne der Primaten. Zeit. Morph. u. Anthrop., 19: 149-254.

Snyder, R. G., A. A. Dahlberg, C. C. Snow, and T. Dahlberg. 1969 Trait analysis of the dentition of the Tarahumara Indians and Mestizo of the Sierra Madre, Occidental, Mexico. Am. J. Phys. Anthrop., 31: 65-76.

Sprawson, E. 1922 On the significance of the extra cusp commonly found on the antero-internal aspect of the maxillary first permanent molar in man. Roy. Soc. Med. Sec. Odont. Proc., 15: 72-74.

Tsuji, T. 1958 Incidence and inheritance of the Carabelli's cusp in a Japanese population. Ja. J. Hum. Genet., 3: 21-31.

Vallois, H. 1955 Ordre des Primates. In: Traite de Zoologie, Anatomie, systematique, biologie. Tome XVII. Mammiferes (second fascicule). Masson and Cie, Paris, pp. 1854-2206.

Von Koenigswald, G. H. R. 1957 Verslag Discussie-voordracht. De evolutie van het menselijk gebit door. C. A. W. Korenhof. Tidschr. voor Tandheelk. 64: 477-478. (As reported by Korenhof, 1960).

Weidenreich, F. 1937 The dentition of Sinanthropus pekinensis. A comparative odontography of the hominoids. Pal. Sinica. New series D. No. 1, Whole Series No. 101 (I).

TABLE 3.

Frequency of occurrence of the different expressions of Carabelli's structures in Wainwright Eskimos.

			smooth		single furrow		pit		Y-furrow		double furrow		slight bulging		small cusp	
		N	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)
Right	M	53	4	(8)	14	(26)	1	(2)	13	(24)	7	(13)	9	(17)	5	(9)
First	F	63	5	(8)	12	(19)	0	(0)	18	(29)	13	(21)	13	(21)	2	(3)
Molar	total	116	9	(8)	26	(22)	1	(1)	31	(27)	20	(17)	22	(20)	7	(6)
Left	M	50	3	(6)	19	(38)	0	(0)	7	(14)	8	(16)	8	(16)	5	(10)
First	F	62	6	(10)	13	(21)	0	(0)	18	(29)	7	(11)	16	(26)	2	(3)
Molar	total	112	9	(8)	32	(29)	0	(0)	25	(22)	15	(13)	24	(21)	7	(6)
Right	M	33	17	(52)	11	(33)	0	(0)	1	(3)	2	(6)	2	(6)	0	(0)
Second	F	41	22	(54)	12	(29)	0	(0)	3	(7)	2	(5)	2	(5)	0	(0)
Molar	total	74	39	(53)	23	(32)	0	(0)	4	(5)	4	(5)	4	(5)	0	(0)
Left	M	35	22	(63)	11	(31)	0	(0)	0	(0)	1	(3)	1	(3)	0	(0)
Second	F	37	21	(57)	12	(32)	0	(0)	1	(3)	2	(5)	1	(3)	0	(0)
Molar	total	72	43	(60)	23	(32)	0	(0)	1	(1)	3	(4)	2	(3)	0	(0)
First	M	103	7	(7)	33	(32)	1	(1)	20	(19)	15	(15)	17	(16)	10	(10)
Molar	F	125	11	(9)	25	(20)	0	(0)	36	(29)	20	(16)	29	(23)	4	(3)
Totals	total	228	18	(8)	58	(25)	1	(1)	56	(25)	35	(15)	46	(20)	14	(6)
Second	M	68	39	(57)	22	(32)	0	(0)	1	(2)	3	(4)	3	(4)	0	(0)
Molar	F	78	43	(55)	24	(31)	0	(0)	4	(5)	4	(5)	3	(4)	0	(0)
Totals	total	146	82	(56)	46	(32)	0	(0)	5	(3)	7	(5)	6	(4)	0	(0)

TABLE 4.

Population comparisons of the frequency of the different expressions of Carabelli's structures

Population	Author	Year		First Molar				Second Molar				Third Molar		
			N	s (%)	p/g (%)	p/c (%)	N	s (%)	p/g (%)	p/c (%)	N	s (%)	p/g (%)	p/c (%)
Wainwright Eskimos	Hershey	1976	228	8	66	26	146	56	40	4				
Skolt Lapps	Kirveskari	1974	182	20	64	16	166	78	19	4	43	74	16	10
Alaskan Eskimos	Bang & Hasund	1972	95	58	26	17								
E. Greenland Eskimos	Pedersen	1949	106	—100—		0	162	99	—1—					
N. Pacific Aleuts	Moorrees	1957	60	87		13								
Arizona Pima Indians	Dahlberg	1963	400	17	59	24	200	77	20	3	13	100		
Tarahumara Indians	Snyder, et al.	1969	165	2	34	63	98	17	79	4				
Valparaiso Chileans	Pinto-Cisternas & Figueroa	1968	705	73	—27—									
Iowa Whites	Meredith & Hixon	1954	100	—16—		84								
Tuscon Whites	Kraus	1959	600	44	10	45								
Chicago Whites	Dahlberg	1968	289	14	31	55	200	57	29	14	24	92	8	
American Whites	Keene	1968	773	40	38	22	778	97	2	1				

TABLE 4-- continued

Population	Author	Year	First Molar				Second Molar				Third Molar			
			N	s (%)	p/g (%)	p/c (%)	N	s (%)	p/g (%)	p/c (%)	N	s (%)	p/g (%)	p/c (%)
British Whites	Goose & Lee	1971	602	21	58	19								
Yemen Jews	Rosenzweig & Zilberman	1967	30	7	26	67								
Cochin Jews	Rosenzweig & Zilberman	1967	30	38	26	26								
Java Malayans	Korenhof	1960	1431	76	4	20								
Nasioi Melanesians	Bailit, et al.	1968	134	81	10	9	113	94	6		69	97	2	1
E. African Blacks	Barnes	1969	10284	90		10								
Tuscon Blacks	Kraus	1959	548	42	28	30								
Gujarat Hindus	Joshi, et al.	1972	978	35	38	27								
Liverpool Chinese	Goose	1976	134	70	20	10	133	99	1					
Easter Islanders	Turner & Scott	1976	70	67	23	10	129	90	8	2	39	89	7	4

s = smooth p/g = pitted or grooved p/c = protuberance or cusp

A consideration of the "*Dryopithecus* pattern"

DONALD C. JOHANSON

OSSA

Nearly all anthropological investigations of hominoid dentitions include a consideration of the "*Dryopithecus* pattern". Although it was clearly defined by Gregory (' 16) and Gregory and Hellman (' 26a, b) it has often been misunderstood and misused by investigators. Its usefulness in pointing out phylogenetic affinities and as a descriptive device in anthropological studies demands that the correct definition be properly applied.

The "*Dryopithecus* pattern" has undergone considerable evolutionary alteration from its primitive configuation of Y-5. Several schemes have been proposed for the sequence of change, but based on studies of human molars the sequence Y-5 to +-5 to +-4 to Y-4 appears to be quite plausible.

Почти все антропологические исследования зубов гоминидов включают рассмотрение "модели дриопитека". Хотя она и была точно определена Gregory /'16/, а также Gregory и Hellman /'26, a,b/, она часто неправильно понимается и употребляется исследователями. Польза ее состоит в том, что она указывает на филогенетическое родство. Для применения этой модели в качестве дескриптивного приспособления в антропологических исследованиях необходимо пользоваться правильным определением.

"Модель дриопитека" подверглась значительным эволюционным изменениям со времени ее примитивной конфигурации Y-5. Для последовательности изменений были предложены различные схемы, однако, изучение человеческих больших коренных зубов показывает , что последовательность от Y-5 к +-5 и к +-4 является вполне приемлемой.

Donald C. Johanson, Laboratory of Physical Anthropology, The Cleveland Museum of Natural History, Wade Oval, University Circle, Cleveland, Ohio, 44106 U.S.A.

Vol. 6, pp. 125-138, Lund. ISSN 0345-8865.

Introduction

Most investigations which consider hominoid dentitions include discussion of the "*Dryopithecus* pattern" found on lower molars. The pattern was initially discussed by Gregory (' 16) and after recognizing that the pattern is "characteristic of all species of *Dryopithecus* , both European and Indian" (' 16:294) he chose the name "*Dryopithecus* pattern". The evolutionary significance of the "*Dryopithecus* pattern" is that it is characteristic of all Hominoidea, and is a useful feature for establishing phylogenetic affinities. It led Gregory to write "that the ancestors not only of the modern anthropoids but also of man would have the known generic characters of the jaws and dentition of *Dryopithecus*" (' 26:30).

It is not the intention of this presentation to review the numerous studies which have reported on the "*Dryopithecus* pattern" in various hominoid samples. The main objective is, however, to review the definition of the pattern, its misinterpretation and misapplication and to present a consideration of the evolutionary alteration from the primitive Y-5 configuration.

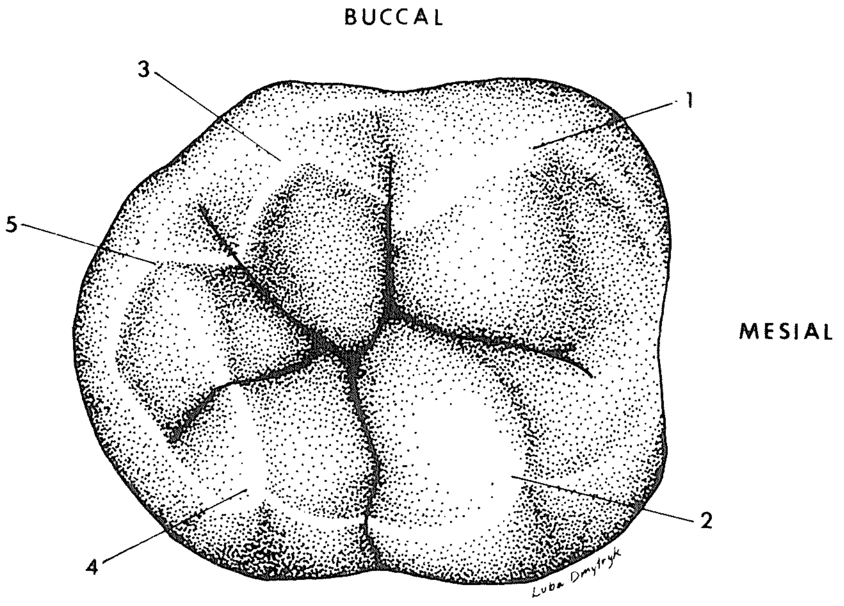


Fig. 1. Idealized *Dryopithecus* lower molar (left) displaying the Y-5 pattern. (1) Protoconid, (2) Metaconid, (3) Hypoconid, (4) Entoconid, (5) Hypoconulid

Definition and Evolutionary Alteration of the "*Dryopithecus* pattern"

Robinson and Allin ('66) have drawn attention to the widespread misuse of the "*Dryopithecus* pattern" and suggest that this, "could rapidly lead to the complete destruction of this nomenclature as a useful descriptive tool," ('66:323). Because of its prominent role in dental studies as well as its frequent misinterpretation and misapplication, a further discussion and evaluation is warranted.

It seems best, therefore, to begin with the complete definition given by Gregory and Hellman ('26b:300) for the "*Dryopithecus* pattern":

> In this five-cusped type ... the most conspicuous feature (is) a more or less irregular Y, the stem of which is the inner transverse groove between cusps 2 and 4, the fork being formed by the outer half of the transverse groove (between cusps 1 and 3) and by the deep oblique furrow between cusps 3 and 5. There is no 1 - 4 contact but there is a prominent 2 - 3 contact. Near the front border of the crown between cusps 1 and 2 there is frequently a prominent transverse groove or crack which has been called the "fovea anterior" (f. a.), while on the hinder inner border, between cusps 5 and 4, a smaller fissure is called the "fovea posterior".

The core of this definition (also that in Gregory, '16; Gregory and Hellman, '26a) is found in the first paragraph, i. e. a five-cusped lower molar with a "Y" groove configuration exhibiting contact between the metaconid and hypoconid. Although the initial definition by Gregory (' 16:294) and this later elucidation by Gregory and Hellman (' 26b:300) are straight forward and unambiguous, a number of incorrect renderings have appeared (Anderson, '62; Simons, '64; Day, '65; Hill, '66). This may be in part due to different investigators depending on unreliable secondary sources for their definitions. In addition there are several possible "Y" configurations which can be delineated on lower molars and some authors simply guess as to which pattern is correct. Even now after a clear presentation of the misinterpretations of the "*Dryopithecus* pattern" by Robinson and Allin ('66) there are some investigators (Biggerstaff, '68; Morris, '70) who still misunderstand the pattern.

Gregory and Hellman ('26a, b), but predominately Hellman ('28), noted that in some hominoid molars, particularly those of man, the primitive "*Dryopithecus* pattern" has undergone alteration. They pointed out that instead of the characteristic contact between the metaconid and hypoconid, there occur situations where there is contact between the protoconid and the entoconid and this situation they termed the, "typical plus-shaped human pattern," ('26a:105). Jørgensen ('55) takes issue with this description and says that a protoconid -entoconid contact is more properly designated as an "X" pattern and only in cases where a point contact exists between the protoconid, metaconid, hypoconid and entoconid should the "+" designation be employed.

Recognition of the "X" pattern is useful in studies of human teeth where advanced alteration of the groove pattern has occurred. However, in the Pongidae its use is not required because alteration from the "Y" pattern is not as pronounced (Johanson, '70).

Hellman ('28) noticed that the number of cusps on lower molars may also vary Certain cusps can be lost so that only four or even three (rare) are present. Usually the cusp which is lost is the hypoconulid and the pattern is designated as a Y-4 or a +-4. On the other hand, lower molars may also manifest supernumerary cusps such as the C_6 and/or C_7. However, the supernumerary cusps are not reflected in the designation of the pattern because a Y-6 designation does not distinguish between a five cusped lower molar with a C_6 and one with a C_7. So all molars with at least five cusps should be designated as Y-5 or +-5 (or X-5).

Hellman ('28) studied the various modifications of the "*Dryopithecus* pattern" in different racial groups and arrived at several conclusions which have figured prominently in succeeding investigations. Although the pattern varied in the human dentition and differed from the primitive pattern found in *Dryopithecus* it could be easily traced to the primitive situation. The changes which occur and modify the primitive pattern are brought about "by a gradual and progressive process of evolution " (Hellman, '28:174). Such changes take place in four clearly delineated stages defined by Hellman as: 1) the primitive "*Dryopithecus* pattern", 2) a stage in which the cusp number has been reduced from 5 to 4 with the groove pattern remaining a "Y", 3) a stage in which the groove pattern has been modified from a "Y" to a "+" and the number of cusps has remained as 5, and 4) a stage in which both the cusp number has been reduced and the groove configuration changed, resulting in a a +-4 pattern. Hellman regarded these as reflecting various stages of evolutionary advancement and concluded that the most advanced condition is found among modern "Whites", the "Mongols" being intermediate, and the West African "Negroes" the most primitive.

Although Hellman ('28) gives no reason why he considered the +-4 condition to be the most advanced modification of the "*Dryopithecus* pattern" it may be assumed that it was because it involved changes both in cusp number and in groove pattern. Hence, Hellman considered the hypoconid - metaconid contact to be more stable than the cusp number. In Hellman's scheme there is a single linear arrangement of the stages of alteration: Y-5 to Y-4 to +-5 to +-4. Although Dahlberg ('49) basically follows Hellman's scheme he does not see each stage as constituting a position in a phylogenetic sequence but suggests two alternative routes: 1) Y-5 to Y-4 and 2) Y-5 to +-5 to +-4. Dahlberg's scheme is evolutionarily simpler since Hellman's scheme would dictate regaining a cusp between the Y-4 and +-5 stages. Both Remane ('60) and Frisch ('65) concur with Dahlberg's suggestion on the basis of comparisons of fossil and recent dentitions.

A third evolutionary scheme for the modification of the "*Dryopithecus* pattern" is suggested by Erdbrink ('65). He suggests that Y-4 is the most advanced stage of alteration and outlines the following sequence: Y-5 to +-5 to +-4 to Y-4.

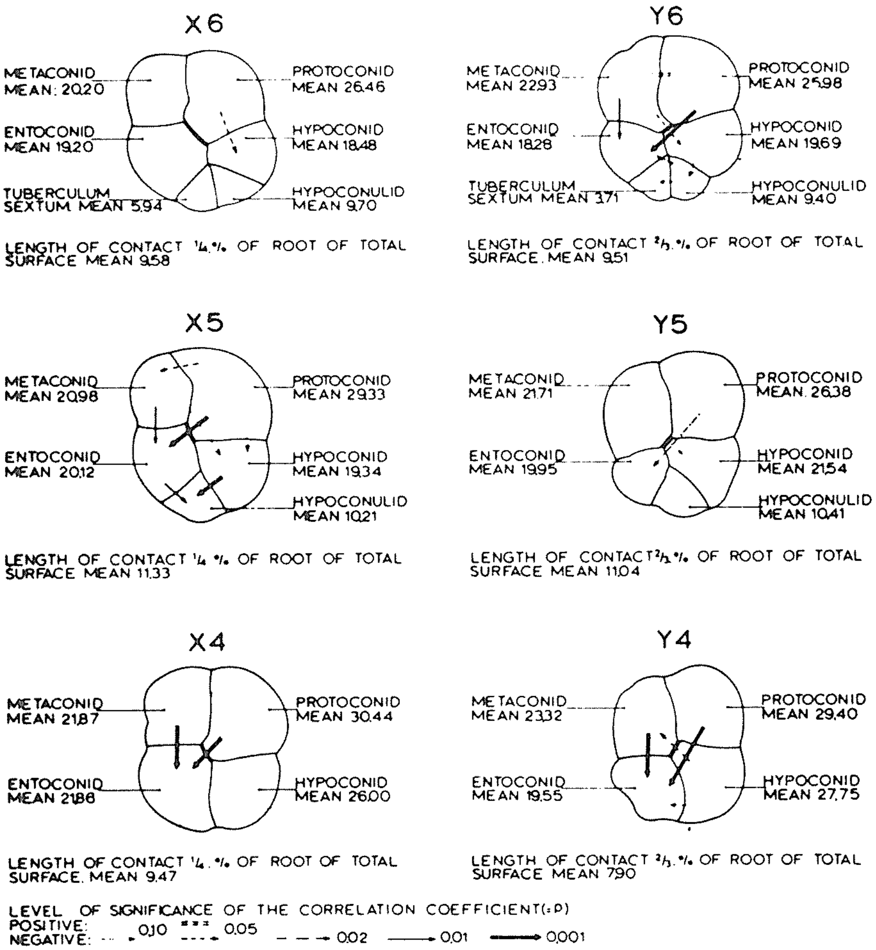


Fig. 2 Correlations between cusp sizes of lower molars (after Erdbrink, '65).

In order to evaluate these different schemes it is best to consider the manner in which such modifications of the groove pattern occur. Originally Gregory and Hellman ('26a, b) pointed out that stages of graduations from the "Y" to the "+" pattern are seen in a series of teeth. They postulated that the modification occurs in the following manner:

> The hypoconid reduces and tends to fuse with the hypoconulid, the protoconid becomes relatively large, the apex of the hypoconid Y withdraws from contact with the base of the metaconid, either enabling all four cusps to meet in the center or enabling the forwardly displaced entoconid to gain contact with the protoconid base; meanwhile the hypoconulid is fused with the hypoconid and becomes secondarily more median in position ('26a:105).

Jørgensen ('55) considers the major cause of the modification to be the distal movement (relative to the lingual groove) of the buccal groove separating the protoconid and hypoconid. This results in a larger protoconid and smaller hypoconid in the +-5 pattern, but in the +-4 pattern the protoconid would be larger and the hypoconid would be larger because of its incorporation of the hypoconulid.

Remane ('60) on the other hand, believes that the major reason for a protoconid-entoconid contact, hence a "+" pattern, is the enlargement of the entoconid resulting in a mesial migration of the lingual groove and a reduction in size of the metaconid.

In order to evaluate these two hypotheses we can turn to the excellent contribution by Erdbrink ('65). He attempted to quantify the "*Dryopithecus* pattern" by measuring from photographs, using a planimeter, the area occupied by the different cusps. He did this for all three lower molars exhibiting modifications of the "*Dryopithecus* pattern" (including Jørgensen's "X" category). After measuring the different cusp areas Erdbrink calculates the correlation coefficients between various cusps and considers significant negative and positive correlations. Reproduced in Figure 2 are the results of Erdbrink's investigation ('65:86, fig. 4) which are used throughout this discussion.

Jørgensen's model predicts an increase in size of the protoconid and a decrease in size of the hypoconid in the transition from a Y-5 to a +-5 (X-5) pattern. Erdbrink's data substantiates this because the mean area of the protoconid increases from 26.38 to 29.33 and the mean area of the hypoconid decreases from 21.54 to 19.34.

In the transition from a Y-5 to a +-5 according to Remane's model the lingual groove moves mesially resulting in a decrease in metaconid area and an increase in entoconid area. Erdbrink's data also supports this hypothesis in that the mean area of the metaconid decreases from 21.71 to 20.98 and the entoconid mean area increases from 19.95 to 20.12.

Hence, it is seen that Erdbrink's data supports <u>both</u> Jørgensen's and Remane's models indicating that alteration of the cusp configuration involves both a mesial shifting of the lingual groove and a distal shifting of the buccal groove.

Erdbrink's data may be used to test Dahlberg's ('49) model which postulates two independent sequences. We have established that the modification from Y-5 to +-5 is a reasonable transition. Does Erdbrink's data support a transition from a +-5 stage to a +-4 stage? What is involved here is the loss of the hypoconulid and its incorporation into the hypoconid following Gregory and Hellman ('26a). In addition Erdbrink ('65) believes that on the basis of a significant negative correlation (p=.01) a portion of the hypoconulid will be incorporated into the entoconid but that most of it will be incorporated into the hypoconid as is indicated by a highly significant negative correlation (p=.001) between these two cusps. Thus we see a strong tendency for the hypoconulid to be lost in a transition from a +-5 to +-4 stage. Indeed, the hypoconid mean area increases from 19.34 to 26.00 and the entoconid mean area from 20.12 to 21.86. Thus, the sequence +-5 to +-4 is fully supported by Erdbrink's data.

The second sequence, Y-5 to Y-4 to +-4 may also be tested. In the Y-5 condition there are not strong negative correlations of the hypoconulid indicating a loss of this cusp. Indeed, the negative correlation between the metaconid and hypoconid is contradicted in a Y-5 to Y-4 modification because the metaconid and the hypoconid both increase in size. Therefore the data presented by Erdbrink do not support a Y-5 to Y-4 modification. The transition from a Y-4 to a +-4 is, however, possible because the protoconid and entoconid increase in size as opposed to the metaconid and hypoconid which decrease in size. Thus it is seen that the second independent sequence, Y-5 to Y-4 to +-4, does not find support in Erdbrink's data. Supporting evidence for Erdbrink's data comes from observations by Gregory and Hellman ('26) and Frisch ('65) which suggest a change in groove pattern preceded cusp reduction.

Up to this point I have shown that only one sequence is possible, i.e. from Y-5 to +-5 to +-4. However, this does not include the stage Y-4. The next logical hypothesis to test is whether or not it is possible to go from a +-4 to a Y-4. (A change from a "+" to a "Y" would suggest a distal movement of the lingual groove and a mesial movement of the buccal groove. This would result in an increase in size of the metaconid and hypoconid along with a decrease in size of the protoconid and entoconid.) Indeed this is what happens: the metaconid increases in mean area from 21.87 to 23.32 and the hypoconid from 26.00 to 27.75. The protoconid decreases in size from 30.44 to 29.40 and the entoconid from 21.86 to 19.55. A look at the significant correlations present in the +-4 pattern indicates some contradiction in the sequence +-4 to Y-4. The significant negative correlation between the metaconid and entoconid indicates an increase in metaconid size and decrease in entoconid size, which does occur. However, the significant negative correlation between the protoconid and entoconid indicates an increase in entoconid size, which does not occur. When one looks at the strength of the correlations in Erdbrink's data I find that the metaconid -entoconid correlation (-0.4887) is stronger than the protoconid - entoconid correlation (0.3296). This indicates that the former is more important in determining entoconid size; hence the entoconid decreases in mean area.

Utilizing Erdbrink's data it is therefore possible to establish a hypothetical sequence of alteration in the "*Dryopithecus* pattern" which differs from those of Hellman ('28) and Dahlberg ('49). This new sequence is: Y-5 to +-5 to +-4 to Y-4. The implication of this sequence is that the Y-4 pattern is the most advanced stage and not the +-4 as postulated by Hellman ('28) and Dahlberg ('49).

This sequence is based entirely on human molars. The few pongid specimens included by Erdbrink ('65) do not permit conclusive statements to be made about the sequence among these primates. Erdbrink ('65:84) indicated that the significant correlations differ greatly between these two groups. Hence, it is possible that the sequence is not the same among the pongids as among the hominids and such a hypothesis should be investigated.

The "*Dryopithecus* pattern" in pongids

It is possible to compare the frequency of occurrence of certain occlusal patterns occurring in hominids and pongids. Using the data presented by Jørgensen ('55) confirms that +-4 patterns are much more frequent than are Y-4 patterns, the most advanced stage of Erdbrink. Using the comparative data I collected on the chimpanzee (Johanson, '74), the results are somewhat sporadic (Tables 1, 2, 3, 4). In the *paniscus* and *troglodytes* samples Y-patterns are more frequent and in the *schweinfurthi* and *verus* samples the +-4 patterns predominate. It is difficult to reach conclusions on the basis of such observations but it appears that not only in some instances do chimps show a different pattern than human molars, but there are even varying patterns between the groups.

It was noted by Hellman ('28) and most subsequent observers (Dahlberg, '49; Schuman and Brace, '54; Jørgensen, '55; Frisch, '65; Johanson, '70) that the first molar tends to retain the "Y" pattern in a higher frequency than the second or third molars. Modification of the "Y" pattern into a "+" pattern occurs more frequently on the distal two molars but not in any regular fashion. Using the data found in Jørgensen's paper ('55) illustrates that among the human groups listed about half show a regular decrease in "Y" patterns from the first to the third molar while the other half show a higher frequency of "Y" patterns on the third molar than on the second. In pongid dentitions with available data there is always a trend in which the "Y" pattern is highest on the first molar, intermediate on the second, and lowest on the third (Schuman and Brace, '54; Frisch, '65; Johanson, '70; Skaryd, '71).

With regard to cusp number, investigators (Jørgensen, '55; Dahlberg, '49; and others) of human dentitions report that the first molar retains five cusps in the highest frequency, the third is intermediate and the second shows the lowest frequency. However, studies of the gibbon (Frisch, '65), the chimpanzee (Schuman and Brace, '54; Johanson, '70; Skaryd, '71) and the gorilla (Skaryd, '71) show that the trend towards loss of the hypoconulid is more regular with first molars being very conservative, second molars intermediate, and third molars most progressive.

Although modifications of the "*Dryopithecus* pattern" of the actual cusp contact and the cusp number are seen in both contemporary hominids and pongids the frequency of alteration is considerably higher among the former. An exception to this statement is the work by Schuman and Brace ('54) on the Liberian chimpanzee. They report frequencies of 76% and 99% for the occurrence of "+" patterns on second and third molars, respectively. [1] In an earlier work Johanson ('70) suggested that this discrepancy may be in part due to the scoring of molars with a very short metaconid-hypoconid contact as a "+" pattern instead of a "Y" pattern. In addition errors in scoring metaconid - hypoconid contact may be due to other reasons as Remane has written:

> Differences in evaluation whether a *Dryopithecus* pattern or a plus pattern, originate evidently from the fact that some authors count molars with a uniform transverse groove as plus patterns even when the longitudinal groove is not present, but the metaconid and hypoconid are still in contact. Here the plus pattern is attributed only to the absences of such a length of contact ('60:716, my translation). [2]

This points out that in situations where the lingual groove has moved mesially to line up with the mesialbuccal groove there may be an impression of a "+"pattern. However, in instances when this is not accompanied by a point contact or a clear contact between the protoconid and entoconid it must be scored as a "Y" (see fig. 3). An untrained observer might incorrectly record such an instance as "+" pattern and not a "Y" pattern.

Adaptive significance of the "*Dryopithecus* pattern"

Persistence of the "*Dryopithecus* pattern" in the Hominoidea since the earliest dryopithecine times is striking. This leads one to question the adaptive advantage of this pattern as opposed to other possible patterns.

It is established that the buccal half of the lower molars sustains a more rapid degree of attrition than does the lingual half (Welsch, '67). Three of the principal cusps, the protoconid, hypoconid and hypoconulid are located on the buccal half of the lower molar. Hence, it is possible that in hominoids which masticate a considerable amount of tough food between the molars, like the gorilla, selection would tend to retain the five-cusped molar pattern. The data presented by Jørgensen ('55) for hominid groups substantiates this hypothesis. Among such groups as the Eskimo, the Australians, and African Negroes the five-cusped tooth is found more frequently than is the four-cusped tooth, while the latter predominate among Chicago and European Whites (Dahlberg, '63). The first molar, a tooth which sustains the heaviest forces and is subject to wear for the longest time, retains the five-suped tooth pattern in higher frequencies than do the other two molars. Even among the pongids, the chimpanzee for example, there is a strong tendency for retention of the five-cusped molar on M_1

What the adaptive significance of the "Y" versus the "+" pattern is, has not been worked out. Independence of cusp number and groove pattern has been demonstrated by several studies (Jørgensen, '55; Garn *et al.*, '66a, '66b). However, when alterations in the "*Dryopithecus* pattern" of groove configuration and cusp number are compared and considered independently it is found that alterations in groove pattern are more frequent than alterations in cusp number (Gregory and Hellman, '26a, b; Frisch, '65; Johanson, '70, '74). It appears, therefore, that selection is strong for five-cusped lower molars and reduced for retention of the "Y"pattern of groove configuration.

---

[1] My observations on the same sample are at considerable odds with those of Schuman and Brace. I found the following frequencies of "+" patterns: M_2-3.1%; M_3-40.1%

[2] Unterschiede in der Bewertung, ob *Dryopithecus* muster oder Kreuzmuster, entstehen offenbar dadurch, dass manche Autoren Molaren mit einheitlicher Querfurche bereits als Kreuzmuster zählen, auch wenn die Längsfurche noch nicht besteht, sondern Metaconid und Hypoconid noch in Kontakt sind. Hier wird das Kreuzmuster erst vom Fehlen einer solchen Kontaktstrecke an gerechnet ('60:716).

Fig. 3. A "Y" pattern which may be mistaken for a "+" pattern. Right lower M_2, Harvard Specimen N/6962.

Recent misinterpretations of the *"Dryopithecus* pattern"

Recently the usefulness of the *"Dryopithecus* pattern" has been criticized (Biggerstaff, '68; Morris, '70). I feel that these criticisms arise from a misunderstanding of the *"Dryopithecus* pattern", are only minimally instructive, and have unnecessarily confused the literature.

Biggerstaff ('68) contends that a classification of the mandibular molars should include observations on the distal marginal ridge, cusp size, cusp number, and distal fovea. He argues that the presence of a distal marginal ridge and a distal fovea are necessary for a lower molar pattern to qualify as a *"Dryopithecus* pattern" because these morphological features were mentioned in the original definition (Gregory, '16: 294; Hellman, '28:161; Gregory and Hellman, '26b:300). However, there is no mention of a distal marginal ridge in these definitions at all. Furthermore the presence of both a distal fovea and an anterior fovea is mentioned. Why then should Biggerstaff choose only the distal fovea and not the anterior fovea? Why not both?

Most investigators (see Robinson and Allin, '66) have considered the anterior and posterior fovea as being of minor importance and hence ignored them. This has been the usual practice since the "form of contact and the number of cusps do not appear to be influenced by their (fovea) being present or absent" (Erdbrink, '65:71).

Biggerstaff contends that, "range of variation existed among the Dryopithecinae lower molars as it exists among populations or individuals of *Homo sapiens* " ('68:442). To illustrate this he refers to published figures by Gregory and Hellman, and points out that they "demonstrate the absence of the posterior fovea and distal marginal ridge even though these teeth are presented as representing typical molar patterns of the Dryopithecinae" ('68:442). In particular he refers to figure 6 (which he incorrectly cites as figure 16) of Hellman's publication ('28:164) and remarks that the figure "depicts variations which further establish the fact that the Dryopithecinae molars, as a group manifested a range of variation and could not be unequivocally defined as a single type" (68:442). Figure 6 of Hellman does not depict the dentition of a Dryopithecinae but of an American Indian! In fact it is the same illustration that occurs in Gregory and Hellman's earlier work ('26e: Plate XIII B). Gregory and Hellman never contended that variation did not exist among the Dryopithecinae lower molars in the *"Dryopithecus* pattern" and they wrote "the *"Dryopithecus* pattern" (was) subject to extreme variation in regard to proportions but is singularly constant in the fundamental arrangement of the five principal cusps and of the several grooves at their bases" ('37:256). From this one statement it should be clear that Gregory and Hellman not only recognized that variation existed in dryopithecine lower molars but also that the important features of the lower molar in defining the *"Dryopithecus* pattern" are the cusp number and the groove pattern. Therefore, Biggerstaff's criticisms of the original definitions, descriptions, and illustrations of the *"Dryopithecus* pattern" by those most familiar with the morphology fall away. In addition, Biggerstaff states that in his new classification cusp size should also be included despite the fact that his "new" classification contains no mention of cusp size ('68:444)

Morris ('70) suggests that the presence of a deflecting wrinkle on the mandibular molars of some humans produces a "Y"pattern that is spurious and not comparable with that found in the dryopithecine specimens examined by Gregory and Hellman. Morris criticizes dental investigators for not reporting the frequencies of a deflecting wrinkle in the dentitions which they studied. He contends that data reported on lower molar occlusal groove patterns are therefore questionable.While it is true that most observers have not reported the incidence of deflecting wrinkles it does not follow that frequencies of mandibular molar patterns are unreliable. Illustrations by Hellman ('41: fig. 17) show human molars with a Y-5 pattern and a deflecting wrinkle, so that it appears Hellman considered teeth with a deflecting wrinkle classifiable as a "Y" pattern.

Morris reproduces a figure from Jørgensen ('55) that exhibits a "Y" and a "+"pattern. The "Y" pattern shows a slight distal deflection of the lingual groove which has led Morris to consider this a deflecting wrinkle. The molar illustrated showing a "+" pattern lacks any expression of a deflecting wrinkle and Morris remarks, "thus he (Jørgensen) evidently identified the types on the basis of presence of . . . , the deflecting wrinkle" ('70:100). Such a conclusion is unfair because Jørgensen clearly states that he determines a "Y"pattern on the basis of a metaconid-hypoconid contact. Also human molars can show "Y" patterns without the presence of a deflecting wrinkle (Morris, '70: fig. 3).

Conclusion

It is hoped that this presentation has provided a clearer understanding of the "*Dryopithecus* pattern", its alteration, evolutionary importance and usefulness as a descriptive tool. Reference to the original descriptions by Gregory ('16) and Gregory and Hellman ('26a, b) indicate that the configuration of the "*Dryopithecus* pattern" is straightforward and unambigouous. Although a number of interpretations of the sequence of evolutionary alteration from the primitive Y-5 pattern have been proposed, the sequence Y-5 to +-5 to+ -4 to Y-4 is most reasonable. This is particularly true for hominids but has not been confirmed by the study of pongid dentitions.

Acknowledgements

Gratitude is expressed to the following individuals for providing access to chimpanzee collections: Dr. Max Poll, Curator of the Vertebrate Laboratory at the Musée Royal de L'Afrique Centrale, Tervuren, Belgium; Dr. H. Hackethal, Curator of Collections at the Museum für Naturkunde in Berlin; Mr. L. R. Barton, Curator of Collections at the Powell-Cotton Museum, Birchington, England; and Dr. W. W. Howells, Harvard University.

This project was supported by the Wenner-Gren Foundation for Anthropological Research and by the USPHS DE173 training grant in physical anthropology.

Dr. Albert A. Dahlberg was responsible for the encouragement to conduct this study and I owe him special thanks for all his kind assistance.

Luba Dmytryk drew Figure 1.

References

Andersen, J. E. 1962 The Human Skeleton. A manual for archaeologists. National Museum of Canada, Ottawa.

Biggerstaff, R. H. 1968 On the groove configuration of mandibular molars: The unreliability of the "*Dryopithecus* pattern" and a new method for classifying mandibular molars. Am. J. Phys. Anthrop. 29, 441-444.

Dahlberg, A. A. 1949 The dentition of the American Indian. Papers on the Phys. Anthrop. of the American Indian, Fourth Viking Fund Summer Seminar. W. S. Laughlin, (ed): The Viking Fund, Inc., New York, 138-176.

______ 1963b Analysis of the American Indian dentition. In Brothwell, D. R. (ed.): Dental Anthropology, 149-177. New York. Pergamon Press.

Day, M. H. 1965 Guide to Fossil Man. Cleveland. World Publishing Company.

Erdbrink, D. P. 1965 A quantification of the *Dryopithecus* and other lower molar patterns in man and some of the apes. Z. Morph. Anthrop. 57, 70-108.

Frisch, J. E. 1965 Trends in the evolution of the hominoid dentition. Bibl. Primat., Fasc. 3, 1-130.

Garn, S. M., Lewis, A. B. & Kerewsky, R. 1966a: Sexual dimorphism in the buccolingual tooth diameter. J. Dent. Res. 45, 1819.

______ 1966b Bilateral asymmetry and concordance in cusp number and crown morphology of the mandibular first molar. J. Dent. Res 45, 1820.

Gregory, W. K. 1916 Studies on the evolution of primates. Bull. Am. Mus. Nat. Hist. 35, 239-355.

Gregory, W. K. & Hellman, M. 1926a The dentition of *Dryopithecus* and the origin of man. Anthropl. Pap. Am. Mus. Nat. Hist. 28, 1-123.

______ 1926b The crown patterns of fossil and recent human molar teeth and their meaning. Nat. Hist. 26, 300-309.

______ 1937 The evidence of the dentition on the origin of man. In MacCurdy, G. G. (ed.): Early Man, 243-256. Philadelphia. Lippincott Co.

Hellman, M. 1928 Racial characters in human dentition. Proc. Am. Phil. Soc. 67, 157-174.

______ 1941 Factors influencing occlusion. In Gregory, W. K., Broadbent, B. H. & Hellman, M. (eds.): Development of Occlusion, 49-72. Philadelphia. University of Pennsylvania Press.

Hill, W. C. O. 1966 Primates, Comparative Anatomy and Taxonomy. Vol. VI: Cercopithecinae. New York. Interscience Publishers, Inc.

Johanson, D. C. 1970 Morphological and metrical variability in the chimpanzee molar dentition. Unpublished M. A. thesis, Department of Anthropology, The University of Chicago, Chicago.

______ 1974 An odontological study of the chimpanzee with some implications for hominoid evolution. Doctoral Dissertation, University of Chicago, Chicago.

Jørgensen, K. D. 1955 The *Dryopithecus* pattern in recent Danes and Dutchmen. J. Dent. Res. 34, 195-208.

Morris, D. H. 1970 On deflecting wrinkles and the "*Dryopithecus* pattern of mandibular molars. Am. J. Phys. Anthrop. 32, 97-104.

Remane, A. 1960 Zähne und Gebiss. Primatologica III, 637-846.

Robinson, J. T. & Allin, E. F. 1966 On the Y of the *Dryopithecus* pattern of mandibular molar teeth. Am. J. Phys. Anthrop. 25, 323-324.

Schuman, E. L. & Brace, C. L. 1954 Metric and morphologic variations in the dentition of the Liberian chimpanzee; comparisons with anthropoid and human dentitions. Hum. Biol. 26, 239-268.

Simons, E. L. 1964 The early relatives of man. Sci. Am. 211, 51-62.

Skaryd, S. M. 1971 Trends in the evolution of the pongid dentition. Am. J. Phys. Anthrop. 35, 223-239.

Welsch, U. 1967 Die Altersveränderungen des Dauergebisses der Primaten. Gegenb. Morph. Jb. 110, 1-188.

TABLE 1.

Frequency (%) of lower molar groove patterns in *Pan paniscus*

	Sex	N	Y-4	Y-5	+-4	+-5	?-4	?-5
M_3	M	17	11.8	64.7			5.9	17.6
	F	14		85.7				14.3
	Unk.	1		100.0				
M_2	M	24		95.8				4.2
	F	29		100.0				
	Unk.	7		85.7			14.3	
M_1	M	37		100.0				
	F	47		100.0				
	Unk.	19		100.0				
dm_2	M	22		100.0				
	F	22		100.0				
	Unk.	14		100.0				
Combined Sexes								
M_3		32	6.2	75.0			3.1	15.7
M_2		60		96.6			1.7	1.7
M_1		103		100.0				
dm_2		58		100.0				

TABLE 2.

Frequency (%) of lower molar groove patterns in *Pan troglodytes schweinfurthi*

	Sex	N	Y-4	Y-5	+-4	+-5	?-4	?-5
M_3	M	23		87.0		13.0		
	F	32		75.0	6.3	18.7		
	Unk.	7						
M_2	M	29		100.0				
	F	35		100.0				
	Unk.	17		100.0				
M_1	M	36		100.0				
	F	52		100.0				
	Unk.	36		100.0				
dm_2	M	10		100.0				
	F	20		100.0				
	Unk.	39		100.0				
Combined sexes								
M_3		62		82.3	3.2	14.5		
M_2		81		100.0				
M_1		124		100.0				
dm_2		69		100.0				

TABLE 3.

Frequency (%) of lower molar groove patterns in *Pan troglodytes verus*

	Sex	N	Y-4	Y-5	+-4	+-5	?-4	?-5
M_3	M	47	2.1	48.9	12.8	27.8	4.2	4.2
	F	48	6.3	60.4	10.4	20.8		2.1
	Unk.	2		50.0		50.0		
M_2	M	46		93.5		6.5		
	F	50	2.0	98.0				
	Unk.	2		100.0				
M_1	M	47		100.0				
	F	43		100.0				
	Unk.	5		100.0				
			Combined sexes					
M_3		97	4.1	54.7	11.3	24.7	2.1	3.1
M_2		98	1.0	95.9		3.1		
M_3		95		100.0				

TABLE 4.

Frequency (%) of lower molar groove patterns in *Pan troglodytes troglodytes*

	Sex	N	Y-4	Y-5	+-4	+-5	?-4	?-5
M_3	M	45	31.1	53.3	2.2	4.5		8.9
	F	81	6.2	80.3	3.7	4.9		
	Unk.	3		100.0				
M_2	M	62	1.6	95.2				3.2
	F	106		100.0				
	Unk.	7		100.0				
M_1	M	79		96.2				3.8
	F	119		98.3				1.7
	Unk.	13		100.0				
dm_2	M	32		100.0				
	F	32		100.0				
	Unk.							
			Combined sexes					
M_3		129	14.7	71.3	3.1	4.7		6.2
M_2		175	0.6	98.3				1.1
M_1		211		97.6				2.4
dm_2		64		100.0				

The histogenetic specificity of embryonic cartilage

CLARKE L. JOHNSON

OSSA

Embryonic avian cartilage fragments from Meckel's cartilage, nasal, scleral, quadrate, limb and sternum were dissected and apposed in organ culture in various permutations. Combinations of cartilage fragments and dissociated aggregated chondrocytes were made. Co-aggregations of dissociated aggregated chondrocytes were also made. All were studied histologically.

Differential fusion was noted between the cartilages in different combinations. For all permutations, fusion declined with increasing explant age. Fragments of cartilage combined with itself revealed the best fusion. Cartilage fragments sharing a common origin from neural crest or from mesoderm revealed an intermediate degree of fusion. Pairs of cartilage where one is neural crest, the other mesoderm revealed the least fusion.

The differential fusions of cartilage in vitro reveal the existence of embryonic cartilage subphenotypes, which express their developmental peculiarities in culture.

Эмбриональные птичьи хрящевые фрагменты меккелева хряща, носа, склеры, квадратной кости, конечностей и грудины были расчленены и приложены друг к другу в культуре органа в различных комбинациях. Применяли комбинации фрагментов хряща и диссоциированных агрегатных хондроцитов. Проводили также совместную агрегацию диссоциированных агрегатных хондроцитов. Все комбинации изучали гистологически.

Отмечено дифференцированное слияние хрящей в различных комбинациях. У всех комбинаций слияние снижалось по мере увеличения возраста эксплантата. Объединение фрагментов хряща друг с другом продемонстрировало наилучшее слияние. Фрагменты хряща, имевшие общее происхождение из нервного гребня /neural crest/ или из мезодермы, демонстрировали промежуточную степень слияния. Пары хрящей различного происхождения обнаруживали наименьшую степень слияния.

Дифференциальное слияние хрящей in vitro показывает наличие эмбриональных хрящевых субфенотипов, отражающих особенности развития в культуре.

Ключевые слова: эмбриональный хрящ, гистогенетическая специфичность.

Clarke L. Johnson, 970 East Court Street, Kankakee, Illinois, 60901 U.S.A.

Vol. 6, pp. 139-150, Lund. ISSN 0345-8865.

Introduction

Cartilage, the predominant skeletal material of all vertebrate embryos, is widespread in the animal kingdom and evidence of it is present in the fossil record. It is a tissue amenable to study in the laboratory and is an important element in the growth of the vertebrate embryo. Further, the individual histogenetic differences among embryonic cartilage as discussed here suggest the early acquisition of specific biochemical characteristics. From a developmental standpoint, these differences relate to the origin, functional development, and fate of these cartilages. From an evolutionary, these difffferences relate directly to the unique morphological features acquired by these tissues through evolution. The cell and tissue affinities presented here are also directed to basic problems of orofacial development, in addition to their more general impact for studies of growth and development.

In studies of postnatal growth, the concept of functional matrices (Moss and Salentijn, '69) has opened new avenues in anatomical investigations of postnatal development and growth. In this conceptual approach, skeletal units are no longer viewed as the discrete bones of classical osteology, but rather as the micro- or macro-components of functional cranial units. Skeletal morphology is seen not as the product of "bone cell" encoding, but rather as a net result of the influences of investing soft tissues comprising a functional system -- the functional matrix.

Whereas in the postnatal period the head and neck may be understood in terms of a series of related functional matrices, in the embryonic period orofacial growth can best be seen as a set of developmental cellular systems derived from interacting cell populations, each with its own developmental history. Thus, the study of embryonic systems in developmental biology has a logical relationship to the post-natal functional matrix concepts as a study of systems in development after birth.

In the embryonic period, growth processes have been shown to stem from the progressive acquisition and expression of cell characteristics that are sequentially exhibited during cellular differentiation. Growth and change can be understood in terms of programmed cell division, inductive interactions, cellular migrations, cell aggregations, and cytodifferentiation. These cellular events play a central role in the dynamics of orofacial growth and development, in which the cranial neural crest is dominant.

Von Bauer's classic germ layer theory of the derivation of distinct classes of tissues from three primary germ layers has led to the acceptance of the view that the skeletal and connective tissues are mesenchymal derivatives. Accumulating evidence (Hörstadius, '50); Weston, '70), however, indicates that certain mesenchymal cells and tissues of the head, including odontoblasts, osteocytes, certain dermal bones of the skull and cartilages of the visceral and cranial skeleton are products not of mesoderm but rather of the cranial neural crest.

Embryonic cartilage, therefore has two distinct embryonic origins: 1) mesoderm for the axial, appendicular, otic, certain of the chondrocranial cartilages, and 2) neural crest for much of the nasal capsule, scleral cartilage, gill bar, Meckel's cartilage, and much of the remaining branchial skeleton (except the second basibranchial cartilage). The various embryonic cartilages differ in their origin, course of development, and fate.

Selective fusion has been reported for embryonic cartilage (Chiakulas, '57). Young embryonic cartilages tend to appear histologically similar initially, but subsequently develop characteristic phenotypic expressions.

In order to test cell affinities between chondrocytes, Chiakulas ('57) used various combinations of intact fragments of mesodermally-derived femur, humerus, prescapula, and chondrocranium as well as neural crest-derived gill bar and Meckel's cartilage were implanted in physical apposition in the tail fin of larval hosts for 21 days. An examination of all combinations revealed selective differential fusion between the cartilages. There was complete fusion between cartilages of similar origin; however, there was poor or no fusion between cartilages of dissimilar origin. Thus, Chiakulas ('57) demonstrated a specificity of cartilage on the basis of embryonic origin.

Selective fusion was used by Chiakulas as a measure of histogenetic affinity, itself a function of biological distance. The underlaying premise was that differential fusion was the counterpart of embryonic cell recognition.

Zwilling ('68) has extended these findings to studies of dissociated and aggregated embryonic chick cells. Histogenetic sorting of embryonic somite and limb cells was observed when these cells were dissociated, homogeneously dispersed, aggregated by centrifugation, and cultured in vitro for only 18-20 hours.

Since the 1957 report by Chiakulas on differential fusion in amphibia, critical new evidence has become available through the use of tritiated thumidine (Johnston, '66; Weston, '70) and chick-Japanese quail combinations in transplant studies (Le Douarin, '73; Le Lievre and Le Douarin, '75; Johnston, '74) which provide elegant and detailed mapping of the contribution of the neural crest to cranial and visceral cartilage in avian embryos.

It is the expressed purpose here to confirm and extend the Chiakulas ('57) study to analyses of the avian embryo. In vitro experiments have been designed to confront four types of embryonic cranial cartilages of neural crest origin (Meckel's, nasal, scleral, and quadrate) and two post-cranial cartilages (limb and sternum) in all possible paired combinations.

Research strategy

The design of this research was directed toward providing additional information about the histogenetic affinities of cartilages in the avian ambryo by culturing four neural crest cartilages (Meckel's, nasal, sclera, quadrate) and two mesodermal cartilages (limb,sternum) as pairs in vitro. There are three major sections in the study.

I. Cartilage Fragments in Apposition

In these studies, intact fragments of pre-cartilage and cartilage were paired in apposition, cultured in vitro, and examined histologically.

Meckel's, nasal, scleral, quadrate, limb, and sternum cartilages were obtained whenever available from chick embryos in daily increments, incubation ages six through thirteen days. The cartilage pairs were cultured for seven days.

Meckel's, nasal, limb, and scleral cartilages were obtained at incubation ages of 6, 7, and 8 days of incubation and cultured in pairs for fourteen days.

Meckel's, nasal, scleral, quadrate, limb, and sternum pre-cartilage and cartilage fragments were respectively paired according to their day of first appearance, and cultured for seven days.

II. Cartilage Fragments and Dissociated Aggregated Chondrocytes in Apposition

Meckel's, nasal, sclera, quadrate, limb, and sternum intact cartilage fragments were confronted with dissociated aggregated chondrocytes in all possible permutations at incubation ages from 6 through 13 days. These were cultured for seven days.

III. Co-Aggregates of Dissociated Aggregated Chondrocytes

Meckel's., scleral, and limb cartilages at 8 days of incubation were enzymatically freed of their matrix, homogenously dispersed in equal numbers, aggregated by centrifugation, and cultured for seven days.

Materials and Methods

Chick cartilage fragments were dissected from White Leghorn embryos, incubated from 5 to 13 days at 37.5°C. Quail cartilage fragments were dissected from Japanese quail, Coturnix. These were incubated at 37.5°C.

For this study, four cranial and two postcranial cartilages were used. Because of differences in the onset of development, not all cartilages were available at all ages. Cartilages were dissected free of investing tissue and later cut with sharp cataract knives into intact fragments.

Explants were maintained in vitro on 3 ml of BGJb medium, 50 units each of pencillin and streptomycin solidified with 0.4% agar placed in organ culture dishes. An atmosphere of 5% CO_2 - 95% air was maintained and the explants incubated at 37° for 7-14 days with media changed every two or three days.

Cartilage or pre-cartilage mesenchyme fragments, approximately 1.0 mm^3, were obtained from chick embryos and combined as pairs in all possible combinations at each stage of incubation in daily increments from 5 through 13 days.

The conclusions drawn from the portion of the investigation testing the confrontation of cartilage fragments in all permutations in vitro for seven days was based on the histological analyses of 728 explant combinations. In the long term organ culture test, 145 explant combinations were examined. A total of 235 pre-cartilage and first appearance cartilage combinations were analyzed.

For dissociation, cartilages were cut into pieces with a cataract knife to approximately 0.5 mm^3 in size. After rinsing three times in calcium- and magnesium-free Tyrode's solution (CMF), the tissues were placed in a conical centrifuge tube containing 1 ml CMF, gassed with 5% CO_2-95% air mixture for 15 seconds, and incubated in stoppered tubes at 37.5° for 90 minutes. Excess CMF was removed, 1 ml of 1.35% trypsin in CMF added, the solution was gassed with 5% CO_2-95% air mixture for 15 seconds, and incubated in stoppered tubes at 37.5° for 60 minutes. Fragments were then carefully rinsed three times with excess CMF and transferred to a culture medium consisting of BGJb medium with 10% horse serum and penicillin and streptomycin at a concentration of 50 units each per ml of medium. The fragments were dispersed into single cells in the culture medium by flushing them briskly for at least 20 seconds in and out of a Pasteur pipette with a fine tip. Residual fragments and fibrous material was removed by filtering the suspension through a Swinney filter with a single thickness of lens paper.

The cell suspensions were centrifuged for one minute at 2,000 rpm; the resulting pellets were incubated at 37°C for one hour to allow the cells to cohere before transferring them from the centrigue tubes to a Maximove slide. Then, the pellets were carefully divided into aliquots. These were carried gently within the meniscus between the tongs of fine surgical forceps to the cartilage fragments placed on solidified nutrient medium and cultured for seven days as outlined previously. For the analyses of these tests, 1226 explant combinations were examined.

Chick and quail chondrocytes were prepared separately as outlined. Following determination of cell concentrations with a hemocytometer, the two suspensions were mixed in such proportions as to provide an equal number of chick and quail cells. This cell suspension was centrifuged at 2,000 rpm for one minute; the resulting pellets were incubated for one hour to allow the cells to cohere. The resulting pellet was transferred to a Maximov slide, carefully divided into $1mm^3$ aliquots, transferred to a solidified nutrient medium, and incubated for seven days.

The conclusions drawn from this portion of the investigation are based on a total of 40 explanted combinations. Harvested explants and pelleted aggregates were fixed in Carnoy's fixative, embedded in paraffin, sectioned at 8 microns, and stained with hematoxylin and eosin for chick tissues or by the Feulgen method for chick-quail cell combinations.

A statistical analytical technique as suggested by Elton and Tickle ('71), and modified by Spiegel ('76), was used to quantify the histogenetic affinities between various chondrocyte combinations in the co-aggregates. The detailed discussion of the specific application has been described elsewhere (Johnson, '76).

Results

Intact fragments of chick embryonic cartilage from four cranial cartilages (Meckel's, nasal, scleral, quadrate) of neural crest origin and two postcranial cartilages (limb, sternum) of mesodermal origin were cultured in vitro for seven days.

Intact fragments of chick embryonic cartilage from three cranial cartilages (Meckel's, nasal, scleral) of neural crest origin and one postcranial cartilage (limb) of mesodermal origin were cultured in vitro for fourteen days.

Intact fragments of chick embryonic cartilage and precartilage mesenchyme from four cranial cartilages (Meckel's, nasal, scleral, quadrate) of neural crest origin and two postcranial cartilages (limb,sternum) of mesodermal origin were cultured in vitro for seven days.

Harvested explants were fixed, sectioned, stained with hematoxylin and eosin (parts I and II) or Feulgen reagent (part III). For part III, the α factor as a measure of cell sorting (Elton and Tickle, '71) was calculated.

The degree of fusion, a parameter of cell homology and histogenetic affinity was rated as complete, incomplete, or no fusion. Complete fusion was a clear and unmistakable continuity of matrix and cellular pattern with no distinct line of demarcation. Where there was an integration into a common tissue fabric, but a line of demarcation remains between the fragments, the fusion was rated as incomplete. If the two cartilage fragments displayed little or no histological continuity and revealed a distinct boundary or even a cleft between them, the histological pattern was described as healing with no fusion.

On the basis of embryological origin, the cartilage combinations fall into three groups: 1) isotypic pairs; i. e., two cartilage fragments of identical phenotype; 2) homologous pairs; i. e., neural crest cartilage apposed with another type of mesodermal cartilage; 3) heterotypic pairs; i. e., neural crest cartilage apposed with a mesodermal cartilage.

All isotypic combinations of cartilage fragments cultured for seven days exhibited complete fusion at the earliest stages and diminished healing as the explant age increased. All four cartilage phenotypes cultured long-term for 14 days displayed complete fusion at the earliest ages. The six pre-cartilage phenotypes all exhibited complete fusion after 7 days, a result conistent with the other two tests.

All homotypic combinations of cartilage fragments cultured for seven days exhibited no fusion by the 13th day of explantation. As a group, the homotypic combinations show less fusion tendency than did the comparable isotypic pairs (Table 1). Three homotypic pairs of cartilage fragments derived from neural crest were cultured long term for 14 days: only one revealed complete fusion at the earliest stages of development. Viewed overall, these combinations exhibited less fusion than the comparable isotypic group (Table 1).

Four of the seven homotypic pairs of pre-cartilage mesenchyme revealed complete fusion; the remaining revealed incomplete fusion (Table 1). This group exhibited less capacity for fusion than the comparable isotypic group.

Only two of the eight heterotypic combinations of cartilage combinations for seven days revealed good fusion at the earliest explant age. The heterotypic combinations reveal less fusion than the homotypic group and much less than the isotypic group of cartilage pairs. Viewed as a group, the isotypic group showed the best propensity for fusion, the homotypic group an intermediate tendency, and the heterotypic group the least capacity for fusion when cultured for fourteen days. The pre-cartilage mesenchyme pairs revealed a similar pattern.

These studies in perspective revealed that isotypic pairings achieved the most fusion, homotypic pairings an intermediate degree of fusion and heterotypic pairings the least degree of fusion. There was declining fusion with advancing explant age. Extended time in culture led to a breakdown of the zone of healing. The characteristics of the individual cartilages were reflected in their growth and fusion characteristics in vivo.

For this series of tests, using intact cartilages and dissociated aggregated chondrocytes, cartilages of neural crest origin (Meckel's, nasal, scleral, quadrate) and two postcranial embryonic chick cartilages were obtained at incubation ages 6 through 13 days. Cartilage cells were dissociated, aggregated by centrifugation, and placed in apposition with an intact cartilage fragment.

These were cultured for seven days, harvested and prepared for histological examination. In cases where complete fusion between intact cartilage and dissociated cells were obtained, there was usually some reconstruction of the characteristic cartilage tissue fabric by the dissociated cells. This occurred usually, though not invariably, at the younger ages. The ability of dissociated cells to reconstruct cartilage was a general finding in this study; however, the ability to reconstruct the histotypic structre of the derivative cartilage was more limited.

At the earliest ages, all of the isotypic combinations exhibited complete fusion except for nasal cartilage which alone was the only incomplete fusion. Fourteen permutations were possible in homotypic combinations of cartilage fragments and dissoicated cells. Twelve of the pairs revealed incomplete fusion at the youngest explant age, while only two revealed complete fusion. None of the 16 possible permutations of heterotypic pairings of cartilage fragments and dissociated cells revealed complete fusion. These findings reveal the decline of the ability for fusion with increasing explant age. Further, the general trends noted in the earlier tests are replicated here: isotypic combinations show the most fusion, homotypic combinations show an intermediate degree of fusion, and heterotypic ones show the least degree of fusion.

For the co-aggregates of dissociated chondrocytes, embryonic chick 8 day cartilages and embryonic quail cartilage tissues of equivalent developmental age were dissociated, comingled in equal numbers, pelleted by centrifugation, and then cultured as a pellet on agar for seven days in vitro. Centrifugation permitted retrieval of all of the cells in the suspension. The cells of the two species were distinguished by use of the Feulgen reaction. The quail nucleus by this method shows large heterochromatic masses, whereas in the chick nucleus the DNA is uniformly distributed in the nucleoplasm. Thus, the quail cells serve as markers for the study of the degree of dispersion or segregation of the two cell types.

Initial inspection of the histologic sections did not reveal a readily apparent pattern of homogeneous dispersion or segregation of the cells within the aggregates. Therefore, a quantitative measure, α, of the degree of segregation of the two cell types, as suggested by Elton and Tickle (' 71) and modified by Spiegel (' 76) was used. Eight co-aggregation combinations were analyzed and the results are summarized in Table 1. The results suggest that the isotypic co-aggregate cell populations remain randomly dispersed. The mean of three experiments reveals a cross ratio that is somewhat intermediate between that observed for isotypic co-aggregates and heterotypic co-aggregates.The heterotypic combinations of dissociated cartilage cell populations show that the mean cross ratios of the tests of these combinations reveal a significantly lower value for cross ratios than those seen in the isotypic or homotypic combinations. This would tend to suggest that cell sorting has occurred.

Discussion

The objective of the experiments reported here was to examine the histogenetic specificity of a variety of embryonic cartilages and to relatethe results to the larger problems of growth and development. The present study used as its starting point the observation by Chiakulas (' 57) that the various cartilage tissues that developed in different regions of amphibian larva were not all alike, and expressed their identities by their ability or failure to fuse when apposed in selected pairs based on their embryological origin from neural crest or from mesoderm.

Organized cartilage and pre-cartilage fragments placed in apposition for seven or fourteen days in vitro revealed that the best degree of fusion resulted from isotypic pairings; an intermediate degree of fusion resulted when cartilages were paired homotypically, and the least degree of fusion occurred in heterotypic pairs. These results suggest that differential fusion of embryonic cartilages is based on recognition of finely regulated tissue-specific cues. They confirm the findings of Chiakulas' study (' 57) and extend it in several critical ways. The Chiakulas' study treated isotypic and homotypic pairings as a single group, the heterotypic pairings as a second group, then compared the fusions between these two groups. In the study reported here, the poorest fusions were seen in heterotypic pairings of cartilages derived from neural crest and mesodermal origins (e.g., Meckel's and limb cartilages), confirming the Chiakulas observations that cartilage subphenotypes of widely different ontogenetic derivation exhibited significant differences in histogenetic behavior. However, in this present study, an essential difference between isotypic and homotypic pairings was also noted. When homotypic pairs of cartilage subphenotypes, both of neural crest origin, were apposed (e.g., Meckel's and scleral cartilages), they were less able to fuse than corresponding isotypic pairs (e.g., Meckel's-Meckel's, or scleral-scleral). The same was true for homotypic pairs of cartilage subphenotypes both of mesodermal origin (limb and sternum cartilage pairs).

These results suggest that the tissue specificity of cartilage is based not only on its derivation, but on some other unique characteristic possessed by each of the individual cartilages studied.

The present study also examined the fusion between cartilages removed from the embryo and explanted at various stages of development. It was a consistent finding that the potential for fusion declined with increasing age of the tissue at the time of explantation. This may reflect increasing matrix rigidity, fewer perichondrial cells at the older ages, and loss of cellular pleuripotency at later developmental stages. Tissue fusion involves cell release, migration, mitosis, differentiation, and tissue integration. These events, in essence, mirror normal processes in embryonic growth and development. What are the environmental cues to the cells for cell release? What directs cell migration? How is localized mitosis governed? What elicits cell differentiation? How do the cells communicate (as they must) to achieve functional integration in tissue formation? These intriguing questions provoked by many studies in developmental biology await answer.

After fourteen days in culture, the results showed that there was no improvement in fusion compared with the seven-day studies; in both cases, the best fusion occurred between isotypic pairs, less complete fusion resulted between homotypic pairs, and the least fusion was found between heterotypic pairs. Thus, differential fusion was not an artifact of insufficient time in culture, rather it was a consequence of cellular origin and a reflection of in vivo development and fate as noted earlier. It is likely that where healing was less after fourteen days than at seven, that regression of the repair zone had occurred.

The series of pre-cartilage - cartilage tests sought to determine whether the pre-cartilage blastemata also would produce differential fusion. As a group, all of the isotypic pairs yielded complete fusion, whereas the heterotypic pairs yielded either incomplete or no fusion. Homotypic pairs produced either incomplete or complete fusion. The differential fusion results seen here corroborate the results of the earlier apposition studies of differentiated cartilage tissues. This is interpreted to demonstrate the existence of distinct embryonic cartilage subphenotypes, which reflect the derivation, developmental program and fate of each individual cartilage.

One of the basic questions to be raised in this regard is the role that the chondrocytes and the matrix each play in the recognition of subphenotypes leading to differential fusion.

When dissociated aggregated chondrocytes were confronted with intact fragments earlier results were corroborated; however, the degree of fusion was dimished, not enhanced. The younger the age of the dissociated cartilage, the more successful were the aggregated cells in reconstructing cartilage with a recognizable histotypic pattern. Although most of the dissociated cells of the various cartilages were able to reconstitute cartilage, the cells revealed a variable capacity to produce cartilage with a histotypic pattern that resembled the donor tissue. Limb cells were very competent in organizing into tissue, the other cartilages were less competent.

These tests demonstrated the differential fusion of intact cartilages paired with dissociated chondrocytes and the results were consistent with the findings of the previous apposition studies using intact cartilage pairs. These results again suggest that, the greater the biological distance between the cartilage subphenotypes, the less the fusion seen in vitro.

To test whether cartilage cells would exhibit discriminatory properties when allowed to interact in the absence of matrix and organized tissue structure, co-aggregation studies were performed using dissociated cells of different phenotypes in isotypic, homotypic, and heterotypic combinations. This test of cell-cell affinities complements the rationale of confronting pairs of intact tissues, or pairing intact tissue with dissociated cells.

In these tests done with 8-day chick and quail of equivalent staging, the precise identification of each cell type was facilitated by the prominent quail nucleus displayed by Feulgen staining. This then permitted a statistical evaluation of cell interactions as suggested by Elton and Tickle ('71).

The average cross ratios shown in Table 1 reveal a general trend of more cell sorting in the heterotypic co-aggregates than in the isotypic or homotypic combinations. It should be noted, however, that the individual cross ratios of each group in some cases overlap other groups and are not mutually exclusive. The comparison of mean cross ratios between each experimental group showed that they were notably different. The isotypic cross-ratios which should approximate 1.0 with a homogenous dispersion of the cells come close to doing so; however, the heterotypic cross ratios are not considerably different from the isotypic group, although they do trend toward cell segregation.

It would appear that several biological phenomena must be considered in the interpretation of the co-aggregation tests of cartilage subphenotypes. First, we are dealing with a cell population that produces matrix; the cells are in contact only briefly before forming matrix. Second, after matrix forms, cell division results in the formation of many clones within the aggregate. Third, the tests here deal with subphenotypes, and it is possible at this sensitive level of cell interactions that the species differences between chick and quail may contribute to the appearance of limited segregation of cells in the isotypic co-aggregates. Fourth, it may be possible that both cell and matrix are necessary in order for cartilage cells to recognize their subphenotype. In the dissociated state, therefore, in which the extracellular matrix has been removed, the cells may sort out as well as in the presence of matrix. When the matrix is reformed, cells no longer move about freely and cannot re-arrange themselves with respect to one another without more complex remodeling processes. This may explain why the heterologous cross-ratios revealed less cell sorting than might be predicted in comparison with homotypic or isotypic co-aggregates.

The in vitro tests of cell recognition reported here reveal that cartilage cells derived from regionally differentiated skeletal rudiments in the body represent distinct subphenotypes. The histogenetic significance of this recognition is confirmed by the differential fusion seen in the apposition studies of intact cartilage tissues, combinations of intact cartilage tissues, combinations of intact cartilage and dissociated cells, and co-aggregations of dissociated chondrocytes. These conclusions are based on 2374 tests and observations.

Weinmann and Sicher ('55) distinguished between bone as a tissue and bones as organs. It is appropriate here to extend this concept to cartilage. Although all cartilage tissues share certain basic morphological and biochemical characteristics, it has become clear that individual cartilages produced in various regions of the developing organism exhibit special attributes which impart a histogenetic individuality to each. These particular characteristics of individual cartilage subphenotypes and their morphogenetic interactions provide important clues for discovering the developmental mechanisms controlling skeletal growth and differentiation.

Viewed teleologically, each cartilage has a specific developmental role. For example, Meckel's is a temporary strut in mandibular growth. Scleral cartilage molds and protects the developing eyeball. Limb cartilage is a precursor to bone; it is both capable of support and rapid interstitial growth. Since histogenetic specificity has been demonstrated for these cartilages differing in origin and fate, it is important to explain such differences and the extent which they exist in other tissues as well,and how they relate to their functional role in the organism.

In this study, the histological differences between chick and quail cells was exploited as a cell marker technique (Le Dourain, '73). Chick and mouse combinations have been used with equal success (Moscona, '57). Implicit in this technique is an important phenomenon relevant to anthropology: homologous cells in different species share common histogenetic properties.

Homologous cartilages in two different species are more closely identified histogenetically than two different cartilages in the same species. In anthropology, therefore, tissue culture may offer a means of evaluating homologies between tissues. The differences between the cartilages examined in this thesis implies that the underlying cytogenetic and molecular changes are phylogenetically ancient evolutionary events.

The property of embryonic cartilage histogenetic specificty relates to serological studies, themselves exploites as a device for determining the biological differences between species. The fusion experiments reported here reveal the affinities between cartilage tissues and are used as an assessment of the underlying biochemical peculiarities of these subphenotypes. Just as serological differences between species suggest the time and degree of species divergence, the differential fusion between embryonic cartilages reflects the morphological and developmental differences between them.

The contribution of tissue culture studies to dental science and to anthropology are well recognized. The contribution of cartilage tissue culture studies of growth and development are a necessary adjunct to the classic studies of craniofacial growth that are so much a part of the literature of physical anthropology.

Summary and conclusions

1. Embryonic cartilages were combined as pairs in organ culture as apposed explants or pellets of co-aggregated cell suspensions. Based on their derivation, they may be classified as isotypic, homotypic, or heterotypic combinations. Isotypic combinations were paired cartilage tissues of identical origin: Meckel's, nasal, scleral, quadrate, limb, or were represented by paired cartilage tissues both of neural crest origin, or both of mesodermal origin: e.g., Meckel's-scleral; limb-sternum. Heterotypic combinations were represented by paired cartilage tissue of different origin, i.e., neural crest versus mesodermal origin, e.g., Meckel's-limb.

2. Apposition of cartilage and pre-cartilage tissues cultured in vitro resulted in:
   a, the most complete fusion between isotypic pairs;
   b, an intermediate degree of fusion between homotypic pairs;
   c, the least complete fusion between heterotypic pairs;
   d, declining fusion with the age of the tissue at the time of explantation and;
   e, less fusion after fourteen days in culture than at seven days in culture.

3. Combinations of intact cartilage tissue and dissociated chondrocytes cultured in vitro resulted in:
   a, the most complete fusion between isotypic pairs;
   b, an intermediate degree of fusion between homotypic pairs;
   c, the least fusion between heterotypic pairs and;
   d, rapidly declining fusion with the age of the tissue at the time of explantation.

4. Co-aggregation of dissociated chondrocytes cultured in vitro resulted in:
   a, the least cellular sorting in isotypic combinations;
   b, an intermediate degree of cellular sorting in homotypic combinations and;
   c, the most cellular sorting in heterotypic combinations.

5. The histogenetic specificity and recognition of embryonic cartilage subphenotypes was demonstrated.

6. The conclusions reported here are based on 2374 tests and observations.

Acknowledgements

This work was funded at its outset by a fellowship grant from the Walter G. Zoller Memorial Fund; thereafter by a Postdoctoral Fellowship, DE-52897 from NIDR. Gratitude is expressed to Dr. Edward J. Kollar, Dr. Beatrice Garber, Dr. Thomas Graber, and Dr. Russell Tuttle for their encouragement, guidance, and support. I thank Mrs. Linda Satterwhite for her assistance in the typing and preparation of this manuscript.

To Dr. Albert A. Dahlberg, I express special thanks for my opportunity to do research and graduate study at the University of Chicago. Dr. Dahlberg: teacher, scholar, friend.

Literature cited

Chiakulas, J. 1957 The specificity and differential fusion of cartilages derived from mesendoderm and mesectoderm. J. Exp. Zool., 136: 287-300.

Elton, R. and Tickle, C. 1971 The analysis of spatial distributions in mixed cell populations: a statistical method for sorting out. J. Embryol Exp. Morph., 26: 135-156.

Hörstadius, S. 1950 The Neural Crest. Oxford Univ. Press, London.

Johnson, C. 1976 The histogenetic specificity of embryonic cartilage. Doctoral Thesis, The University of Chicago.

Johnston, M. 1966 A radioautographic study of the migration and fate of the cranial neural crest cells in the chick embryo. Anat. Rec., 156: 143-156.

Le Douarin, N. 1973 A biological cell labeling technique and its use in experimental biology. Dev. biol., 30: 217-222.

Le Lievre, C. and N. Douarin 1975 Mesenchymal derivaties of the neural crest: analysis of chimaeric quail and chick embryo. J. Embryol. Exp. Morp., 34: 125-154.

Moscona, A. 1957 The development in vitro of chimaeric aggregates of dissociated embryonic chick and mouse cells. Proc. Nat. Acad. Scie. U.S.A., 43: 184-194.

Moss, M. and L. Salentijn 1969 The primary role of functional matrices in facial growth. Amer. J. Orthodont., 55: 566-577.

Spiegel, J. 1976 Enhancement of cell sorting in brain cell co-aggregates by nerve cell recognition factors. Doctoral Thesis, The University of Chicago.

Weinmann, J., and H. Sicher 1955 Bone and Bones. C.V. Mosby Company, St. Louis.

Weston, J. 1970 The migration and differentiation of neural crest cells, in Advances in Morphogenesis, 8. Abercrombie, M. and J. Brachet, eds. Academic Press, New York, pp. 41-114.

Zwilling, E. 1968 Morphogenetic phases in development. Dev. Biol., 2: 184-207.

TABLE 1

DEGREES OF FUSION AND CO-AGGREGATE CELL SEGREGATION IN CARTILAGE COMBINATION EXPERIMENTS

I. Cartilage and Pre-Cartilage Fragments Cultured in Apposition

A. Intact Cartilage Fragments Apposition Cultured for Seven Days

Fusion	Isotypic	Homotypic	Heterotypic
Complete	41.5%	6.8%	4.4%
Incomplete	43.9%	40.9%	20.0%
None	14.6%	52.3%	75.6%

B. Cartilage Fragments Cultured for Fourteen Days

Fusion	Isotypic	Homotypic	Heterotypic
Complete	63.6%	14.3%	0%
Incomplete	36.4%	57.1%	25.0%
None	0.0%	28.6%	75.0%

C. Pre-Cartilage and Cartilage Fragments Cultured for Seven Days

Fusion	Isotypic	Homotypic	Heterotypic
Complete	100 %	35.7%	0.0%
Incomplete	0.0%	28.6%	37.5%
None	0.0%	35.7%	62.5%

II. Cartilage Fragment and Dissociated Chondrocyte Combinations Cultured for Seven Days

Fusion	Isotypic	Homotypic	Heterotypic
Complete	34.1%	2.3%	0.0%
Incomplete	46.3%	28.4%	15.7%
None	19.5%	69.3%	84.3%

III. Co-Aggregate of Dissociated Aggregate Chondrocytes Cultured _In Vitro_

	Isotypic	Homotypic	Heterotypic
Cross Ratio of Factors as a Measure of Cell Sorting	.561	.505	.384

Quantification of the shovel shape of incisor teeth

PENTTI KIRVESKARI AND LASSI ALVESALO

OSSA

Mesiodistal tooth diameter and depth of the lingual fossa of maxillary incisors are measured in two genetically different populations: Skolt Lapps of northern Finland and Finns of Hailuoto Island. A highly significant correlation is found between the two variables, and also between the relative depth of fossa and the mesiodistal diameter. An analysis of variance after logarithmic transformation reveals highly significant positive allometry of the depth of fossa versus the mesiodistal diameter. The general power function model of allometry explains 19.7% of the total variance in central incisors and 15.2% in lateral incisors.

Keywords: Shovel Shape - Allometry.

Были измерены мезодистальный диаметр зуба и глубина лингвальной впадины верхних резцов у двух генетически различных популяций: лопарей-сколтов из северной Финляндии и финнов с острова Хайлуото. Корреляция с высоким уровнем значимости найдена между двумя переменными, а также между относительной глубиной впадины и мезодистальным диаметром. Анализ вариабильности после логарифмического преобразования обнаруживает высокий уровень значимости положительной аллометрии глубины впадины по сравнению с мезодистальным диаметром. Аллометрическая модель, построенная с помощью общей степенной функции, объясняет 19.7% общей вариабильности у центральных резцов и 15.2% - у латеральных резцов.

Ключевые слова: лопатообразная форма зуба, аллометрия.

Pentti Kirveskari, *Lassi Alvesalo*, *Institute of Dentistry, University of Turku, SF-20520 Turku 52, Finland.*

Vol. 6, pp. 151-156, Lund. ISSN 0345-8865.

A large number of studies on populations of known racial background suggest that the shovel shape of anterior teeth is a reliable racial marker trait. Theoretical support to its use comes from genetic studies (Portin and Alvesalo, '74; Blanco and Chakraborty, '76) that indicate a large genetic component of variation.

The desirability of quantification of the shovel trait was pointed out by Dahlberg and Mikkelsen ('47) who also introduced a method of measuring the depth of the lingual fossa. Later on, Dahlberg et al. ('56) reported that the depth of the lingual fossa is not a simple function of the shovel shape but other morphologic features are associated. Specifically, the mesiodistal tooth diameter was correlated with the depth of the fossa. Similar conclusions have been presented by Suzuki and Sakai ('66), and Lombardi ('75). The shovel shape was visually scored in these studies, and the statistical evidence was not conclusive in the latter one.

The depth of the fossa and the subjective shovel shape score are correlated, but the inter-observer error in the subjective scoring is considerable (Turner and Hanihara, '77). The error of method is less serious in the depth measurements (Rothhammer et al., '68). Measuring the depth of the fossa has replaced subjective scoring in most publications. The indications of an association between tooth size and degree of shoveling give reason to study it further, because such an association - if it exists - has at least theoretical importance in the use of the shovel trait in anthropologic and genetic studies.

Material and method

We examined two genetically different populations in Finland in 1966-1970. Finns are represented by the population of Hailuoto, an island off the west coast of the mainland in the Gulf of Bothnia of the Baltic Sea. The total population was 1265 in 1966, and of these 730 volunteered to undergo the examination. A detailed description of the population and field studies is given by Alvesalo (' 71). Lapps are represented by Skolt Lapps, one of the Lapp tribes in northern Scandinavia and the Kola Peninsula. They are a relatively pure stationary genetic isolate with considerable inbreeding. Their number in Finland totalled 515 in 1967 and over 90% of these could be examined. For further details see Lewin (' 71).

The measurements were made from dental stone casts prepared in the field. Only casts that showed at least one measurable maxillary incisor were included. Great care was taken to exclude all teeth in which wear or fillings could have altered the original dimensions. Teeth of the right side were measured and those on the left side were used only as a substitution for missing or unmeasurable teeth. The great majority of measurable teeth were from children aged between 7-15 years.

Mesiodistal tooth diameter was measured with a sliding caliper following the method defined by Moorrees (' 57:78-80). The readings were rounded off to the nearest tenth of a millimeter. The greatest depth of the lingual fossa was measured at right angles to the lingual surface using modified dial gauges with fixed lateral shoulders and a moving central measuring rod (see Kirveskari, ' 74). Malalignment of teeth sometimes prevented the measuring. The readings were rounded off to the nearest twentieth of a millimeter. All measurements were made by the same worker.

A relative depth of lingual fossa (depth/M-D diameter x 100) was computed for the statistical analysis. Using that, the mesiodistal diameter and the depth of the fossa in both incisors, a correlation matrix was then computed.

Results

The mesiodistal diameters were almost the same in both samples, and very close to the values reported earlier of the whole populations (Alvesalo, ' 71; Kirveskari et al., ' 78). In Skolt Lapp boys, I^1 measured 8.86 mm and I^2 6.92 mm, in girls I^1 8.60 mm and I^2 6.69 mm. In Finnish boys I^1 was 8.90 mm and I^2 6.93 mm, and in girls I^1 8.64 mm and I^2 6.72 mm.

The depth of the lingual fossa (table 1) of the central incisor was greater in the Finns of Hailuoto than in Skolt Lapps ($t = 2.46$, 407 df, $0.02 > p > 0.01$). Comparisons of measurements for the lateral maxillary incisors revealed no statistically significant differences between the populations; the same was true for sex comparisons of both incisors.

The relative depth of the lingual fossa (table 2) of the central incisor was significantly ($t = 2.53$, 406 df, $0.02 > p > 0.01$) greater in Finns of Hailuoto than in Skolt Lapps. The difference was not significant in the lateral incisor. Females showed but slightly more shoveling than males excepting the lateral incisor in Hailuoto Finns which was significantly ($t = 2.16$, 219 df, $0.05 > p > 0.025$) more shoveled in males.

A comparison of the correlation matrices of the two populations showed that none of the correlation coefficients in one population differed significantly from its counterpart in the other population. The correlation coefficients computed separately for the sexes differed even less. We therefore decided to pool the materials, and computed a correlation matrix for the combined population (table 3).

All of the variables showed a positive and significant correlation. Because the positive correlation between the relative depth of fossa and the mesiodistal diameter suggests allometry we made a logarithmic transformation of the general formula of simple allometry:

$$y = bx^{\alpha}.$$

We computed the value of the exponent, and made an analysis of variance to test its significance. The regression equation explained 19.7% of the total variance ($F = 99.535$, $df_1 = 1$, $df_2 = 407$, $p < 0.001$) in the central incisor, and 15.2% ($F = 64.264$, $df_1 = 1$, $df_2 = 360$, $p < 0.001$) in the lateral incisor. The regression coefficient (the value of alpha in the power function) was 3.73 for the central incisor, and 2.81 for the lateral incisor, both of which are highly significantly different from 1.00, indicating positive allometry.

Discussion

The occurrence of shovel shaped incisors has been studied previously both in Finns and in Skolt Lapps (Koski and Hautala, '52; Zubov, '72; Kirveskari, '74; Portin and Alvesalo, '74). Although the results are not fully comparable they suggest that shovel shape in both populations is somewhat more common than generally found in Caucasoid populations. The present results indicate that Finns apparently have slightly but significantly more shoveled central incisors than Skolt Lapps.

The variability of the fossa depth is larger in the lateral incisor than in the central one. The same pertains to the relative depth, which in itself seems somewhat larger in the central than in the lateral incisor. Furthermore, the allometric association is weaker in the lateral incisor. These results agree with Dahlberg's ('45) interpretation of the field concept. Skolt Lapps show higher variability than Finns. It is tempting to interpret this as the result of harder environmental stress and perhaps of the higher inbreeding in Skolt Lapps. To be sure, the socio-economic conditions are poorer among Skolt Lapps.

Allometry in mammalian dentitions is the rule rather than the exception, as was recognized long ago by palaeontologists (Kurtén, '54). The apparent lack of direct selection pressure on the dentition of modern man probably explains why dental anthropologists have not interested themselves greatly in allometry. Yet, lateral ridges do make an incisor biomechanically stronger. The natural explanation of positive allometry of the fossa depth versus mesiodistal tooth diameter would thus be the need to alter form when the tooth becomes larger, if the strength is to be maintained. An isometric increase would mean biomechanic weakening (cf. Gould, '66).

However, allometric trends are also subject to evolutionary alterations (Gould, '66). Such alterations must be kept in mind when the depth of fossa in different populations of modern man is being considered. For instance, Australian Aborigines who possess the largest modern human teeth, do not express a particularly deep lingual fossa (Hanihara, '77).

Because of the positive allometry of the fossa depth versus mesiodistal tooth diameter, the quantification of shovel shape by simply using the depth measurement is not theoretically sufficient. However, overlooking the effects of allometry does not necessarily lead to serious errors in population comparisons, because tooth sizes seldom differ very much. After proper adjustment, Mongoloid populations still express the strongest degree of shovel shape. But when, for instance, population distances or trait heritabilities are calculated, the failure of observing the allometry may considerably distort the picture. A simple way of eliminating much of the error is to use the relative depth of the fossa.

Literature cited

Alvesalo, L. 1971 The influence of sex-chromosome genes on tooth size in man. Suom. Hammaslääk. Toim., 67:1-54.

Blanco, R. and R. Chakraborty 1976 The genetics of shovel shape in maxillary incisors in man. Am. J. Phys. Anthrop., 44: 233-236.

Dahlberg, A.A. 1945 The changing dentition of man. J. Am. Dent. Ass., 32:676-690.

Dahlberg, A.A., P.J. Epling and J.A. Brown 1956 Analysis of the shovel-shaped incisor trait. Am. J. Phys. Anthrop., 14: 386.

Dahlberg, A.A. and O. Mikkelsen 1947 The shovel-shaped character in the teeth of Pima Indians. Am. J. Phys. Anthrop., 5: 234-235, n.s.

Gould, S.J. 1966 Allometry and size in ontogeny and phylogeny. Biol. Rev., 41: 587-640.

Hanihara, K. 1977 Dentition of the Ainu and the Australian Aborigines. In: World Anthropology, Orofacial Growth and Development. A.A. Dahlberg and T.M. Graber, eds. Mouton Publishers, The Hague, pp. 193-200.

Kirveskari, P. 1974 Morphological traits in the permanent dentition of living Skolt Lapps. Proc. Finn. Dent. Soc., 70: Suppl. II, 90 pp.

Kirveskari, P., H. Hansson, B. Hedegård and U. Karlsson 1978 Crown size and hypodontia in the permanent dentition of modern Skolt Lapps. Am. J. Phys. Anthrop., 48: 107-112.

Koski, K. and E. Hautala 1952 On the frequency of shovel-shaped incisors in the Finns. Am. J. Phys. Anthrop., 10: 127-132.

Kurtén, B. 1954 Observations on allometry in mammalian dentitions; its interpretation and evolutionary significance. Acta zool. fenn., 85: 1-13.

Lewin, T. 1971 Introduction to the biological characteristics of the Skolt Lapps. Suom. Hammaslääk. Toim., 67: Suppl. I, 104 pp.

Lombardi, A.V. 1975 Tooth size associations of three morphologic dental traits in a Melanesian population. J. Dent. Res., 54: 239-243.

Moorrees, C.F.A. 1957 The Aleut Dentition. Harvard University Press, Cambridge, Massachusetts.

Portin, P. and L. Alvesalo, 1974 The inheritance of shovel-shape in maxillary central incisors. Am. J. Phys. Anthrop., 41: 59-62.

Rothhammer, F., E. Lasserre, R. Blanco, E. Covarrubias and M. Dixon 1968 Microevolution in human Chilean populations IV. Shovel shape, mesial-palatal version and other dental traits in Pewenche Indians. Z. Morph. Anthrop., 60: 162-169.

Suzuki, M. and T. Sakai 1966 Morphological analysis of the shovel-shaped teeth. Zinruigaku Zassi, 74: 202-218.

Turner II, C.C. and K. Hanihara 1977 Additional features of Ainu dentition V. Peopling of the Pacific. Am. J. Phys. Anthrop., 46: 13-24.

Zubov, A.A. 1972 Einige Angaben der dentalen Anthropologie über die Bevölkerung Finnlands. Ann. Acad. Sci. fenn. A5, No. 150.

TABLE 1.

Depth (in mm) of lingual fossa of maxillary incisors in Skolt Lapps and Finns of Hailuoto Island.

		Central incisor			Lateral incisor		
		N	mean	S.D.	N	mean	S.D.
Skolt Lapps	♂	91	0.52	0.25	80	0.38	0.24
	♀	82	0.57	0.28	73	0.40	0.25
	♂+♀	173	0.54	0.27	153	0.39	0.24
Finns of Hailuoto	♂	112	0.61	0.25	120	0.43	0.21
	♀	124	0.60	0.27	102	0.36	0.19
	♂+♀	236	0.61	0.26	222	0.40	0.21

TABLE 2.

Relative depth of lingual fossa (depth/M-D diameter x 100) of maxillary incisors in Skolt Lapps and Finns of Hailuoto Island

		Central incisor			Lateral incisor		
		N	mean	S.D.	N	mean	S.D.
Skolt Lapps	♂	91	5.76	2.70	80	5.37	3.22
	♀	82	6.56	3.04	73	5.92	3.57
	♂+♀	173	6.14	2.89	153	5.63	3.39
Finns of Hailuoto	♂	112	6.83	2.59	119	6.10	2.84
	♀	124	6.88	2.94	102	5.28	2.75
	♂+♀	236	6.86	2.77	221	5.72	2.82

TABLE 3.

Correlation matrix computed for the combined Skolt Lapp and Hailuoto Finn population. Only cases in which both incisors could be measured are included (N = 283).

	I^1 depth of fossa	I^2 depth of fossa	I^1 M-D diameter	I^2 M-D diameter	I^1 relative depth of shovel	I^2 relative depth of shovel
I^1 depth of fossa	1.000					
I^2 depth of fossa	.573	1.000				
I^1 M-D diameter	.430	.295	1.000			
I^2 M-D diameter	.385	.432	.605	1.000		
I^1 relative depth of fossa	.987	.559	.294	.310	1.000	
I^2 relative depth of fossa	.530	.983	.195	.279	.532	1.000

Observations on the trigonid of the last lower deciduous molar (m_2) of man and some higher primates

G. H. R. VON KOENIGSWALD

OSSA

The lower molar consists of an anterior portion termed the trigonid. In its primitive condition the trigonid is composed of three cusps and in higher primates the paraconid is normally absent. Remane ('60), however, reports an occurrence of this cusp in 90% of gorilla deciduous dentitions. It is also seen in the deciduous teeth of Sinanthropus and Meganthropus.

Observations of the trigonid, including the occurrence of a paraconid on m_2's in fossil and extant hominoids has led to an interpretation of the trigonid cresting pattern different from that of Remane ('21).

Передняя часть нижнего большого коренного зуба называется тригонидом. В его примитивном виде тригонид состоит из трех конусов, причем у высших приматов параконид обычно отсутствует. Remane /'60/, однако, сообщает, что этот конус встречается у 90% молочных зубов гориллы. Он был также обнаружен у молочных зубов синантропуса и мегантропуса.

Изучение тригонида, включавшее обследование распространенности параконида на m_2 у ископаемых и современных гоминидов, вело к отличающейся от Remane /'21/ интерпретации модели расположения гребней на тригониде.

Ключевые слова: сравнение человек - высшие приматы, тригонид нижнего молочного большого коренного зуба /m_2/.

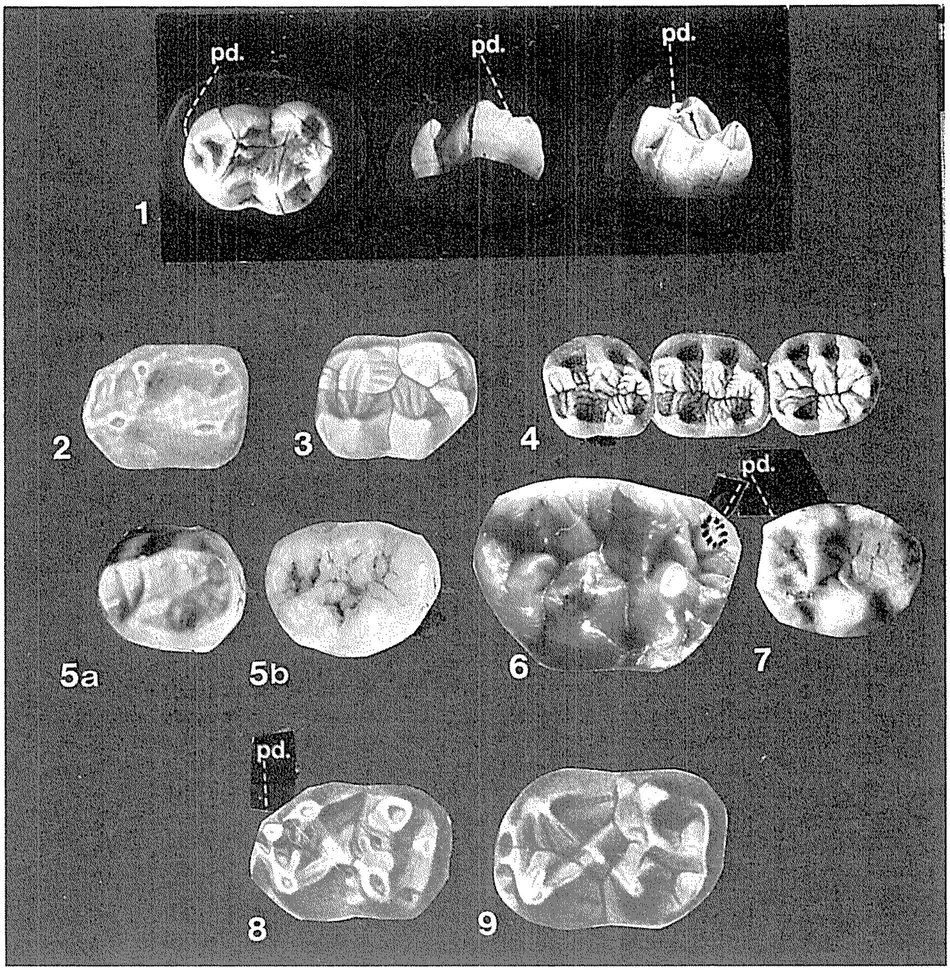
G. H. R. von Koenigswald, Natur-Museum Senckenberg, Forschungsinstitut Senckenberg, 6 Frankfurt - M 1, Senckenberganlage 25, W.Germany.

Vol. 6, pp. 157-162, Lund. ISSN 0345-8865.

The lower molar consists of two parts, the trigonid part in front and the talonid part behind. On the trigonid part of the lower molars of *Tarsius* and many modern and fossil lemurids, the original pattern of three cusps can be distinguished: the protoconid on the lingual and the metaconid on the buccal side, both connected by a crest, and in front of the metaconid connected by its own crest to the protoconid, the paraconid. In the course of evolution in the higher primates the paraconid has vanished (except in very rare cases), and the metaconid has been shifted towards the anterior border.

The presence of a paraconid in modern apes and in man is a question of considerable interest. As the reduction begins at the third molar, the first and still more commonly, the last deciduous molar may retain most of the original structure. Adloff ('08) was the first to observe a paraconid in the last milk molar of a gorilla. This has been challenged by Weidenreich "I am not convinced about the correctness of such a conclusion" ('37:86). Jørgensen, reviewing Remane's and Weidenreich's papers, is also not convinced and remarks, "that the statement about the presence of a paraconid of m_2-inf. in pongids and hominids should be regarded with considerable skepticism" ('56:45).

We have observed two cases, also in the gorilla, where traces of a paraconid can be found. In one case from our collection, on the last deciduous molar of a gorilla, there is a faint, but clearly developed cusp in front of the protoconid (plate, 1). Its independence is underlined by a crest, connecting the cusp with the top of the metaconid while in front of the cusp is a slight indentation. Protoconid and metaconid are set obliquely, so there is more space in front of the metaconid than in the permanent molars, where both cusps are situated opposite one another. A similar condition is found in a specimen of the Anthropological Institute in Zürich, No. 6612 (Schultz



Plate

1) Last lower deciduous molar of gorilla with paraconid (pd). Length 13.0 mm. Author's collection.
2) The last lower deciduous molar of *Pliopithecus antiquus* from the upper Miocene of Göriach, Austria. Twice actual size. After Hürzeler 1951, fig. 4.
3) First lower permanent molar of gorilla with "the classical three crests". After Selenka.
4) The three lower molars of an orang, the first with the "three classical crests". The second and third molars demonstrate the disintegration. About actual size. After Selenka.
5) Last lower deciduous molar of *Homo sapiens* from Sangiran, sub-recent. a)endocast with three crests, hardly recognizable; b) occlusal surface.
6) Last lower deciduous molar of *Meganthropus*, Lower Pleistocene, Sangiran, Central Java. Length 13,5 mm. Paraconid-area (pd) slightly damaged.
7) *Sinanthropus* last lower deciduous molar, with a paraconid, Specimen No. 139'.
8) First lower permanent molar of *Oreopithecus bambolii* from the Lower Pliocene of Mr. Bamboli, Italy, with large paraconid (pd). Twice actual size. After Hürzeler 1949, fig. 3.
9) Second lower permanent molar of same specimen. The paraconid has been incorporated in the mesial wall, which is partly doubled. idem.

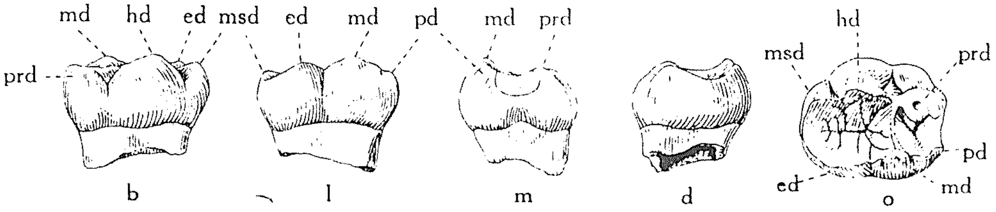


Fig. 1. Last lower deciduous molar of *Sinanthropus* specimen No. 139'. Length 10.9 mm. After Weidenreich 1937, fig. 343.
b-buccal, l-lingual, m-mesial, d-distal, ed-entoconid, hd-hypoconid, md-metaconid, msd-mesoconid, pd-paraconid, prd-protoconid.
A photograph of the cast is shown in plate, 7.

collection). Remane also reports definite occurrences of paraconids in pongid deciduous molars. According to him, this cusp occurs in about 90% of the deciduous teeth of gorilla and he even mentions five cases where it occurs on first permanent molars and even some cases of paraconid traces - "Paraconidreste" - on the first permanent molar of the chimpanzee ('60:699).

In fossil anthropoids, this archaic cusp also seems to be very rare. It is well developed in the first molar of *Oreopithecus* (plate, 8; note paraconid absent in M_2, plate 9) and is also present in one lower first molar of *Dryopithecus fontani* from the Upper Miocene of St. Gaudens, France (Remane, '60, fig. 45). In fossil man we know of two cases of a paraconid in the deciduous teeth. One is of *Sinanthropus* from Chou Kou Tien (Weidenreich, '37, No. 139') seen in our figure 1 (and plate, 7). Here a faint paraconid is situated practically at the mesial edge in front of the metaconid, separated by a small indentation. The large anterior basin is empty and metaconid and protoconid are set obliquely. The connecting crest has its origin at the tip of the metaconid, and is set at a right angle to the length of the tooth. It meets the protoconid not at the tip, but is shifted towards the distal slope of this prominent cusp. In *Meganthropus* from the Lower Pleistocene of Java, the topography is essentially the same, but the paraconid area is larger (this part unfortunately is somewhat damaged) and the basin is filled by a prominent wrinkle originating from the slope of the metaconid (plate, 6). On the mesial edge there are four cusplets, the most lingual must be the paraconid. The condition in that tooth demonstrates clearly that a small elevation sometimes appearing in the middle of the mesial marginal ridge and termed "pseudoparaconid" (Remane, '60, fig. 40e) really is an accessory cusp.

The appearance of the paraconid in hominoids is rare indeed. Its distribution can be matched with another cusp in the upper molar, the protoconulus, which occasionally survives in *Dryopithecus*, in the orang and even in man (Remane, '60, figs. 19 and 20)

A difficult question of much discussion concerns the interpretation of the trigonid crests. Remane describes the here presence of three transverse ridges (fig. 2 and plate, 3). The most mesial one of them is the mesial marginal ridge which forms an arched connection between the protoconid and the metaconid. Distally there are two straight bridges, each of which is formed by two strong wrinkles emerging directly from the tip of the protoconid and the metaconid respectively. Both ridges are interrupted by a fine longitudinal fissure and between them is a deep transversal fissure. "Remane considers the mesial of the straight crests to be the 'anterior trigonid crest', the distal one as the 'posterior trigonid crest' and the fissure between them as the trigonid basin (fovea anterior). I consider the mesial marginal ridge proper to be the anterior trigonid crest, the mesial straight ridge the posterior trigonid crest, the pit between these as the trigonid basin and the distal straight ridge merely as secondary

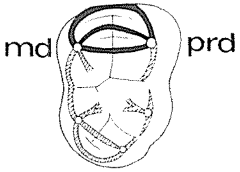


Fig. 2. The "three classical crests" in the trigonid part of the first lower permanent molar of the gorilla. md-metaconid, prd-protoconid. Redrawn after Remane 1921. fig. 15.

inconstant acquisition" (Weidenreich, '37:84). "I am inclined to consider ... the presence of one or two bridges merely as secondary acquisitions in spite of their occupying the region in which the persistance of the distal trigonid crest could be expected" (Weidenreich, '37:87).

That the paraconid is shifted to the lingual-mesial corner of the trigonid has already been mentioned. A classical case can be found in *Necrolemur* (see Hürzeler, '48, fig. 20), and we can accept the same condition for the higher primates. The original connection between paraconid and protoconid now forms the mesial edge of the tooth. This correction has already been made by Remane ('60) and requires no further discussion.

The posterior trigonid crest is the direct connection between protoconid and metaconid. For Weidenreich it is a secondary crest, for Remane it is the posterior trigonid crest ("hintere Trigonidleiste") and, in spite of a number of variations ('60, fig. 40), a remnant of the original trigonid. In Miocene apes, notably in *Proconsul* and *Limnopithecus* from Kenya the crest, uninterrupted or interrupted by a small fissure, connects the tip of the protoconid to the tip of the metaconid (Le Gros Clark & Leakey, '52, figs. 12. 32. 33. 46. 50. 55). In *Propliopithecus* and *Moeripithecus* from the Oligocene of Egypt, the ridge is uninterrupted and prominent (Kälin, '61, fig. 6) and it has been argued by Kälin that this might be the original condition. In the first molar of *Pliopithecus* from the Miocene of France a crest is normal, but in a single case the cusps seem to isolated as in *Parapithecus* (Hürzeler, '54, fig. 25). We regard, beginning with the lemuroid condition, that the posterior trigonid crest, or in view of the whole tooth, the "crista transversa anterior" is the primary element.

The great variation of this crest, the development of secondary crests ("Nebenleisten" of Remane), the dissection by a furrow, the occasional complete reduction by which protoconid and metaconid are isolated, and the bewildering variability of this part urges us to interpret these as various stages of a still incomplete tendency towards reduction of the posterior crest (plate, 4). In front of this crest, as the result of the disappearance of the anterior crest, is the trigonid basin of the original "fovea anterior". If we begin with Oligocene and Lower Miocene forms already mentioned, this basin is smooth and empty as a transverse fissure. A typical broad basin can be observed in the second deciduous molar of *Proconsul* (Hopwood, '33, fig. 2), otherwise that region is more or less compressed. We might call this part the anterior basin.

In specimens of *Proconsul* and *Limnopithecus* from the Miocene the basin is empty. However, with the beginning of the Pliocene (after the appearance of *Hipparion*) the pattern becomes more complicated, and the basin is filled by secondary wrinkles originating from the protoconid and the metaconid respectively ("Randleisten" of Remane). Sometimes only one transverse wrinkle is present, generally arising from the protoconid. Sometimes both meet in the middle and are separated by a longitudinal furrow, while other times the wrinkles are crowded and the tips have no contact.

In *Dryopithecus* from the Pliocene of Salmendingen, the only known m_2 shows an uninterrupted transverse crest which fills the anterior basin (see Hürzeler, '51, fig 3). Also for the first time in Siwalik anthropoids a three fold ridge system occurs. This is found in "Dryopithecus cautleyi", (Lewis, '34, plate, 2, fig. 2), in "Sugrivapithecus salmontanus" (Gregory, *et al.*, '38, plate, 3, fig. 2) and in a fine unpublished specimen from Chinji in our collection. From that point on the conditions are foreshadowed which we find in the present day pongids and in man. There is, by the way, a most interesting difference between the Miocene apes from Kenya and the Pliocene ones from the Siwaliks: *Proconsul* and related forms and *Limnopithecus* have in the upper molars an exaggerated cingulum, even around the hypöcone, while such a structure is completely absent from any species in the Pliocene. Only two upper M^1's from the Siwaliks show a slight and normal cingulum at the anterior lingual corner (Pilgrim, '27, fig. 5; Gregory, *et al.*, plate 5, fig. b and c). In all other cases the lingual side is smooth.

The filling up of the anterior basin by secondary wrinkles might be the consequence of an increase in wrinkling, perhaps initiated by changing feeding habits in connection with the Alpine orogenesis, which changed the climatic conditions, especially in the northern hemisphere.

In the endocasts of the enamel crown of a lower molar of *Dryopithecus* from Melchingen a single connecting ridge between the two main cusps is indicated (Branco, 1898, plate 1,fig. 6). In endocasts of human molars from Central Java we sometimes find three crests (plate, 5a), while at the occlusal surface of the crown not much of a structure can be observed (plate, 5b). We might suppose that "the three bridges" only occur from the beginning of the Pliocene period on, and that this can be taken to indicate a closer relationship between man and the living pongids.

With respect to *Dryopithecus* from the Pliocene of Southern Germany, we found no counterpart to the deciduous tooth already mentioned in our collection. That is not astonishing, as here the metaconid has already been shifted towards the mesial edge, so both main cusps are nearly opposite one another. The large wrinkle filling the anterior basin, no longer regarded as an "original crest", can also be observed in this species. Also in our gorilla (plate, 1) this wrinkle does not reach the tip of the paraconid. The topography of the paraconid area shows great variation (Remane, '60, fig. 139), and without this knowledge one could only too easily be inclined to interpret a complete or partial ridge as the remnant of the original anterior trigonid crest.

Otherwise the *Dryopithecus* lower molars from Germany are very human-like. The classical description by Branco, 1898, has the title (translated), "On the human-like teeth from Bohnerz of the swabian Jura", because for many years serious scientists could not agree. The famous French palaeontologist Gaudry, discoverer of *Dryopithecus*, found the teeth only a little more ape - than human-like. Branco, who made a detailed comparison, still had his doubts, even if he found the greatest resemblance with anthropoid teeth. Why could these not probably be the teeth of a Tertiary forerunner of man? This interpretation has been discarded long ago, and the species name, *Dryopithecus rhenanus*, Pohlig has been accepted. But in the arrangement of cusps in the lower molars, the "*Dryopithecus* - pattern" (Gregory and Hellman, '26) has survived and still is recognizable in the dentition of modern man.

Summary

Our observations confirm the revised interpretation of the trigonid by Remane ('60). His first suggestion ('21) that the three crests (or ridges) generally found in the trigonid part of the lower molars of living pongids - and sometimes as relics even in man - could be traced back to the original trigonid crests of lemuroid dentitions can no longer be maintained. To the contrary, while the topography of this area might be similar to what probably could be expected, as in the case of gorillaitis, very suggestive indeed, that this part has been thoroughly remodeled.

1) The mesial marginal ridge turns out to be the outer wall of the tooth with which the anterior trigonid crest has merged. The paraconid has vanished, except in a few rare cases. In modern pongids in the deciduous dentition it seems to be restricted to the gorilla; in early man it has been observed in the last deciduous teeth of *Sinanthropus* and *Meganthropus*.
2) The anterior crest, situated in the original "fovea anterior", is entirely a new formation and often incomplete or absent.
3) The posterior crest - or "crista transversa anterior" (the crista transversa posterior is situated in the talonid portion) - is the latest remnant of the old connection between the protoconid and metaconid. This crest is extremely variable. It might be present, uninterrupted or interrupted by a small fissure, might be obscured by secondary wrinkles or shifted towards the distal slope of the protoconid or, more often, might be completely absent, leaving the base of the cusps free.
   The variability within the part in the human dentition is enormous, but not without an underlying pattern.

References

Adloff, P. 1908: Das Gebiss des Menschen und der Anthropomorphen. Berlin, J. Springer.

Branco, W. 1898: Die menschenähnlichen Zähne aus dem Bohnerz der Schwäbischen Alb. Jah. Ver. vaterl. Naturkunde, Württemburg 54, 1-144.

Gregory, W.K. and M. Hellman 1926: The dentition of *Dryopithecus* and the origin of man. Anthrop. Pap. Am. Mus. Nat. Hist. 18, 1-123.

Gregory, W.K., M. Hellman and G.E. Lewis 1938: Fossil anthropoids of the Yale-Cambridge India Expedition of 1935. Carnegie Inst. Wash. pub No. 495, 1-27.

Hopwood, A.T. 1933: Miocene primates from Kenya. J. Linn. Soc. Lond., Zool. 38 (260), 437-464.

Hürzeler, J. 1948: Zur Stammesgeschichte der Necrolemuriden. Schweiz. Pal. Abh. 66, 1-46.

——— 1949: Neubeschreibung von *Oreopitheeus bambolii* Gervais. Schweiz. Pa. Abh. 66. 1-20.

——— 1951: Contribution à l'étude de la dentition de lait d' *Oreopitheeus bambolii* Gervais. C.R. Soc. Pal. Suisse 44, 404-410.

——— 1954: Contribution à l'odontologie et à la phylogénèse du genre *Pliopitheeus* Gervais. Ann. Paléont. 40, 1-63.

Jørgensen, K.D. 1956: The deciduous dentition. Act. odont. Scand. 14, suppl. 20, 1-220.

Kälin, J. 1961: Sur les Primates de l'Oligocene inferieur de l'Egypte. Ann. Paléon. 47, 1-48.

Le Gros Clark, W.E. 1952: Report on hominoid material collected by the British--Kenya Expedition, 1949-1951. Proc. Zool. Soc. Lond. 122, 173-286.

Le Gros Clark, W.E. and L.S.B. Leakey 1951: The Miocene Hominoidea of East Africa. Fossil Mammals of Africa, 1, 1-117. Brit. Mus. (Nat. Hist.), London.

Lewis, G.E. 1934: Preliminary notice of new man-like apes from India. Am. J. Sci. 27, 161-179.

Pilgrim, G.E. 1927: A *Sivapitheeus* palate and other primate fossils from India. Paleont. Indica, n.s. 14, 1-26.

Remane, A. 1921: Beiträge zur Morphologie des Anthropoidengebisses. Arch. Natgesch. 11, 1-179.

——— 1960: Zähne und Gebiss. Primatologica, III, 637-846.

Weidenreich, F. 1937: The dentition of *Sinanthropus pekinensis:* A comparative odontography of the hominids. Palaeontologia Sinica, New Series D, 1 (whole series 101), 1-180.

Odontogenesis: Interaction between isolated enamel organ epithelium and dental papilla cells

EDWARD J. KOLLAR AND MICHAEL A. KERLEY

OSSA

The importance of tissue interactions between the dental papilla and the enamel organ has been examined after isolation and recombination of these tissue components. The isolated tissues were dissociated and passaged as cell cultures. Experimental combinations of cultured dental papilla cells and isolated enamel epithelium did not result in overt cellular differentiation in either tissue. Instead the epithelium invaded the cellular mat of the cultured dental papilla cells and displaced the dental papilla cells from the plastic substrate. However, these cells had not lost their ability to differentiate. If the cultured cells were recombined as a pellet of cells and allowed to grow as a tissue, the cells responded to each other and teeth were formed in the grafts. Enamel and dentin matrices present in the crown and a complete root and supporting structures were formed. The importance of the three dimensional structure of the substrate, extracellular matrix, and stromal architecture are stressed as integral elements of tissue interactions during odontogenesis.

Изучение взаимодействия тканей зубного сосочка и эмалевого органа было проведено после выделения и рекомбинации этих компонентов ткани. Выделенные ткани диссоциировали и пересеивали как клеточные культуры. Экспериментальные комбинации культивируемых клеток зубной папиллы и выделенного эпителия эмали не обнаружили явной клеточной дифференциации в обеих тканях. В противоположность этому, эпителий проникал в клеточную пленку культивируемых клеток зубного сосочка и вытеснял клетки зубного сосочка из пластичного субстрата. Однако, эти клетки не теряли способности к дифференциации. В том случае, когда рекомбинация культивируемых клеток осуществлялась в виде клеточных пленок, которые могли далее развиваться в форме ткани, клетки соответствовали друг другу, и зубы формировались в виде трансплантантов. В коронке имеются матрицы для дентина и эмали; благодаря этому образуется полностью сформированный корень и опорные структуры. Подчеркивается важность трехразмерной структуры субстрата, экстрацеллюлярной матрицы и архитектуры остова как неотъемлемых элементов взаимодействия тканей в течение одонтогенеза.

Ключевые слова: одонтогенез, взаимодействие эпителия эмалевого органа и клеток зубного сосочка.

Edward J. Kollar, Michael A. Kerley, Department of Oral Biology, School of Dental Medicine, University of Connecticut Health Center, Farmington, Connecticut, 06032 U.S.A.

Vol. 6, pp. 163-170, Lund. ISSN 0345-8865.

The current interest in the developing tooth as an experimental model can be traced to a paper by Huggins, McCarrol and Dahlberg ('34) who demonstrated the phenomenon of heterotypic tissue interactions and the directive role of the dental mesoderm with remarkable clarity. These pioneering experiments demonstrated the obligatory dependence of the enamel epithelium on the dental papilla for its maintenance as an enamel-secreting epithelium. In addition, the stability of the odontoblasts as dentin-secreting cells was noted following their interaction with the enamel epithelium. But, the most interesting insight in the paper was the observation that the dental mesoderm interacted with the dental epithelium, maintained it as an enamel epithelium, and controlled the hard tissue deposition. That is, the dental mesoderm controlled tooth form. These conclusions were made forty years before the recently renewed interest in the nature of tissue interactions and their influence on the structure, size,form, and pattern of embryonic tissues in general and dental structures in particular.

In the intervening decades, investigators have examined these problems in embryonic tissues and have utilized technical refinements such as enzymatic separation of the tissues (Rawles, '63) and transfilter culture methods (Grobstein, '56; Koch, '67; Thesleff et al., '77). These experiments have confirmed and extended the conclusions reached by Huggins, McCarroll and Dahlberg ('34).

The dental mesoderm does maintain the dental character of the epithelial components of the tooth germ. In isolation, the enamel organ reverts to a surface-like epithelium which sometimes keratinizes in the absence of a mesodermal stroma or in the presence of stroma from non-dental sources (Kollar and Baird, '70a, '70b; Kollar, '72a, '76; Osman et al., '77). In addition, the shape of a particular tooth is determined not by the epithelial enamel organ but by the dental mesoderm (Kollar and Baird, '69, '70a). Thus, the influence of the dental papilla on the oral epithelium was shown to be inductive. That is, the dental mesoderm can evoke the expression of genes for enamel synthesis in ectopic, non-dental epithelium (Kollar and Baird, '70b) both from the oral cavity such as vestibular lamina and from integumental sites such as the plantar surface of the footplate. In addition, we demonstrated (Kollar and Baird, '71; Kollar, '72a; Kerley and Kollar, '77) as an extension of the work of Main ('66) that the isolated cells of the dental papilla retain their inductive capabilities after passage in vitro for extended periods of time. This last result was surprising since the inductive potential of these cells seems weakend or absent when the tissue is isolated from older animals.

We describe, here, further experiments that examine the ability of isolated dental epithelium and dental papilla to interact when recombined in experimental associations after enzymatic dissociation and passage through monolayer culture. Our experiments probe several intriguing problems in developmental biology, and they owe their origin to Professor Dahlberg's active interest in odontogenesis.

Materials and methods

Mandibular molars from 17 or 18 day old embryonic CD-1 Swiss mice were dissected free of surrounding tissues and treated for two hours at 4^{o} C in a 1% trypsin (Bacto-Difco, 1:250) solution in Hanks calcium-and magnesium-free salt solution. We had demonstrated earlier (Kollar and Baird, '69) that following this enzymatic treatment the enamel organ can be cleanly separated from the dental papilla using gentle teasing. The isolated dental tissues were then subjected to an additional trypsinization at 37^{o} C and dissociated into a cell suspension (Moscona, '61). The cell suspensions were seeded onto plastic tissue culture flasks containing MCDB 103 medium (Pacific Biologicals) supplemented with 10% fetal calf serum (Gibco) and 0.1% Gentamycin (Schering). The monolayer cultures of either dental papilla or enamel organ were used during the first week of cultivation or at the end of the second week. If the cultures were incubated for two weeks, the primary culture was split 1:2 at the end of the first week.

The monolayered cells were released from the plastic culture dish with dilute trypsin (0.25% at room temperature) and resuspended with freshly isolated cells of the corresponding heterotypic tissue from 15- or 17-day embryonic molars. The comingled cell suspensions were centrifuged at low speed for one minute. The resulting pellets were cultured overnight on agar-solidified Eagles basal medium. The pellets were cut into suitably small fragments and placed into the anterior chamber of eyes of isologous hosts. The grafts were recovered after two weeks and processed for histological examination.

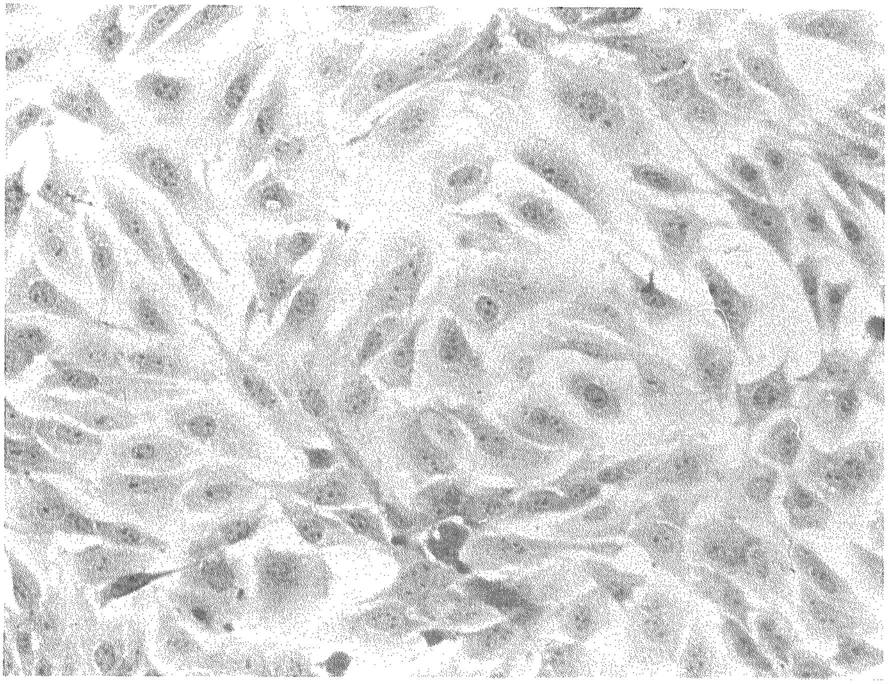


Fig. 1. Dental papilla cells grown as a monolayer culture on plastic dishes for one week. 140X.

Results and discussion

As we reported earlier (Kollar, '72b) dental papilla cells can be cultivated with ease as monolayer cultures. The cells have a typical stellate, fibroblast-like appearance in young, sparcely populated cultures but they can assume a more polygonal shape in dense confluent cultures. There is no evidence of dentin matrix deposition under the conditions described here (fig. 1). After one week in vitro a distinctly different population of long, bipolar, spindle-shaped cells appears on the surface of the monolayer (fig. 2). Daily observation of these cultures suggests that these cells arise from a proliferating population of cells that can be inferred from the large number of mitotic figures seen in the confluent cultures. This distinctly different population of cells does not distribute itself randomly over the surface of the monolayer; rather, they form discrete fusiform configurations on the surface of the culture. The origin and cytological-characteristics of this cell population is being investigated.

Of greater interest, perhaps, is the ease with which the enamel epithelium can be cultivated in monolayer culture. The cells form characteristically confluent sheets of polygonal cells. The epithelial cells do not differentiate into keratinocytes in monolayer cultures despite their ability to do so when combined with a heterologous mesodermal cell population. As in the dental papilla cultures, there is no evidence of differentiated cell function (fig. 3).

These data corroborate the conclusions of Huggins, McCarroll and Dahlberg ('34). The isolated tissues of the tooth germ can not interact after physical separation and, therefore, the characteristic cytology and biosynthetic activity is abolished. The absence of dentin secretion can be explained by the immaturity of the dental papilla at

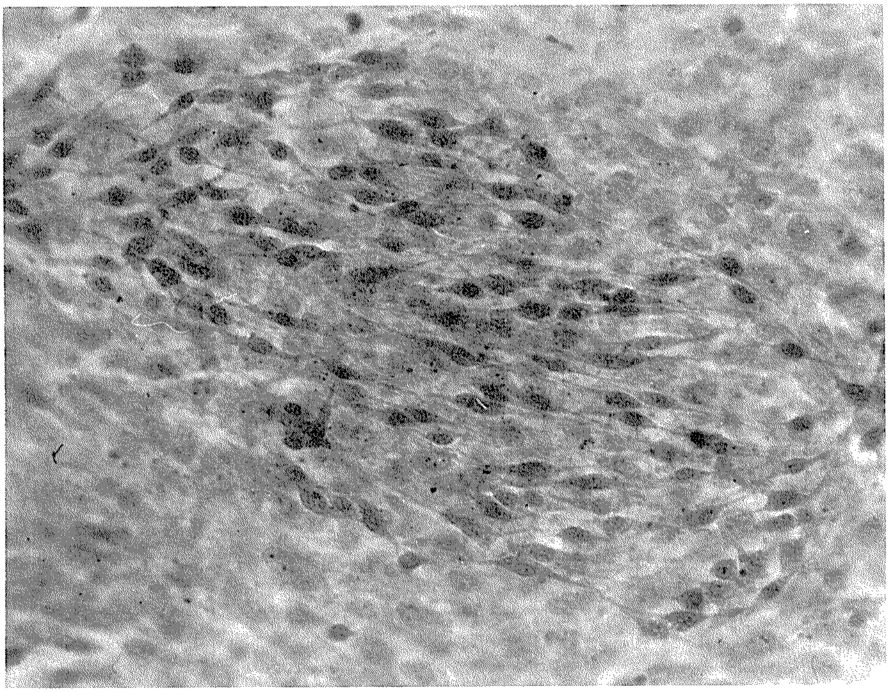


Fig. 2. Bipolar cells appear on the surface of the dental papilla monolayers as a distinct cell population. The cells display long cell processes and a centrally placed nucleus. X300.

the time of isolation when dentin secretion had not yet begun. Presumably, only after dentin secretion is established in the odontoblasts do these cells achieve a stability of differentiated function. In addition, these cells are dissociated and plated as single cell suspension. Such treatment may suppress the previously functioning odontoblasts; or, alternatively, the treatment may select out a more immature population which profilerated in cell culture. The retention of differentiated function in the explanted dental papilla described by Huggins et al. (' 34) can be attributed to the later stages of development that were used, the less severe disruption of the tissue, and the superior nutritional characteristics of the explantation site in the abdominal wall.

In contrast to the refractoriness of the embryonic dental papilla and enamel organ epithelium to differentiate in monolayer cultures, the ability of the dental papilla to participate in tooth development when released from the monolayer state and recombined with intact enamel organ epithelium has already been reported (Kollar, and Baird, '71; Kollar, '76). We have repeated this experimental combination adding a variation in which the monolayered dental papilla cells grown for one or two weeks and are then recombined with dissociated enamel organ epithelium isolated at the time of recombination. In such cases, in which the dental papilla had been in long-term cell culture and the enamel organ had undergone dissociation, well-formed teeth displaying enamel and dentin matrices were found in the intraocular grafts of such explants (fig. 4). Thus, an intact enamel epithelium is not an absolute requirement for the reorganization of a dental papilla. The dissociated cells of the enamel epithelium sort out, produce an epithelial sheet, and, then, under the direction of the dental papilla cells,

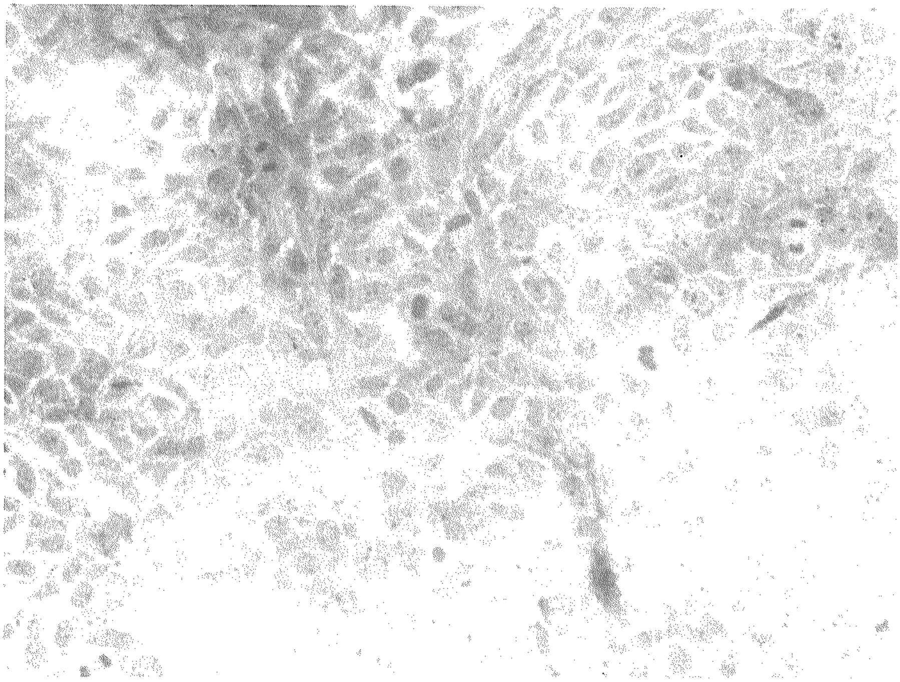


Fig. 3. A culture of enamel epithelium. The isolated epithelial cells form a confluent monolayer. Mitotic figures are apparent throughout the monolayer. X100.

participate in tooth formation. It is not known whether an epithelial sheet must reform in order to direct the reorganization of a dental papillae, or whether the two tissue components can, in fact, reorganize independently. The former alternative would more nearly approximate the events that occur during odontogenesis in vivo. But, the ability of the dental papilla to interact with non-dental epithelium suggests that the organization of the dental papilla as such may not require a specific dental lamina as such.

Because our previous work with odontogenesis and with the developing derivatives of the integument (Garber, Kollar and Moscona, '69; Kollar, '72a) suggested that the epithelium may become stabilized and unresponsive sooner in development and more irreversibly than the mesodermal component, our experiments were extended to examine the effects of long-term cell culture on the responsiveness of the dental epithelium. The molar complex from 17 or 18 day old embryos was dissected and following dissociation plated to monolayer culture. After two weeks these cells were combined with a cell suspension of freshly isolated dental papilla from 16 day old embryos, pelleted, incubated, and grafted to the anterior chamber.

The results shown here (fig. 4) indicated that dissociation followed by prolonged cell culture does not abolish the capacity for the enamel epithelial cells to respond to the inductive stimulus of the dental papilla. In the figure shown here (fig. 4) the enamel and dentin matrices are in a typical crown pattern. Data presented elsewhere (Kerley, unpublished; Kerley and Kollar, '77) indicate that in addition to crown formation the total dental complex including root with cementum and periodon-

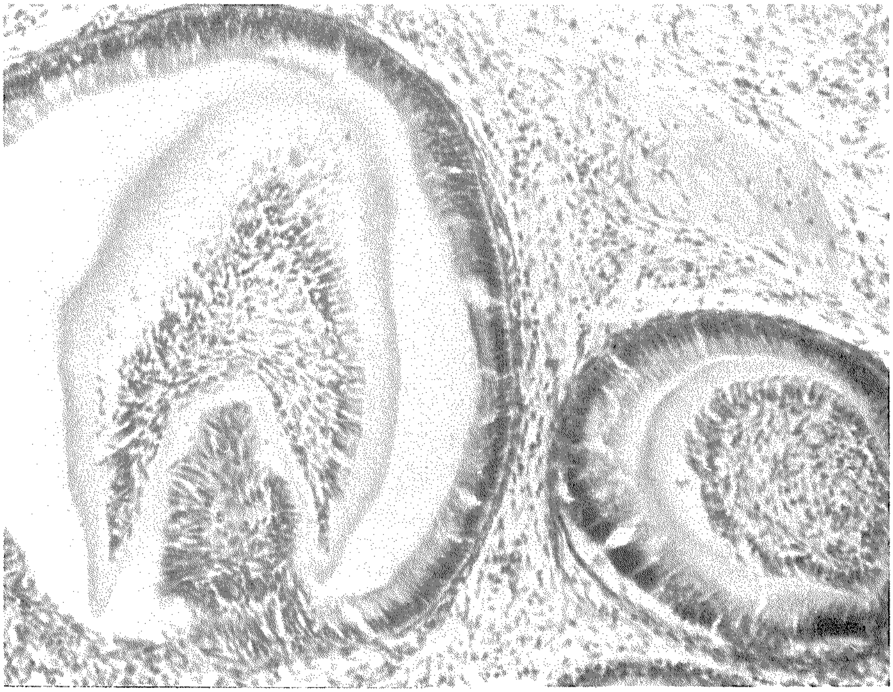


Fig. 4. Developing tooth germs in an intraocular graft. Both dentin and enamel matrices have been deposited. This combination was formed from co-mingled dissociated dental papilla cells combined with monolayered enamel epithelium. X140.

tal ligament can be obtained in these experimental combinations. Obviously the enamel epithelium has not lost any of its potential and can recapitulate its developmental repetoire even after severe alterations of cell position and after cell ageing. Osman et al. ('77) have also presented some evidence to support this conclusion concerning the importance of culture conditions and cell relationships.

The tissue of the developing tooth constitute a most resilient developing complex. Despite the disruption of established cellular patterns and despite long-term cultivation on artificial substrates, the cells retain their ability to interact in a recognizably normal way. This lability of developmental expression suggests that the refractoriness of these cellular elements to differentiate in isolation or as cell cultures indicates a requirement for three-dimensional organization and tissue architecture as a prerequisite for further cytological differentiation and biosynthetic activity.

Another set of experiments carried out recently further support the notion that these tissue interactions require an appropriate stromal-epithelial configuration. Since isolation prevents tooth formation, then association of the epithelial and mesodermal tissues in the simplest manner should provide some indication of restitution of developmental activity. If isolated but intact enamel organ epithelium is placed on dense cell cultures of dental papilla the tissues could interact and, minimally, there might be differentiation in the dental papilla cells with the production of dentin matrix. At best, both tissue components should interact and both dentin and enamel matrices should be laid down, perhaps in a bilamminal sheet-like display.

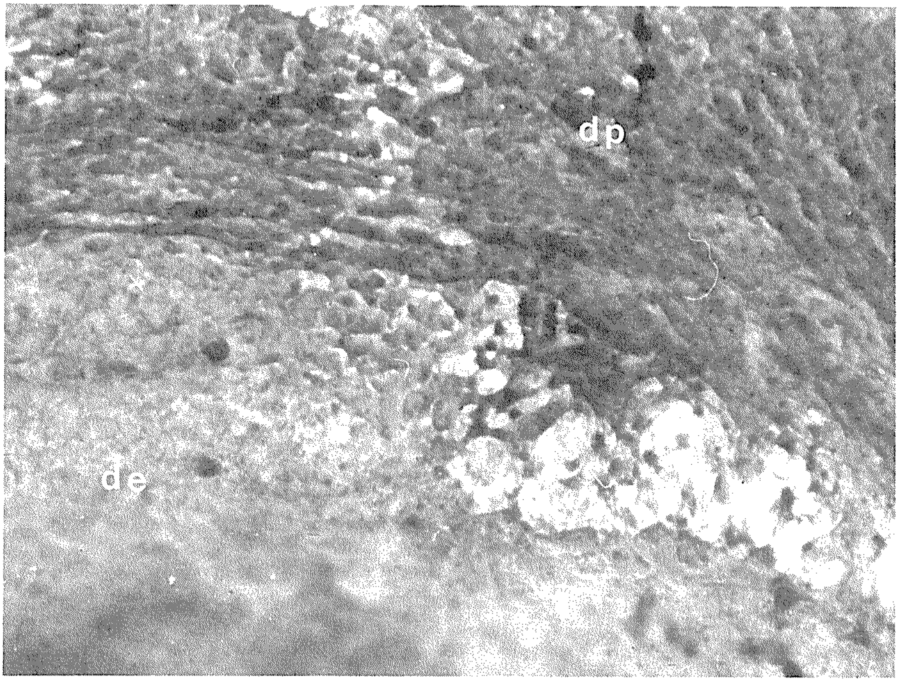


Fig. 5. An island of dental epithelium placed on a confluent monolayer of dental papilla cells. The epithelium fails to interact with the dental papilla. Instead the epithelium penetrates the dental papilla monolayer and migrates along the plastic substrate. There is no evidence of tissue interaction. X 100.

Our data indicate that neither possibility was realized. The enamel epithelium has no effect on the dental papilla cell cultures. Rather, the epithelium invades the papilla cell layer and procedes to migrate along the plastic substrates moving underneath and displacing the papilla cells. Variations of placing the epithelium down first or varying the concentration of papilla cells has no effect on the reaction of these tissues in this experimental model (Fig. 5).

The only variation between this experiment and the results of many combinations of isolated dental papilla cells (even pelleted papilla cells after passage through monolayer culture) and freshly isolated enamel organ epithelium is of topological restriction placed on the papilla cells which are retained in a flattened two dimensional pattern. These observations suggest that an interaction is prevented because an effective interaction with optimal and appropriate deposition of the extracellular matrix molecules is necessary before a characteristic developmental response can be seen in the tissues. A recent paper by Van Der Schueren et al. ('77) examines the changes in cellular structure and behavior as cells move in transition from a pellet to the monolayer substrate. Profound changes are noted both in the cells migrating out into the substrate and those that are retained in the pellet. The importance of substrate, extracellular matrix, and stromal architecture must be stressed or as integral element of tissue interactions.

Acknowledgements

Edward J. Kollar acknowledges, gratefully, the continual and sustaining support of Professor Dahlberg over many years. His interest in odontogenesis and in my work has been a gratifying and encouraging influence.

Both authors wish to thank Mr. J. Benarczyk who did the monolayer cell interaction studies and Ms Joyce D' Amato for typing the manuscript.

Literature cited

Garber, B., Kollar, E.J. and Moscona, A. 1968 Aggregation *in vivo* of dissociated cells. II. Effect of state of differentiation of cells on feather development in hybrid aggregates of embryonic mouse and chick cells. J. Exptl. Zool. 168: 455-472.

Grobstein, C. 1956 Trans-filter induction of tubules in mouse metanephrogenic mesenchyme. Exper. Cell Res., 10: 424-440.

Huggins, C.B., McCarroll, H.R. and Dahlberg, A.A. 1934 Transplantation of tooth germ elements and the experimental heterotopic formation of dentine and enamel. J. Exptl. Med. 60: 199-210.

Kerley, M.A. and E.J. Kollar 1977 Tooth formation from disaggregated dental tissues cultured *in vitro*. Am. Zool. 17: 933.

Koch, W. 1967 *In vitro* differentiation of tooth rudiments of embryonic mice. I. Transfilter interaction of embryonic tissues. J. Exptl. Zool. 165: 155-169.

Kollar, E.J. 1972a The development of the integument: Spatial, temporal, and phylogenetic factors. Am. Zool. 12: 125-135.

______ 1972b Histogenetic aspects of dermal-epidermal interactions. In: Developmental Aspects of Oral Biology (eds., H.C. Slavkin and L.A. Bavetta), Academic Press, New York, pp. 125-149.

Kollar, E.J. and Baird, G. 1969 The influence of the dental papilla on the development of tooth shape in embryonic mouse tooth germs. J. Embryol. Exp. Morph. 21: 131-148.

______ 1970a Tissue interactions in developing mouse tooth germs: I. Reorganization of the dental epithelium during tooth germ reconstruction. J. Embryol. Expt. Morp. 24: 159-171.

______ 1970b Tissue interactions in developing mouse tooth germs. II. The inductive role of the dental papilla. J. Embryol. Expt. Morph. 24: 173-186.

______ 1971 Retention of inductive potential in long-term cultures of dental papillae. J. Dent. Res., Suppl. Abstr. 336.

Kollar, E.J. 1976 The use of organ culture embryonic tooth germs for teratological studies. In: Test of Teratogenicity *In Vitro*. J.D. Ebert and M. Murois, eds. North Holland, Amsterdam, pp. 303-334.

Main, J.H. 1966 Retention of potential to differentiate in long-term cultures of tooth germs. Science 125: 778-

Moscona, A.A. 1961 Rotation-mediated histogenic aggregation of dissociated cells. Exp. Cell Res. 22: 184-194.

Osman, M., V. Karcher-Djurick, et J.V. Ruch 1977 Interactions morphogenes entre constituents dentaires. Archs, d' anat et Morph. Exper., 66: 109-118.

Rawles, M.E. 1963 Tissue interactions in scale and feather development as studied in dermal-epidermal recombinations. J. Embryol. Exptl. Morph. 11: 765-789.

Thesleff, I., E. Lehtonen, J. Wartiovaara, and L. Saxen 1977 Interference of tooth differentiation with interposed filters. Devel. Biol. 58: 197-203.

Van Der Schoeren, B., J.J. Cassiman, and H. Van Den Berghe 1977 Out growth of human fibroblast aggregates on a substratum triggers a wide variety of morphogenetic properties in the cells. J. Cell Sci., 26: 101-117.

The human fetal craniofacial skeleton in radiologic cephalograms

KALEVI KOSKI

OSSA

Lateral radiologic cephalograms of 45 human fetuses, ranging from 144 to 245 mm C-R length, were analysed using angular dimensions between lines related to skeletal anatomy. Among the relationships some were found to be stable, others changing during the two-month period covered by the sample. On the basis of this and previous studies on postnatal subjects it appears that while some of the skeletal relationships become fixed already during the fetal life, others may fluctuate until early adulthood. The characteristic mosaic nature of bones such as the mandible is apparent from the early fetal life.

Keywords: Cephalometry - Fetus - Human - Radiology.

В работе были исследованы латеральные радиологические цефалограммы 45 эмбрионов человека, длиной в пределах от 144 до 245 мм C-R, причем использовали размеры угла между линиями, принадлежащими к скелетной анатомии. Некоторые соотношения оказались стабильными, другие же изменялись в течение двухмесячного периода изучения. На основании этих данных, а также - согласно предварительным исследованиям постнатальных образцов - было установлено, что в то время как некоторые из скелетных соотношений фиксируются уже в течение эмбрионального развития, другие могут подвергаться флуктуациям вплоть до раннего взрослого состояния. Характерная мозаичная природа костей, таких, как нижняя челюсть, становится очевидной в раннем периоде эмбрионального развития.

Ключевые слова: цефалометрия, человеческий эмбрион, радиология.

Kalevi Koski, Institute of Dentistry, University of Turku, SF-20520 Turku 52, Finland.

Vol. 6, pp. 171-180, Lund. ISSN 0345-8865.

As a part of the great bloom of craniofacial research during the last couple of decades cephalometry of human fetal material has also flourished. The structure and growth of the craniofacial skeleton has been studied using both direct cephalometry (Ford, '56; Burdi, '65,'69; Kvinnsland, '71a-c, '73) and radiologic cephalometry (Inoue, '61; Levihn, '67; Lavelle and Moore, '70; Houpt, '70; Lavelle,'74; Johnston, '74; Luke, '76). These studies, based on a total of nearly 1000 fetuses ranging from 43 mm C-R length to term, and employing a variety of measurement techniques, have produced a bulk of data which is both impressive and informative.

Cephalometric methodology has by no means reached the stage of fixed standardization, as regards the analysis of cephalograms. The measurement methods vary; the choice of points and lines may be dictated by the purpose of study, the availability of comparative data, etc. Some authors stress the accuracy and reliability of measurements, while others may strive for anatomical meaningfulness even at the cost of technical accuracy. Along the latter line, a series of studies on the structure of postnatal craniofacial skeleton in Homo and Macaca mulatta has been conducted (Koski, '73; Vinkka and Koski, '75; Vinkka, Koski and McNamara, '75). The present investigation is a continuation of that series, an application of the previously used analytical method on a sample of human fetal cephalograms.

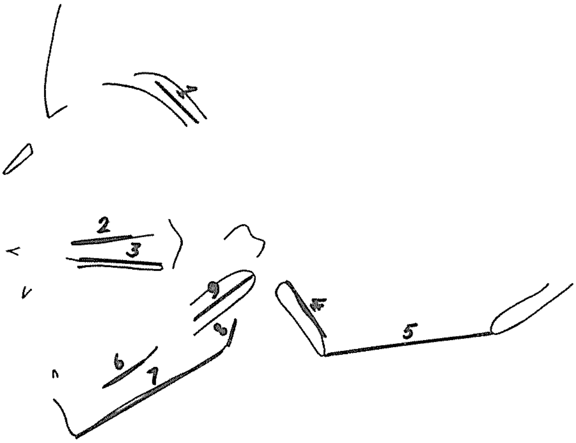


Fig. 1. Tracing of a cephalogram of a 147 mm C-R length fetus, illustrating the lines used for measuring angular relationships. 1 = ORB, tangent to the posterior slope of the orbital roof; 2 = INFRA, line depicting the infraorbital canal (practically identical with the orbital floor); 3 = PAL, tangent to the posterior nasal floor; 4 = CLIVUS, tangent to the cerebral surface of the occipital clivus; 5 = FOR, the foraminal line, basion - opisthion; 6 = AMC, line depicting the anterior part of the mandibular canal; 7 = MAND, tangent to the mandibular base; 8 = RAMUS, tangent to the posterior border of the ascending ramus; 9 = COND, line bisecting the condylar process.

Materials and methods

The material consisted of 45 cephalometric lateral radiograms of human fetuses ranging from 144 to 245 mm C-R length (Table 1). The fetuses, preserved in 10% formalin, had been screened for visible malformations, and specimens with radiographically detectable malformations were excluded from the sample. A special headholder had to be used, the X-ray anode - midsagittal plane distance had been kept constant (50 inches) and the object- film distance to a minimum. A medical X-ray unit was used, with a kV of 42 and an exposure of 200 mA (McNamara, '78).

A small number of cephalograms representing fetuses of 248 to 380 mm C-R length were also available. As they were scattered over a long period of fetal life, and could thus not be trusted to give reliable information about dimensional trends, they were not included in the main material. They were measured, though, and will be referred to in connection with some structural details.

No determination of sex was attempted, as significant sexual dimorphism has not been found to exist in craniofacial dimensions during fetal life (Inoue, '61).

The radiograms were traced on transparent acetate sheets with a sharp pencil, including only structural details of interest. In the tracings a number of lines depicting certain anatomical structures could be visualized (Fig. 1). Using one of these lines, ORB, as a base line, angles were measured between it and all other lines, to the nearest half a degree, with the aid of a special large protractor and a ruled paper placed underneath the tracing. All the other angles were calculated from this basic set of readings.

Since the traced features were quite small, especially in the youngest fetuses, the reliability of the measurements was checked by measuring a set of the 20 smallest tracings about two years after the first measurements. The means of the paired differences between the two sets of measurements ranged from -0.35^{o} to $+0.85^{o}$, with

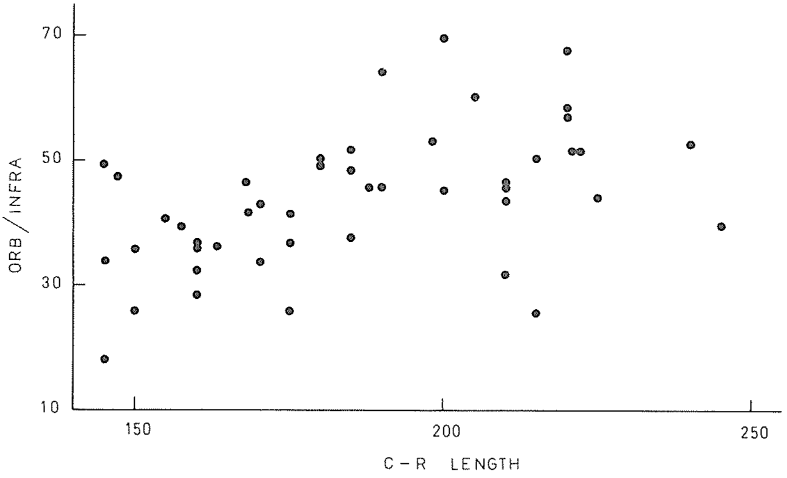


Fig. 2. ORB/INFRA angle by C-R length. Notice the ascending tendency until about 190 mm C-R, and the relatively great variability throughout.

the standard deviations ranging from 2.36° to 3.22°. While the variability of the paired differences was thus fairly large, none of the means was significantly differing from zero at the 0.05 risk level.

Results

Because of the uncertainty of the mandibular position in the fixed fetuses it was decided to calculate the angular relationships within the cranium and mandible separately. A set of ten mutual angles between the five cranial lines and another set of six angles between the four mandibular lines (Fig. 1) were thus measured or calculated.

The series of readings obtained indicated that some of the angles may have a tendency for significant change as a function of age. To check this, scattergrams were drawn for each measured (calculated) angle as a function of C-R length. It appeared that these angle/C-R length relationships could be grouped into three different types, regarding their stableness and variability:

(1) angles which showed a clear tendency to change during the period covered; these included all angles involving the line ORB (Fig. 2), and the angles INFRA/PAL, INFRA/FOR. The variability of these angles was great, except as regards the angle INFRA/PAL;

(2) angles which did not show a significant tendency for change, but appeared moderately or greatly variable, e.g., CLIVUS/FOR (Fig. 3), RAMUS/COND (Fig. 4);

(3) angles which showed neither change nor appreciable variability, e.g., AMC/MAND (Fig. 5).

The visual impression was checked by calculating regression coefficients for all the angle/C-R length relations. The angles of type (1) proved to have coefficients differing significantly from zero. Consequently, the observations related to these angles were not treated statistically any further. However, it was noted from the scattergrams that all the angles between ORB and other cranial lines appeared to increase from the 144 mm C-R length stage until about 190-200 mm C-R length stage, at which point they seemed to become stabilized. The few tracings of older fetuses yielded measurements which, when plotted on the scattergrams, supported this contention. As to the angles INFRA/PAL and INFRA/FOR, their variations through the period

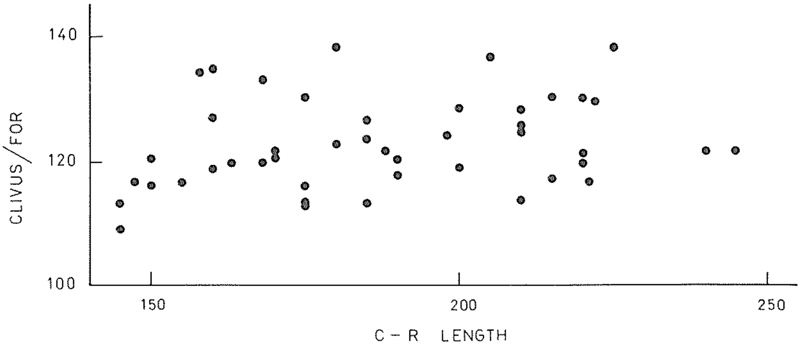


Fig. 3. CLIVUS/FOR angle by C-R length. No significant tendency for change, moderate variability.

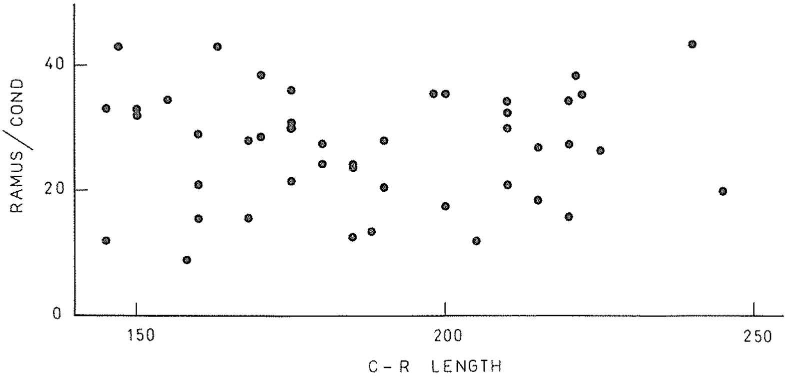


Fig. 4. RAMUS/COND angle by C-R length. No significant tendency for change, great (?) variability.

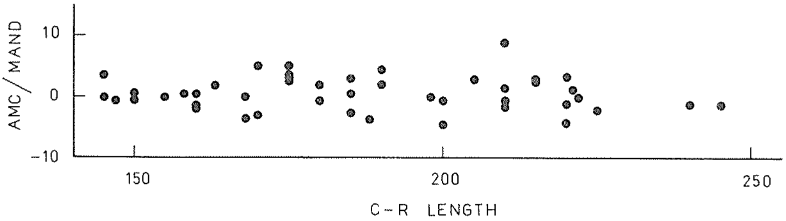


Fig. 5. AMC/MAND angle by C-R length. No change, small variability.

covered by this sample seemed to indicate a rather continuous although slowly increasing trend.

For those angles which did not show a significant change during the age period covered by the sample, means and variances were calculated (Tables 2 and 3).

Discussion

In radiological cephalometry the use of well defined and easily detectable points and connecting lines is recommended because of the guaranteed accuracy and repeatability. However, if the student wishes to follow the skeletal anatomy and pay attention to the functional and growth units to the extent that they are known, it is not always possible to find suitable points, and the connecting lines may cross functional or growth fields in an unwarranted way. The method used in this study is a case in point. It follows the tradition of many craniologists (Pankow, '48; Kummer, '52; Hofer, '60), and it is hoped that its relevancy and meaningfulness compensates for its shortcomings in strict accuracy. At any rate, the method fulfills satisfactory criteria of accuracy as found previously by Vinkka and Koski ('74) and again in the present study.

The employment of angular dimensions only is both a limiting and a broadening factor. Obviously, linear dimensions would be of great interest also. On the other hand, the possible differences in projection magnification inherent in radiological cephalometry are often not so significant in regard to angular as to linear dimensions, although it is obvious that angular relationships between skeletal parts not located in the same sagittal plane may be distorted differently (Slagsvold and Pedersen, '77). In the present study the original radiograms were taken so that even the midsagittal plane magnification varied with the breadth of the head, and the linear dimensions would thus not have been comparable.

Most of the measured angles did not change significantly through the present sample. Although the craniofacial patterns have been claimed to be constant through most of the fetal and during the postnatal life (Inoue, '61; Burdi, '65; Brodie, '41) the present findings cannot be taken to support these claims. The present sample represents only a fourth of the fetal life span, and the fastest period of head growth occurs in human fetuses before this period (Levihn, '67). Many of the craniofacial angular dimensions have been found to fluctuate during the fetal life (Kvinnsland, '71a-c), not to speak of the postnatal life (Koski, '61).

The interrelationship between the brain and the cranial base is common knowledge. The midsagittal structures, planum sphenoidale and the cribriform plate, which are the usual structures studied, are but a small part of the anterior cranial base underlying the brain. By far the largest portion of the floor of the anterior cranial fossa is gradually formed by the sloping parts of the frontal bones forming the roots of the orbits. It is obvious that these structures cannot be adequately represented by any lines visible in the cephalograms, but the orbital roof lines used in this study can be taken as approximations, remembering, of course, that projectional errors introduce a factor of inaccuracy of unknown degree.

The lateral floors of the anterior and middle cranial fossae appear parallel in lateral radiograms of the head in postnatal life (Koski, '73), i.e., the laterally situated major portions of the brain do not show an angulated relationship like the midline structures of the brain. The arrangement of the brain components undergoes a complex process, mainly during the fetal life, involving, among other things, the descent of the lateral parts of the cranial floor in relation to the center of the cranial base (Dabelow, '31). This may explain also the changing angular relationship of the orbital roof to the other cranial structures found in the present sample.

The changes just mentioned did not permit comparison on the basis of means and variances as regards the ORB-angles. However, when the few scattered specimens beyond the 245 mm C-R length were also observed, it appeared that the ORB/INFRA angle had approximately reached the level characteristic of children ($\bar{x} = 49.3^o$; Vinkka and Koski, '75) already at about the 200 mm C-R length stage. As the other ORB-relations were not yet at the postnatal levels, the shape of the orbital cone and the relation between the two first branches of the trigeminal nerve, which happen to be one and the same thing in our analysis, were early maturers among the craniofacial relationships.

While the olfactory bulb, via the cribriform plate, may deserve special attention as a possible determinant of the orientation of the face (Enlow and McNamara, '73), the horizontalisation of the vision axis could be of equal importance (cf. Enlow and Azuma, '75). The changing relationships between the orbital roof on the one hand, and the posterior cranial base and the facial skeleton on the other,may be looked upon as reflecting the rotations of the craniofacial skeleton in relation to the main axis of the body. The stage when the angular relationships involving the orbital roof appear to level off in the present sample, 190-200 mm C-R length, corresponds to approximately the end of the fifth lunar month (Patten, '46; Birkbeck et al., '75), which in turn marks the point of maximum velocity in growth in length of the fetus (Scharf, '74). To what extent these phenomena are causally related to each other remains to be found out.

The clivus has been regarded the best reference structure because its relation to the vertebral column is claimed to be similar in all mammals (Kälin, '46; see also Dabelow, '29; Kummer, '57). Ford ('56) calculated a change of 26.0^o in the basioccipito-foraminal angle (pituitary-basion-opisthion) from the 10-week stage to the 40-week stage, and Kvinnsland ('73) found the angle sella-basion-opisthion to show an increasing trend from 10 to 33 weeks, with a plateau during the third quadrant of this period. Our CLIVUS/FOR angle is not identical with those measured by Ford ('56) or Kvinnsland ('73). Therefore, it is not necessarily surprising that the clivo-foraminal angle of this study does not change; the period covered by our material also approximately coincides with the plateau-period found by Kvinnsland ('73). It is interesting, though, that the means of the CLIVUS/FOR angle measured by us are practically identical in the present fetal sample, 123.1^o, in children of 6-8 years of age, 125.0^o, in young adults, 124.6^o, and even in juvenile Macaca mulatta monkeys, 123.0^o (Vinkka and Koski, '75; Vinkka et al., '75). The claim of the earlier authors thus gains some support; the significance of the choice of structures and dimensions to be measured is also brought into focus. It is true, of course, that the occipital clivus and the foramen are in the same bone postnatally, and they seem to change as a unit, for instance in artificially malformed skulls (Moss, '58). In spite of the fact that the occipital clivus during the fetal life now under observation is still separated from the rest of the foraminal borders by synchondroses, the angular relation between the clivus and the foramen seems to become fixed during fetal life, at least in man. The question of causal relationships between the midsagittal cranial base configuration and the upright position or brain growth (Weidenreich, '41; Dabelow, '29; Biegert, '57; Hofer, '54, '60) is still waiting for a final solution.

The relationship between the palatal plane and the foramen magnum is similar at this fetal stage to that of juvenile Macaca monkeys, -10.3^{o} resp. -10.2^{o} (Vinkka et al., '75). It follows that the angle between the palatal and clival planes is also similar in human fetuses and juvenile monkeys, 46.8^{o} resp. 46.9^{o} (Vinkka et al., '75). On the other hand, no difference was found between young children and young adults in regard to these two angular relationships, (PAL/FOR 7.4^{o} resp. 8.6^{o}, PAL/CLIVUS 62.4^{o} resp. 63.9^{o}; Vinkka and Koski, '75) but these postnatal values were clearly different from the fetal values. As the line PAL also marks the floor of the nasal cavity, the latter, which is claimed to maintain its shape from the third month of pregnancy (Moss and Salentijn, '69) is still in the process of finding its way to the proper postnatal relation to the cranial base. The similarity between the human fetus and the juvenile monkey may remind us of the recapitulation theory, but there may be a more plausible explanation. In the microcephalic skull illustrated by Weidenreich ('41) the relations between the foramen magnum, clivus, and palate are almost identical with our fetal values, which strongly indicates the growth and development of the brain as the influential factor.

In the mandible, the angle AMC/MAND is not significantly different from the corresponding angle in young children ($\bar{x} = 0.8^{o}$; Vinkka and Koski, '75), nor from that of juvenile monkeys ($\bar{x} = 1.4^{o}$; Vinkka et al., '75). The variance of this angle is also of a very low order. Although the close spatial relationship may partly explain these findings, they may also reflect a biological tie between the two elements of the lower jaw.

Except for the relation between the mandibular canal and base, the fetal angular relations within the mandible are not at the postnatal levels. As has been seen in postnatal studies, the different constituents of the seemingly single mandible continue their search for final mutual relationships throughout the adolescence (Vinkka and Koski, '75).

The variability of the angular dimensions in the fetal craniofacial skeleton are of the same magnitude as those found postnatally, with only a few exceptions towards greater variability; this, of course, may also result from the difficulties in measuring angles between small structures.

It is of special interest that the variances of the angles involving the mandibular ramus are the greatest as they are also in postnatal faces. This, too, may depend partly on the technical difficulties referred to above. Nevertheless, it is in agreement with the postulate that the ramus forms a relatively independent and variable link between the corpus mandibulae and the cranium (Koski, '73). If the present findings are accepted at their face value, then the ascending ramus follows its own path from the very beginning, in accordance with the views stressing the function-dependent mosaic nature of bony structures (van der Klaauw, '48; Moss and Salentijn, '69).

In conclusion, the findings of this study, while not of definite nature, indicate that the growth of the fetal craniofacial skeleton is not a simple process following a fixed pattern. Some of the structural details, e.g., the clivus-foramen magnum angle and the shape of the orbit seem to become fixed early. Their relations to other parts of the craniofacial skeleton may continue to change, and parts of complex bones such as the mandible may follow their relatively independent paths of growth from the very start.

Acknowledgements

I wish to thank Dr. J. A. McNamara for letting me trace the cephalograms taken by him of fetuses in the Bradley Patten Embryology Collection, Department of Anatomy, The University of Michigan. Further thanks are due to Dr. O. Rönning for critical reading of the manuscript, to Ms. Leena Tuomarila for drawing the graphs, and to Ms. Sirpa Laakso for typing the manuscript. The study was aided, in part, by grants from the U.S. Public Health Service (DE-02272, DE-43120), while the author was a Visiting Scientist at the Center for Human Growth and Development, The University of Michigan, 1969-1970.

Literature cited

Biegert, J. 1957 Der Formwandel des Primatenschädels. Morph.Jb., 98: 77-199.

Birkbeck, J.A., W.Z. Billewicz and A.M. Thomson 1975 Foetal growth from 50 to 150 days of gestation. Ann. hum. Biol., 2: 319-326.

Brodie, A.G. 1941 On the growth pattern of the human head from the third month to the eighth year of life. Am. J. Anat., 68: 209-262.

Burdi, A.R. 1965 Sagittal growth of the naso-maxillary complex during the second trimester of human prenatal development. J. Dent. Res., 44(1): 112-125.

——— 1969 Cephalometric growth analyses of the human upper face region during the last two trimesters of gestation. Am. J. Anat., 125: 113-122.

Dabelow, A. 1929 Über Korrelationen in der phylogenetischen Entwicklung der Schädelform I. Die Beziehungen zwischen Rumpf und Schädelform. Morph.Jb. 63: 1-49.

——— 1931 Über Korrelationen in der phylogenetischen Entwicklung der Schädelform II. Beziehungen zwischen Gehirn und Schädelbasisform bei den Mammalien. Morph. Jb. 67: 84-133.

Enlow, D.H. and J.A. McNamara 1973 The neurocranial basis for facial form and pattern. Angle Orthod., 43: 256-270.

Enlow, D.H. and M. Azuma 1975 Functional growth boundaries in the human and mammalian face. D. Bergsma (ed.): Morphogenesis and malformation of face and brain, pp. 217-230, Alan R. Liss, New York.

Ford, E.H.H. 1956 The growth of the foetal skull. J. Anat., 90: 63-72.

Hofer, H. 1954 Die cranio-cerebrale Topographie bei den Affen und ihre Bedeutung für die menschliche Schädelform. Homo, 5: 52-72.

——— 1960 Studien zum Problem des Gestaltwandels des Schädels der Säugetiere, insbesondere der Primaten. Zeits.Morph. u. Anthrop., 50: 299-316.

Houpt, M.I. 1970 Growth of the craniofacial complex of the human fetus. Amer. J. Orthod., 58: 373-383.

Inoue, N. 1961 A study on the developmental changes of dentofacial complex during fetal period by means of roentgenographic cephalometrics. Bull. Tokyo Med. Dent. Univ., 8: 205-227.

Johnston, L.E. 1974 A cephalometric investigation of the sagittal growth of the second-trimester fetal face. Anat. Rec., 178: 623-630.

Kälin, J. 1946 Zum Problem der menschlichen Stammesgeschichte. Experientia, 2: 272-287.

Klaauw, C.J. van der 1946 Cerebral skull and facial skull. Arch. Neerl. Zool., 7: 16-37.

Koski, K. 1961 Growth changes in the relationships between certain basicranial planes and the palatal plane. Suom. hammaslääk. toim., 57: 15-26.

——— 1973 Variability of the craniofacial skeleton. Amer. J. Orthod., 64: 188-196.

Kummer, B. 1952 Untersuchungen über die ontogenetische Entwicklung des menschlichen Schädels. Zeits. Morph.Anthrop., 43: 331-360.

——— 1957 Zur Frage der Orientierung von Primatenschädeln zum morphologischen Formvergleich. Anthrop. Anz., 20: 283-290.

Kvinnsland, S. 1971a The sagittal growth of the foetal cranial base. Acta odont. Scand., 29: 699-715.

——— 1971b The sagittal growth of the upper face during foetal life. Acta odont. Scand., 29: 717-731.

——— 1971c The sagittal growth of the lower face during foetal life. Acta odont. Scand., 29: 733-743.

——— 1973 Changes in the foramen magnum axis during foetal life. Acta odont. Scand., 31: 175-178.

Lavelle, C.L.B. 1974 An analysis of foetal craniofacial growth. Ann. hum. Biol., 1:269-287.

Lavelle, C. L. B. and W. J. Moore 1970 Proportionate growth of the human jaws between the fourth and seventh months of intrauterine life. Arch. oral. Biol., 15: 453-459.

Levihn, W. C. 1967 A cephalometric roentgenographic cross-sectional study of the craniofacial complex in fetuses from 12 weeks to birth. Amer. J. Orthod., 53: 822-848.

Luke, D. A. 1976 Dental and craniofacial development in the normal and growth-retarded human fetus. Biol. Neonate, 29: 171-177.

McNamara, J. A. 1978 Personal communication.

Moss, M. L. 1958 The pathogenesis of artificial cranial deformation. Am. J. phys. Anthrop., 16: 269-286.

Moss, M. L. and L. Salentijn 1969 The capsular matrix. Amer. J. Orthod., 56: 474-490.

Pankow, G. 1948 Untersuchungen über die Schädelbasisknickung beim Menschen. Zeit. menschl. Vererb.- u. Konst. lehre, 29: 69-139.

Patten, B. M. 1946 Human embryology. Blakiston, Philadelphia.

Scharf, J.-H. 1974 Die Lage der Wendepunkte der Wachstumskurven während der Intrauterinperiode bei Homo sapiens. Acta Anat., 88: 520-540.

Slagsvold, O. and K. Pedersen 1977 Gonial angle distortion in lateral head films: A methodological study. Amer. J. Orthod., 71: 554-564.

Weidenreich, F. 1941 The brain and its role in the phylogenetic transformation of the human skull. Trans. Amer. philos. Soc., n. s., 31: 321-442.

Vinkka, H. and K. Koski 1974 Inter-and intraobserver variability in an X-ray craniometric analytical method. Proc. Finn. dent. Soc., 70: 156-160.

——— 1975 Variability of the craniofacial skeleton. II. Comparison between two age groups. Amer. J. Orthod., 67: 34-43.

Vinkka, H., K. Koski and J. A. McNamara 1975 Variability of the craniofacial skeleton. III. Radiographic cephalometry of juvenile Macaca mulatta. Amer. J. Orthod., 68: 1-7.

TABLE 1.

The crown-rump resp. postconceptional age distribution of the fetal material *

C-R length, mm	Postconception age, weeks	N
140 - 153	17	5
154 - 167	18	6
168 - 179	19	8
180 - 191	20	8
192 - 202	21	3
203 - 213	22	5
214 - 224	23	7
225 - 234	24	1
235 - 245	25	2
		45

* Age determinations based on size according to Patten ('46).

TABLE 2.

Means and variances of angles between some basicranial and facial lines, in degrees

	INFRA	PAL *	CLIVUS	FOR *
INFRA			118.7	
PAL			46.8	-10.3
CLIVUS	42.98	50.68		123.1
FOR		48.59	53.64	

* Not measured because of tendency for change.

TABLE 3.

Means and variances of angles between some mandibular lines, in degrees

	AMC	MAND	RAMUS	COND
AMC		0.6	136.9	163.9
MAND	7.57		136.3	163.3
RAMUS	68.93	69.99		27.0
COND	32.07	27.98	82.28	

The surface characteristics of tooth roots and their biomechanical importance

I. KOVACS

OSSA

Traditionally the study of tooth roots has not played a large role in evolutionary studies, comparative anatomical investigations and other areas of odontology. Most often the emphasis has been on the morphology of the tooth crown. A detailed investigation of tooth roots is important from a biomechanical viewpoint and is therefore closely tied to tooth function.

This paper presents observations on the surface characteristics of tooth roots in relation to their "gnathofunction". Observations, by several methods reveals the presence of longitudinal root fossae, rugosities (of various types), corrugations, rough areas and areas of resorption. An understanding of these features, particularly in relation to jaw and tooth function (biomechanics) is important for evolutionary studies, comparative anatomy, determination of dental age and even periodontology.

В силу традиции изучение корней зуба не играет большой роли в исследованиях эволюции, в сравнительных анатомических исследованиях и других областях одонтологии. Чаще всего особое значение придают морфологии коронки зуба. Детальное изучение корней зуба представляется важным с биомеханической точки зрения и поэтому тесно связано с функцией зуба.

Эта статья посвящена изучению свойств поверхности корней зуба в связи с их "челюстной функцией". Наблюдения, сделанные с помощью различных методов, обнаруживают присутствие продольной зубной ямки, складок /различных типов/, волнистости, шероховатых областей и областей резорбции. Понимание этих черт, в особенности, в связи с биомеханической функцией нижней челюсти и зубов, важно для изучения эволюции, сравнительной анатомии, для определения возраста зубов, а также - для периодонтологии.

Ключевые слова: морфология, корни зуба, биомеханическое значение.

I. Kovacs, 132, Avenue du Parc, Bruxelles. 1060 Belgium.

Vol. 6, pp. 181-192, Lund. ISSN 0345-8865.

Introduction

The characteristics of tooth roots have not been examined sufficiently, although they afford a broad research field for investigaton (Kovacs, 1967, 1971). Among the large number of interesting points, we selected the influence of the roots on the development of the teeth in various species including human beings as well as their influence on the periodontium. We feel that the study of roots should constitute the starting point when studying peridontology.

In the past, the study of dental evolution was practically limited to the crowns. Crown morphology is deeply engraved in phylogeny for which its characters are more meaningful than those of the roots. Considering that the roots still grow after the onset of function and that they follow the evolution of this function more readily than the crown, in our opinion, the study of dental evolution should be based primarily on the changes occurring in the roots and secondarily on the crown morphology.

As to the biomechanical problem raised by periodontium, it is closely related to the surface of the tooth roots. We propose to stress the importance of the surface characteristics of the roots, with regard to the biomechanical aspects of peridontium.

In order to evaluate the importance of the surface characteristics of tooth roots, we shall examine first the "gnathofunction", which is determined by the following fundamental elements:

1) How strong is the action?
2) In which direction is it applied?
3) How long is it applied?
4) What is the morphology of the teeth?

A perfect physiological function is achieved when these four elements are perfectly balanced.

1) Strength of the action

The strength of human jaws has been assessed by various authors from 25 to 250 kg (Hildebrand 1937; Klaffenbach, 1936; Pernkopf, 1958; Riechelman, 1958; Tholuck, 1923).

This strength varies idiosyncratically as well as with sex and age. It is also dependent on the bite point since the maximum strength is exerted at the level of the first molars and the minimum strength at the level of the middle incisors. Strength is also determined by the largest opening angle which can be achieved by the jaws and masticatory muscle cross-section, insertion and fiber number. It is to be noted that the strength of this action can be increased with constant practice and reduced by the lack of practice.

As far as we know, the strength of animal jaws has not been investigated or reporte in the literature.

2) Direction of the strength

The direction of the strength is determined by the morphology of the temporomandibular articulation. It is related to function which varies according to the species. In carnivores, the function is vertical, as the temporomandibular articulation allows them only a slicing movement. (This movement occurs on alternate sides of the jaw.)

In herbivores and rodents, the action is horizontal. The omnivorous species combine both actions. But teeth shaped for bearing a vertical strength will perhaps not bear the horizontal strain and its lever action, and they will be damaged. Originally, man had the tooth roots of the omnivorous species, which have now become very similar to carnivores' roots, owing to phylogenetic evolution. But man has retained the function of an omnivore, with lateral movements. This lack of balance between function and morphology is one of the main cause of peridontal disease in man (Kovacs, 1976).

When forces are applied vertically, it means that theoretically they are applied along the tooth axis, but this seldom happens in practice, as the teeth are not always in the best position to receive the axial forces. Then again, the forces are para-axial and the lever effect is present.

3) Duration of the action

The duration of the action is not limited to mastication, but extends to the clenching of the jaws in various circumstances. For instance in man, when a physical or psychical effort is sustained, in anger, or in states of nervous stress, grinding of the teeth occurs. This can occur whether people are awake or asleep. The duration of such grinding can become pathological, for example in epilepsy and have a serious impact on the balance described above. In animals, this duration can be prolonged by adrenergic excitation. Unceasing action may lead to ischemia, resulting in bone resorption.

4) Morphologic data on roots and teeth

This broad subject cannot be examined entirely here, but we want to stress the special interest of some of the points. They are: the real length of the root; the relative length of the root; its curve; the angle of its bifurcation; its quantitative surface; the surface rugosities. Moreover, a direct relation has been observed between the root surface and the strain applied to the teeth by the action of masticating. This relation has been well designed by nature. That is, corresponding to a larger occlusal surface, is a

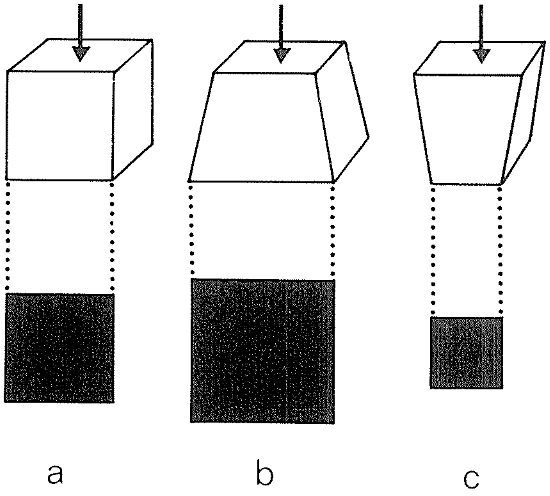


Fig. 1. Schematic example of the biological relationship between the occlusal surface of the crown and the surface area of the root, assuming the intensity and direction of the forces are constant. This question is of course more complex.

a) there is transmission of the forces when the surface area of the root is equal to the occlusal surface area.
b) there is distribution of the forces on the surface of the root when the latter is greater than the occlusal surface area of the crown.
c) there is concentration of the forces on the surface of the root when the latter is smaller than the occlusal surface area of the crown.

larger root surface. For instance, the mesial incisor has a ± 125 mm^2 root surface, the premolar has two roots with a total surface of ± 175 mm^2, and the first upper molar roots have a total surface of ± 375 mm^2.

In carnivores, the premolars have practically no occlusal surface, as these teeth are designed for cutting rather than for crushing, whereas in herbivores, omnivores and rodents broader occlusal surfaces are observed.

In order to elucidate the biological relationship between the occlusal surface of the tooth and the root surface, refer to Figure 1. Here, the schematic example of this relationship supposes that the intensity and direction of the forces are constant, which is not the case in vivo.

We point out that, a) the force is transmitted when the root and the occlusal quantitative surfaces are equal; b) the force is distributed on the root surface when this is larger than the occlusal surface of the crown; c) the force is concentrated on the root surface when the latter is smaller than the occlusal surface of the crown. The biomechanical importance of the root surface is due to the fact that during the mastication the strain is distributed onto the root surface.

Points a) and b) describe normal physiological conditions. Point c) describes a pathological condition. The biomechanical importance of the relation between the root and tooth surface is due to the fact that, in the normal physiological conditions, the strain of mastication is distributed on the root surface, whereas the strain is concentrated on this surface when a pathological condition is present. The latter results in too much strain being applied on a small surface, an important element in the pathology of the periodontium. The strain applied to the crown and distributed on the root surface finally reaches the alveolar bone through the ligament fibers.

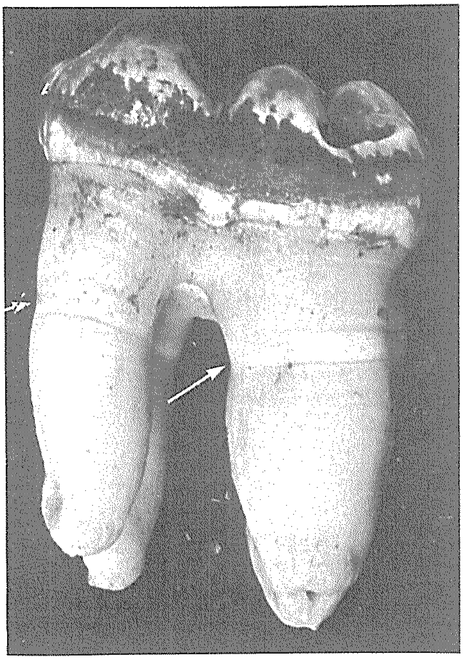


Fig. 2. Third mandibular molar of a mountain gorilla. The proportion of root length developed during the two stages is not exactly the same as in man. In gorilla's teeth, that part of the root developed during the eruptive phase is smaller than in man's teeth.

A well-balanced relation of these various elements is essential to a satisfactory physiological function. The root surface is one of these elements as are the rugosities or smoothness of this surface, which can modify the distribution of the forces. The main characteristics of the root surface will be examined below.

Characteristics of Tooth Root Surfaces

In a previous work, we examined the sizes of the roots in various species. We now propose to study the quality of this surface, since it is clear that any rugosities and corrugations increase the surface area.

Three observation methods were used: 1) direct visual observation; 2) macrophotography and 3) microscopic observation. The field of observation becomes smaller as the picture is enlarged, but the synthesis of the three methods supplies a complete image.

1) Direct visual observation

If we examine various root surfaces, we see that they all show some determined geography following the examined sides. If we apply the usual classification, e.g. mesial, lingual and distal sides, we see more differences between the various roots on the mesial side than on the others.

On the other hand, we know that human teeth show one universal character: the roots are not vertical but show an incline of 18 to 20 degrees with regard to the crown.

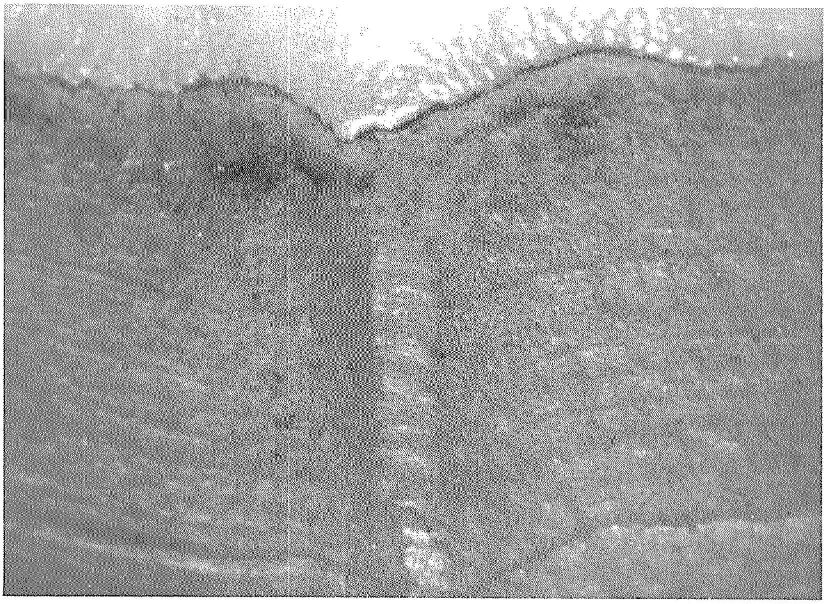


Fig. 3. Macrophotograph (enlarged 30 times) of part of the root of a human maxillary molar, on the distal side. Rather circular undulations are observed which remind us somewhat of enamel perykimata.

Consequently, the strain resulting from the function acts more strongly on the mesial than on the distal side, and that is why the mesial side of the root shows excrescences large enough to be seen by direct observation, whereas the distal side seems smooth. This character shows particularly clearly on a first lower molar root.

- Longitudinal root fossae

When we examine the roots in various species, we see that longitudinal fossae exist on the side of the root bearing the strain. Furthermore they are more numerous and strongly marked in herbivores (of which roots show fossae all around the surface), less numerous and less marked in the omnivores, and that they are seldom seen, superficially marked or even non-existent in carnivores. These fossae increase the quantitative surface area of the root, and also provide the tooth with a firm hold in the area where it has to bear a strain resulting from lateral movements.

- Rugosities

If the root surface is examined in detail, a constant morphologic feature can be observed - the root is divided into two sections: one is the part located nearer to the apex, equal to the third of the total length on the surface of which some small regular or irregular rugosities, corrugations or circular plications are seen. This part of the root has grown during the penetrating phase; the other is constituted by the two remaining thirds which are smoother - this part has developed during the eruptive phase.

This relation allows the timing of the root development to be reconstituted, which was the subject of a previous study to which the interested readers will kindly refer (Kovacs, 1964).

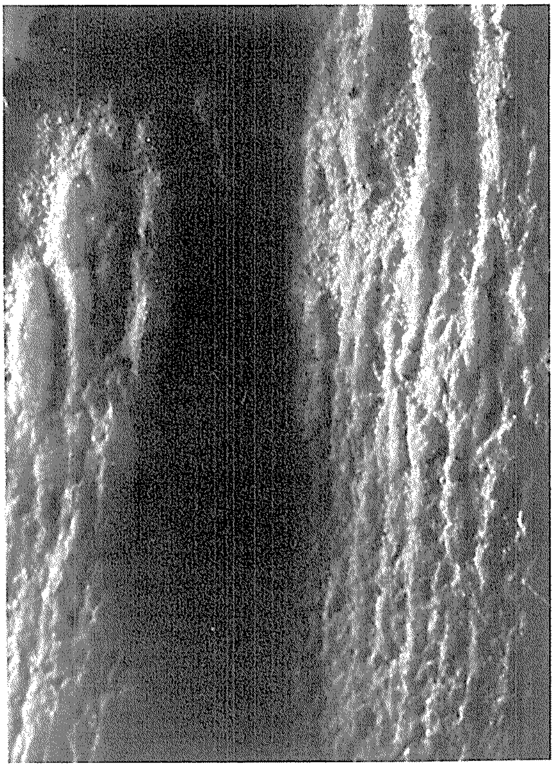


Fig. 4. Macrophotograph (enlarged 15 times) of the surface of a second mandibular molar root of a mountain gorilla. These vertical grooves are rather typical of herbivores.

This study demonstrated that, at the time of occlusion, two thirds of the human tooth root is already developed. This proportion can vary according to the various teeth and individuals. An X-ray study of chimpanzees, gorillas and lions shows a difference in the development of the roots. In anthropoids, the part of the root developed during the eruptive phase is smaller (Fig. 2) whereas in carnivores, the root development is nearly completed before occlusion occurs. It seems that the root rugosities play a big part in the distribution of masticatory forces. Indeed the direction of the force may vary and the teeth with rougher roots can better withstand the strains of laterally applied forces than the teeth with smooth roots.

2) Observation by Macrophotography

The macroscopic study combined with macrophotography is very efficient because a surface which looks smooth and insignificant when observed directly, will show many interesting details when examined through a magnifying lens (enlargement: x10).

In order to give a clearer view of these irregularities, we dyed the roots with printing ink and then rubbed them with moist chamois leather which eliminated the ink on the prominent parts, thus giving a contrasting effect. In this way it was possible to observe:

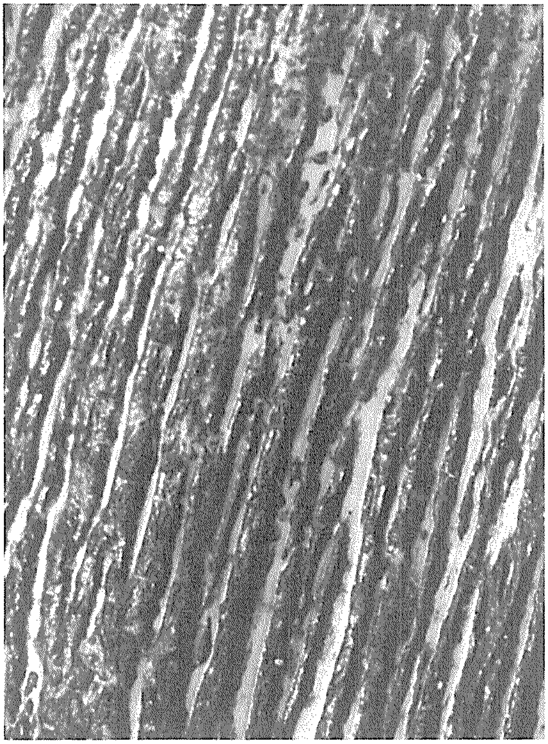


Fig. 5. Macrophotograph of part of the root of an elephant's molar. This picture shows a rather regular vertical pleating which extends over the whole surface of the root and increases the surface area considerably. (Enlarged 9 times).

- The corrugations

If we examine the macrophotograph (Fig. 3) of a root or part of a root, we see that really smooth surfaces are seldom found, though they may have seemed smooth when observed with the naked eye.

Rugosities are generally found, and, on the major part of the surface, they consist of corrugations looking somewhat like perikymata appearing on the crown enamel surface, but larger. These corrugations are more pronounced in young subjects than in older ones, in whom the secondary cement production can modify and even smooth them out. We think that if these rugosities were studied thoroughly, it might help to determine the subjects' age (Fig. 8). In man and anthropoids, the most pronounced corrugations are found in the apical third of the root. In carnivores, they are much less pronounced, like the longitudinal radicular fossae. In gorilla (Fig. 4) and elephant (Fig. 5) roots, we did find vertical corrugations whereas in the horse (Fig. 6), regular corrugations were observed towards the apical third of the molar roots.

- Irregular rugosities

This type of rugosity is observed in all species. It is more pronounced towards the apical third and becomes even more so with old age, owing to secondary hypercementosis (Fig. 7).

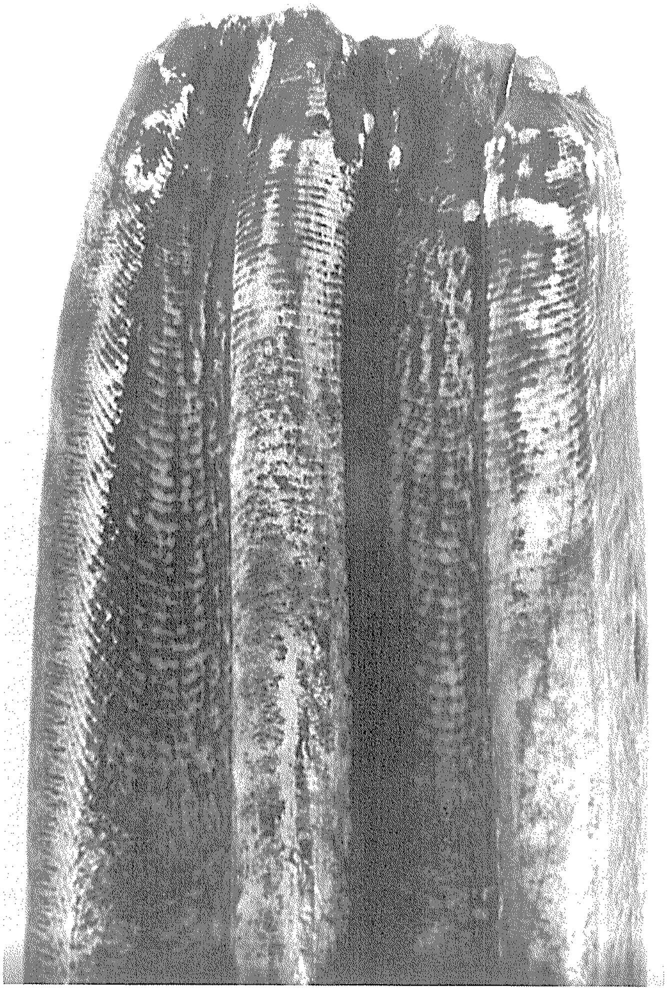


Fig. 6. First molar of a horse. In this picture two deep longitudinal fossae and, on the whole surface of the root, horizontal corrugations are seen. These fossae and corrugations result in a significant increase of the root surface area allowing it to bear lateral strains.

- Resorption

Resorption, according to Bouyssou, Leipp & Zerosi (1965) is often observed, even in the roots of normally functioning teeth in approximately 9 of 10 individuals. These small radicular resorptions occur in areas where the strain is brought to bear the most heavily on the tooth. The resorptions look like small craters in the root surface and occur particularly in the apical part.

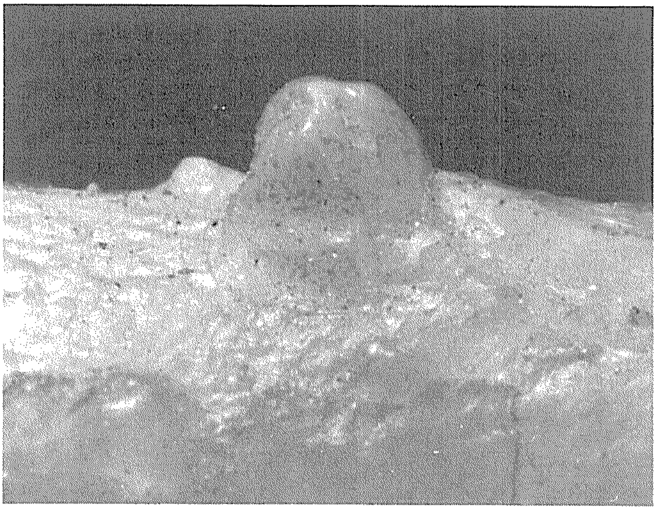


Fig. 7. Rough spots of various sizes are sometimes found on the surface of the root. They appear most frequently on that part of the root which develops during the penetrative phase. This macrophotograph of a human mandibular molar shows such a rough spot enlarged 25 times.

- The rough areas

We know that rough areas develop mainly during the penetrating phase, since they are found most often on the apical third of the root. Numerous observations show them to occur more frequently than was presumed.

3) Observations by means of various microscopes and measuring instruments

The surface rugosities of materials designed for industrial use are generally subject to thorough examination as the surface quality plays an important part in the way in which the pieces or parts will fit together. We examined a few of these techniques which, in our opinion, can be applied to the study of the root surface, and help to improve its knowledge. They are: Mechau's optical system; pneumatic technique by Göttel; electric technique by Perthen; slit-light microscope (Schmaltz method); palpation method of Forster; interference microscope: Zeiss-Linnik' s method (Fig. 9); observation by means of a scanning electron microscope.

The individual investigator is usually not in a position to apply these techniques which require team-work and are quite expensive. However, we are anxious to know the impact which they certainly would have on the completion of our study. This would open new horizons in the field of comparative studies and would provide solutions to numerous problems in the field of pathology and especially of periodontal disease.

This is of some interest to others as well since during a recent conversation on this matter, a proposition was extended to the author, to undertake a root study utilizing a scanning electron microscope. This study will be done in the near future.

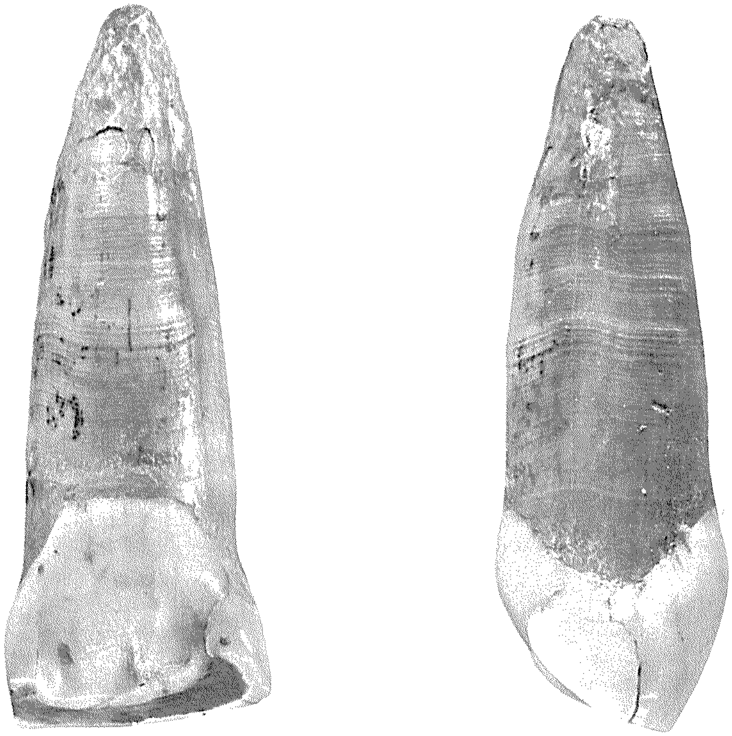


Fig. 8. Neanderthal upper central incisor from Hortus, lingual and distal sides. Photograph courtesy of Mrs. M. A. de Lumley (de Lumley et al. 1972). Horizontal, parallel and regular corrugations appear on the root surface. This phenomenon is seen only in young subjects and disappears with age and secondary cement production. This is why we propose to use these corrugations to determine the subjects' age.

Summary and Conclusions

We have stressed the biomechanical importance of the various elements in the study of tooth roots, and particularly, the quality of the root surface as being an essential aspect in the study on evolution, comparative anatomy, the determination of a subject's age, and periodontology.

Various observation methods were proposed, e.g. direct visual, macrophotograph and microscope examination, as well as various measuring systems. The synthesis of all these observations would supply investigators with a fairly complete picture of the root surface.

We have presented the various types of rugosities which vary according to species, the particular tooth and individual. These include longitudinal radicular fossae, circular, regular or irregular rugosities and plications, the corrugations, the resorptions and the roughness.

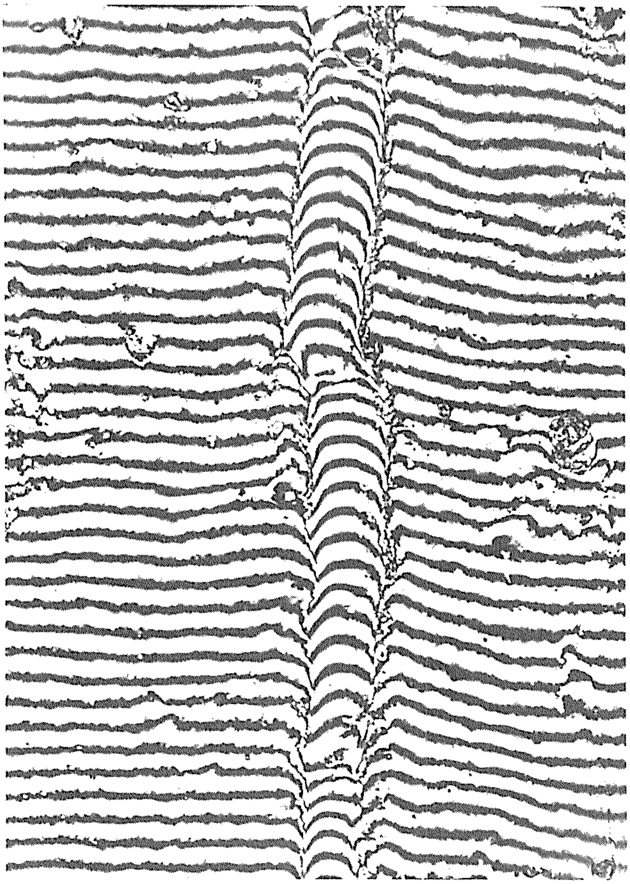


Fig. 9. Microscopic photograph of the root impression of a central incisor. Impression made with acetylcellulose. Interferential microscope Leitz. The regular lines mean that the surface is rather smooth and the microfossa is shown by the corrugations.

Literature cited

Bouyssou, M., F.H. Leipp and C. Zerosi 1965 Résorptions dentaires et biologie osseuse. 1 vol. 613 pp. Sciences et Lettres, éditeur, Liège.

de Lumley, M.A., H. Haltes, R. Brandi, E. Guerrier, F. Pillard and B. Pillard 1972 Haltes et campements de chasseurs neanderthaliens dans la grotte de l'Hortus (Valflaurès Hérault). Etudes quaternaires, Memoire No. 1, pp. 527-624.

Hildebrand, G.J. 1937 Studies in Dental Prosthetics. Vol. I, Chap. 8, Stockholm.

Klaffenbach, A.O. 1936 Gnathodynamics. J. Am. Dent. Assoc. 23, 371.

Kovacs, I. 1964 Contribution à l'étude des rapports entre le développement et la morphologie des racines des dents humaines. Bull, Gr. Int. Rech. Sc. Stom., No. 1.

______ 1967 Contribution to the ontogenetic morphology of roots of human teeth. J. Dent. Res. supp. vol. 46, No. 5.

Kovacs,I. 1971 A systematic description of dental roots. In: Dental Morphology and Evolution, A.A. Dahlberg (edt). University of Chicago Press, Chicago, pp. 211-256.

Kovacs, I. 1976 Eine Ursache der Parodontose: Der Gegensatz zwischen den morphologische Merkmalen des Zahnwurzeln und der Kieferfunktion beim Menschen. Parodontologie, Vol. 2 (5405) 107-110.

Pernkopf, E. 1958 Anatomie des Mundbereiches. Die Zahn-, Mund- und Kieferheilkunde, Vol. I, pp. 56. Verlag von Urbain und Schwerzenberg, München/Berlin.

Riechelman, O. cited in Reichborn-Kjennerud 1958 Protetische Berhandlung und Profylaxe der Zahnlockering usw. Die Zahn-, Mund- und Kieferheilunde, Vol. 4, pp. 496. Verlag von Urbain und Schwarzenberg, München/Berlin.

Tholuck, H.J. 1923 The force of mastication. Deutsche Zahnarzt Wissenschrift 51, 24.

Variations in skull base flexure among twins

ANDERS LUNDSTRÖM

OSSA

Skull base flexure according to the angle basion-sella-nasion has been studied in 100 pairs of twins having the same sex. The material included 50 pairs diagnosed as monozygotic (MZ) and 50 pairs as dizygotic (DZ) twins.

Variations within MZ and DZ pairs were studied using correlation coefficients. Variances were also determined for MZ and DZ twins and compared with the total sample variance after effects due to accidental measurement errors had been eliminated. The findings are discussed and caution recommended as regards interpretation of results.

Keywords: Skull base flexure, twins.

При изучении изгиба основания черепа был использован угол базион-турецкое седло-назион у 100 пар близнецов одинакового пола. Материал включал 50 пар однояйцевых близнецов /monozygotic, MZ/ и 50 пар двуяйцевых близнецов /dizygotic, DZ/ по установленному диагнозу.

При помощи метода корреляционных коэффициентов изучались вариации у MZ и DZ пар. Дисперсии вычислялись также для близнецов MZ и DZ. Их сравнивали с общей дисперсией образца после устранения эффектов, зависящих от случайных ошибок измерения. Проводилось обсуждение обнаруженных результатов, к которым рекомендуется подходить с осторожностью.

Ключевые слова: изгиб основания черепа, близнецы.

Anders Lundström, Faculty of Dentistry, Karolinska Institutet, Box 3207, S-10364 Stockholm, Sweden.

Vol. 6, pp. 193-198, Lund. ISSN 0345-8865.

Introduction

It is well known that in primates especially Homo Sapiens, there is considerably more flexure of the skull base than in most four-legged animals. The phylogenetic development of this flexure has been explained by Weidenreich (1924) as being due to the change in head position brought about by upright locomotion on two feet. The change in the skull base is, according to this hypothesis, designed to accomodate horizontal eyesight. Another hypothesis has been presented by Dabelow (1931) who claimed that skull base flexure was the result of increased brain volume, the site of sella turcica remaining more or less unaffected.

Considerable individual variation has been demonstrated with regard to skull base flexure. Measurements of the basion-sella-nasion angle have given means approaching 130 degrees irrespective of sex and with standard deviations varying between 4.2 and 5.3 degrees (Table 1). Individual growth changes have been investigated by Brodie Jr (1955). Brodie's annual measurements of 30 cases from 5 to 15 years ranged from -6 to +5 degrees with a mean change +1 degree. Björk's figures showed a similar variation (standard deviation 1°9, range 10°5) and mean change (+0°8) between 12 and 20 years. Björk also related the angle at 12 years to the angle at 20 years and found a high degree of correlation (r = 0.91). Knott (1969) concluded from a review of the literature (Björk, Stramrud, Koski) and from studies of her own that there is "little if any change on the average after age about 6 years".

Histologic studies by Melsen (1974) have shown resorption on the occipital part of the clivus, which "per se would tend to reduce the cranial base angle" with age. As, however, greater growth activity was found in the external than in the internal part of the spheno-occipital synchondrosis, this would tend to counteract such a change.

Houston & Brown (1980) calculated partial correlation coefficients for a number of cranio-facial variables including skull base flexure. These were based on fathers, mothers and midparent-values in relation to their sons and daughters. The mid-parent/child correlations for the younger and older children in each sex were -0.04, 0.71, 0.47, and 0.32. The first and last of these differed significantly from the theoretical value of 0.7 obtained on the assumption that polygenetic inheritance alone is responsible for skull base flexure.

The skull base has special orthodontic significance as a basis for superimposition when studying growth or orthodontic treatment effects. The extent of genetic and non-genetic influences as regards the degree of skull base flexure should therefore be of interest. The aim of following presentation is to further contribute to our knowledge in this field.

Material

The twins studied have been described in earlier publications (1954, 1963a). Zygosity determinations were based on anthropological similarity determinations including careful tooth anatomy comparisons. In addition 40 pairs underwent serological and blood-group determinations. Of these, 17 pairs showed discordance and were found to have primary similarity diagnoses indicating dizygosity. For the remaining 23 pairs with concordance of blood-groups and serological tests, 22 had similarity diagnoses of MZ and 1 of DZ. The probability of this latter pair being identical was, according to the blood-groups and serological findings, 0.96 and there is, therefore, reason to question the similarity diagnosis in this case.

The value of tooth-morphology as a basis for zygosity diagnoses has been demonstrated in an earlier publication (1963b) with a 94% concordance between diagnoses based on comprehensive determinations including somatic, serologic and blood-group data on the one hand, and tooth anatomy alone on the other. Discordance was found in 0.8 per cent where tooth anatomy indicated MZ and 4.8 per cent where tooth anatomy indicated DZ. These findings suggest that only in very few cases should MZ pairs be wrongly diagnosed as DZ or vice versa. Altogether 100 pairs of twins were studied including 50 diagnosed as MZ (15 male and 35 male) and 50 diagnosed as DZ (26 male and 24 female). The age range varied between 7 and 20 years. For 41 pairs a second investigation was undertaken some 13 years after the first one, which for most of the twins was performed between 12 and 15 years of age.

Method

Skull base flexure was measured on profile radiographs according to the basion-sella-nasion angle. Basion was defined as the tip of the anterior contour of foramen magnum as seen from sella turcica. Measurements were performed to the nearest tenth of a degree with the help of a digitizer constructed by the Central Institute for Industrial Research, Oslo. Due to difficulties in locating basion on the radiograph 2 MZ and 4 DZ pairs had to be excluded.

In order to determine the extent of accidental measurements errors double determinations were performed using two radiographs from each twin. The error variance was calculated according to the formula:

$$S_i^2 = \frac{n \Sigma d^2 - (\Sigma d)^2}{2n \cdot (n-1)}$$

where d is the measurement difference between the first and second radiographs. The value obtained for the younger series was:

$$S_i^2 = 1.02 \quad (n = 62)$$

This was found to be 4.9% of the total sample variance (V = 20.98) and high enough to be taken into account when analysing MZ and DZ variances.

Results

Earlier studies have shown similar variations of skull base flexure with regard to sex and age (Table 1). It has, therefore, been considered justified to pool all MZ and DZ-twins accordingly. This procedure was further substantiated by the strong correlation between young and old cases shown by Björk (r = 0.91). The present material also suggested a strong association between skull base flexure in different sexes at different ages (r = 0.88). Also, the longitudinal study of 41 pairs resulted in means and standard deviations for young and old twins that were very similar ($\bar{x}$ = 130°3 and 130°1: sd = 4°73 nd 4°72, respectively). Low non-significant partial correlation coefficients between skull base flexure, age and sex (Table 3) give further support to justify pooling the entire twin-material irrespective of age and sex.

Table 2 shows the means and standard deviations found in the two types of twins. It is noted that this variation corresponds closely to what has earlier been found for non-twin populations. No difference could be demonstrated between the MZ and DZ twins or between 1:st and 2:nd born twins. A test of kurtosis and skewness gave no clear indication of any divergence from normal distribution as only one of four corresponding variables showed a significant deviation at the 5% level in each test (Table 4).

Correlation coefficients for skull base flexure were calculated from the following pairs of observations: (1) measurements from duplicate radiographs of the same individual. (2) measurement from MZ twins. (3) measurements from DZ twins. The results are presented in Table 5. The difference between correlation coefficients for MZ (r = +0.72) and DZ (r = +0.41) is significant at the 5 per cent level.

Differences between MZ and DZ co-twins can also be expressed through variances calculated according to the method previously described for measurement errors. These results are presented in Table 6 together with an estimate of the total sample variance for twins. The latter was obtained as the weighted mean of variances from the four standard deviations presented in Table 2. The difference between the DZ and MZ variance was significant at the 5 per cent level.

Discussion

A basic problem in all twin research is the reliability of the twin-diagnoses. As blood-grouping and serological testing has only been performed for part of the present material there is obviously some doubt as regards the validity of the MZ and DZ grouping. The degree of concordance between similarity diagnoses based on general anthropology and tooth-anatomy - as judged by the author - on the one hand, and blood-grouping including serological testing on the other, suggests, however, that the number of erroneous diagnoses was small. Nevertheless, it cannot be excluded that such errors can have occurred. Because of this the difference obtained between the correlations for MZ and DZ pairs is more likely to be somewhat less than would have been obtained had more reliable diagnoses been available.

Differences in skull base flexure within MZ pairs may well be due to developmental inferences acting during the prenatal period or early infancy. The strong correlation from approximately 12 years onwards suggests that later deviations are of a limited degree. The close correspondance of means and standard deviations between non-twin populations presented in Table 1 and the MZ and DZ twins presented in Table 2 indicates that the special twin environment does not, in itself, create circumstances which notably affect the variation in skull base flexure.

The comparisons between MZ, DZ and the total sample variances, show the stepwise increase of variances when, first, genetic differences of the magnitude relevant for brothers and sisters and, secondly, genetic and non-genetic influences operating between families are added.

Thus population and DZ variances, corrected for the effect of accidental measurements errors, were 20.0 and 11.2 respectively. This difference of about 9 represents almost 45 per cent of the total sample variance.

Summary

A study of skull base flexure was carried out on 100 twin pairs of the same sex (50 MZ and 50 DZ) and gave the following results.

1. Twin means and standard deviations for one twin from each pair did not differ significantly from corresponding values for non-related individuals as reported in the literature.
2. A high correlation coefficient ($r = +0.94$) was found between double determinations of skull base flexure measured on duplicate profile radiographs. A slightly lower correlation ($r = 0.88$) was obtained between two measurements of the same individual after an interval of 13 years.
3. Correlation within MZ and DZ twin pairs resulted in coefficients of $r = +0.72$ and $r = +0.41$ respectively. This difference is significant at the 5% level.
4. Variances within MZ and DZ twin pairs and the population were 5.5, 11.2 and 20.0 respectively. The difference between 11.2 and 5.5 was significant at the 5% level.
5. The difference between the total sample variance and DZ variance was 8.8 and represents that part of the total variance which may be explained by genetic and non-genetic influences acting between families.

References

Björk, A. 1955 Cranial base development. Am. J. Orthod. 41: 198-225.

Brodie, A.G. Jr. 1955 The behaviour of the cranial base and its components as revealed by serial cephalometric roentgenograms. Angle Orthod. 25: 148-160.

Dabelow, A. 1929 Über Korrelationen in der phylogenetischen Entwicklung der Schädelform. Morph. Jb. 63:1.

______ 1931 Über Korrelationen in der phylogenetischen Entwicklung der Schädelform. Morph. Jb. 67:84.

Houston, W.J.B. & Brown, W.A.B. 1980 Family likeness as a basis for facial growth prediction. Europ. J. of Orthod. 2:13-18.

Knott, V. 1969 Childhood change in cranial base. Growth 33: 123-142.

Koski, K. 1960 Some aspects of the growth of the cranial base and the upper face. Odont. Tidskr. 68: 344-358.

Lindegård, B. 1953 Variations in human body build. Diss. E. Munksgård, Köpenhamn.

Lundström, A. 1954 The importance of genetic and non-genetic factors in the facial skeleton studied in 100 pairs of twins. Trans. Eur. Orthod. Soc., 92-107.

______ 1963 Tooth morphology as a basis for distinguishing monozygotic and dizygotic twins. Am. J. Hum. Genet., 15: 34-43.

______ 1967 Genetic aspects of variation in tooth width based on asymmetry and twin studies. Hereditas 57: 403-410.

Melsen, B. 1974 The cranial base. Diss. Acta Odontol. Scand., Suppl. 62.

Odenrick, L. 1976 Ansiktets utveckling vid juvenil reumatoid artrit. Diss. Stockholm.

Riolo, M.L., Moyers. R.E., McNamara, J.A. and Hunter, W.S. 1974 An atlas of craniofacial growth. Craniofacial Growth Series No 2. Center for Hum. Growth and Devel., Ann Arbor, Mich.

Stramrud, L. 1959 External and internal cranial base. A cross sectional study of growth and of association in form. Acta Odontol. Scand. 17: 239-266.

Weidenreich, F. 1924 Die Sonderform des Menschenschädels als Anpassung an den aufrechten Gang. Zschr. Morph. und Anthropol., 24: 157-189.

TABLE 1.

Population means ($\bar{x}$) and standard deviations (sd) for the ba-s-n Angle.

Author		Sex	No	Age	$\bar{x}$	sd
Lindergård	(1953)	M	181	20	131.8	4.6
Björk	(1955)	M	223	12	130.8	4.2
		M	234	20	131.6	4.5
Stramrud	(1959)	M	464	3-25	131.5	4.6
Koski	(1960)	M	46	7	133.3^{x}	
		F	37	7	132.3	
		M	38	11	131.4	
		F	34	11	130.8	
		M	38	15	130.5	
		F	49	15	131.8	
		M	43	22	129.6	
		F	46	22	130.8	
Riolo et al	(1974)	M	43	13	129.2	5.3
		F	29	13	130.7	4.7
Odenrick	(1976)	M+F	69	3-6	129.9	5.0
		M+F	76	6-9	131.6	4.6
		M+F	307	9-12	131.3	4.7
		M+F	424	12-16	131.1	5.1

[x] For Koski the medians.

TABLE 2.

Means and standard deviations for the ba-s-n angle in MZ and DZ twins.
A = Firstborn, B = Secondborn twin.

	n	$\bar{x}$	sd
MZ A	48	130.7	4.79
B	49	130.8	4.49
DZ A	48	132.9	4.56
B	46	132.1	4.47

TABLE 3.

Partial correlation coefficients expressing the covariation of skull base flexure (1), age (2), and sex (3) in the twin material.

	MZ (A) 49	MZ (B) 49	DZ (A) 48	DZ (B) 48
$r_{12.3}$	-0.20	+0.15	+0.16	+0.12
$r_{13.2}$	-0.17	-0.18	+0.14	-0.07
$r_{23.1}$	+0.11	+0.17	+0.06	+0.10

TABLE 4.

Kurtosis and Skewness for the ba-s-n angle in MZ and DZ twins

	n	Kurtosis	Skewness
MZ A	49	3.66	0.72^{+}
B	49	4.03^{+}	0.16
DZ A	48	2.62	-0.19
B	48	2.73	0.09

TABLE 5.

Correlation coefficients and degrees of significance for the ba-s-n angle in three pairs of observations.

	n	Correlation coefficient (r)
Double determinations	64	$+0.94^{+++}$
MZ twins	48	$+0.72^{+++}$
DZ "	46	$+0.41^{++}$

TABLE 6.

Variances for skull base flexure within MZ and DZ twins and in the total sample.

	MZ	DZ	Total sample
n	49	46	191
V	6.56	12.20	20.98
V_c [1]	5.54	11.18	19.96

[1] V_c has obtained as $V-S_i^2$ and is thus a corrected value after elimination of the error variance.

The dental morphology of the Inuit of the Canadian Central Arctic

JOHN T. MAYHALL

OSSA

The Inuit (Eskimos) of the Foxe Basin area of the Northwest Territories, Canada were studied to determine the size and shape of their teeth. These individuals were found to have a low number of maxillary incisors displaying an absence of shovel-shaping. In contrast to some reports for Mongoloid populations, a low incidence of premolar occlusal tubercles was noted. Other traits reported include the protostylid, sixth cusp (tuberculum sextum) and seventh cusp (tuberculum intermedium) on mandibular molars. Maxillary molars were examined for the Carabelli's trait. Fourteen percent of the population displayed a cusp expression in contrast to a lower percentage found in the biological precursors of the present day Inuit. Both mesiodistal and buccolingual crown diameters were determined for all teeth. The variability noted in the diameters supports A. A. Dahlberg's field concept.

Keywords: Dental Morphology - Eskimos.

Были изучены размеры и форма зубов эскимосов из области Бассейна Фокс в северозападной Канаде. У этих индивидов отмечалось небольшое число верхнечелюстных резцов, причем отсутствовали резцы лопатообразной формы. В противоположность некоторым сообщениям, касающимся монголоидной популяции, наблюдали низкую распространенность жевательных бугров на малых коренных зубах. Среди других черт отмечали наличие протостилида, шести бугорков /tuberculum sextum/ и семи бугорков /tuberculum intermedium на больших коренных зубах нижней челюсти/. Признак Карабелли был изучен у больших коренных зубов верхней челюсти. 14% популяции обнаруживало наличие бугорков по сравнению с низким процентным показателем, найденным у биологических предшественников современных эскимосов. Как мезодистальные, так и щечно-язычные диаметры коронки были определены у всех зубов. Изменчивость, отмеченная в отношении диаметров, поддерживает концепцию А.А. Дальберга.

Ключевые слова: морфология зубов, эскимос.

John T. Mayhall, Faculty of Dentistry, University of Toronto, Toronto, Canada.

Vol. 6, pp. 199-218, Lund. ISSN 0345-8865.

While the Inuit (Eskimos) occupy the widest latitudinal range of any aboriginal group in the world, the comprehensive studies of their dentition have dealt with those groups living at the extremes of the range. P. O. Pedersen ('49) produced a remarkable monograph on the East Greenland dentition. At the other extreme of the geographic range C. F. A. Moorrees ('57) comprehensively studied the Aleuts, an Eskimoid people. Another study dealt with Alaska Indians, Aleuts and Eskimos (Turner '67). To my knowledge, no comprehensive studies have detailed the dental morphology of the Canadian Inuit, with the exception of my 1976 study which is partially summarized here. It seems odd that with cooperative groups such as the Inuit, with the archeological theories of population movement extant, and with dental morphology having been demonstrated as a useful tool for identifying population affinities, there have been so few studies.

The results presented here will be concerned primarily with the Inuit presently residing in the Foxe Basin area of central arctic Canada. Another paper (Mayhall, '79) has dealt with the dental morphology of the prehistoric Thule culture skeletal material from the same area and has discussed the biological relationship between the Thule culture people and the modern Inuit.

The Inuit of the Foxe Basin were the subject of intensive study by a multidisciplinary project under the auspices of the International Biological study, human adaptability section, between 1969 and 1973. Included in the study was an assessment of oral health, craniofacial growth studies and dental morphology analyses.

Materials and Methods

Dental stone models were made from alginate impressions of all available residents of the two settlements of Igloolik and Hall Beach, Northwest Territories, Canada, as well as from some groups still living outside of the settlements (on the land) in 1969. Every effort was made to see each person in the settlement, and messages to two outlying camps 80 and 120 miles from Igloolik resulted in the residents traveling to Igloolik to be examined. Hall Beach, sixty miles to the south, was included in the study about six months after the initial Igloolik data collection was completed. Table 1 indicates the population of these communities and the numbers examined. It should be noted that, at least, 95 individuals on the R. C. M. P. census list were either no longer resident in the community, were at very distant F. E. C. camps, at a camp too far away to contact, or out of the community for schooling or health care. Thus, we were able to examine 95 percent of the population resident in the settlements. A complete description of the two communities and their history has been provided in earlier papers (Mayhall '76).

It should be noted here that while the residents of the two communities claim to be closely related, they have come from different camps to settle in the villages. The residents of Hall Beach, generally, came from camps to the south of Hall Beach, while the Igloolik residents moved to the community from camps north, west and east of Foxe Basin.

Because of the remote possibility that there might be significant differences in the genetic constitution of the residents of the two communities, the results are reported separately here.

The alginate impressions were made using a solid metal tray to contain the material and to force it into minute spaces, thus improving the accuracy. After the impressions were obtained, they were stored briefly in 100 percent humidity until they could be filled with dental stone. The longest period of time between impression and pouring was about 45 minutes. In the majority of the cases this time was considerably shorter.

The morphological traits to be studied were chosen to alleviate the anticipated problem of obliteration by attrition and abrasion. If traits such as cusp number and groove patterns had been included in the analysis the sample sizes would have been drastically reduced. In order to reduce the chances of genetic interdependence morphological traits were chosen so that they would not be too concentrated in any one tooth class. For the incisor tooth class the presence and degree of shovel-shaping were studied for both maxillary and mandibular centrals and laterals. Canines were not included in the study because of the problems of attrition and abrasion. Premolars were surveyed for the presence of occlusal tubercles. In the maxillary molars the presence and expression of the cusp of Carabelli was observed. In the mandibular molars the sixth and seventh cusp occurrence and expressions were noted. These teeth were also examined for the presence and expression of the protostylid.

The method of recording the expressions will be explained later with each trait as it is discussed. For all of the traits, with the exception of the premolar occlusal tubercles, the plaques issued by Dahlberg (N. D.) and Hanihara ('60) were used as standards. They were constantly referred to in order to assure a continuity of the observations. In addition, the determinations of all of the traits were made in a relatively short time period, consistent with accurate observations. Many reexaminations were also made to increase the accuracy.

In addition to the above traits, mesiodistal and buccolingual crown diameters were determined for all of the teeth. There has been disagreement as to which portions of the crown should be measured to determine "mesiodistal" and "buccolingual" measurements. The definition for the mesiodistal diameter used here is that of Selmer-Olsen ('49) who suggests that this determination is " the distance between the points of contact with normal tooth position". Obiously, this definition still leaves much to one's subjective judgement, but it is rather simple with an adequate knowledge of dental morphology to determine the areas that in a malposed tooth would be the contact points. All measurements were taken parallel to the occlusal or incisal plane.

Those teeth that displayed large amounts of interproximal wear were deleted from analysis. While it is difficult to accurately describe the point at which wear becomes excessive, the best estimate might be near one-half millimeter of tooth substance. In addition, care was taken not to include those teeth that had excessive occlusal wear which might have involved the mesial and distal heights of contour.

Most authors are in agreement that the buccolingual, or labiolingual, diameter is the greatest measurement of the tooth taken as right angles to the mesiodistal measurement. While this measurement is not affected by interproximal wear, care must be taken that heavy or unusual patterns of occlusal wear do not affect the results. Many anterior teeth were unmeasurable because of the inability to determine the lingual height of contour of the teeth from the models. While some authors have deleted this determination, enough teeth were measureable to include it here.

All teeth were measured with a Peacock dial caliper and readings recorded to the nearest one-hundredth of a millimeter. The points of this caliper have been reduced to sharp points and double determinations were made regularly to assure accuracy of technique and measurement. The subsequent computer program rounded the observations to the nearest 0.1 millimeter as reported here.

Throughout the tables teeth are identified by F.D.I. nomenclature (Hrabowsky and Sim '71). Teeth are numbered beginning with the central incisor and proceeding distally to the third molar. Preceeding this digit is another number indicating the quadrant (permanent teeth: 1=maxillary right, 2=maxillary left, 3=mandibular left, 4=mandibular right). For example, the maxillary right permanent central incisor is 11, and the mandibular left permanent first molar is 36.

Results

The results for the morphological traits are reported separately for each side. Right and left sides were not combined because Biggerstaff ('73) has shown that the correlations of the results of the morphological analyses of antimeres reveal that antimere asymmetry is much higher than previously presumed when the classic "presence or absence" categories were abandoned and a more detailed analysis, as is done here, was used.

Maxillary Shovel-shaped Incisors (Table 2)

Without doubt the most typical Mongoloid dental morphological trait is the shovel-shaped incisor. Dahlberg ('49) pointed out that the shovel-shape character is more frequent in American Indians than in any other group. In the same paper he illustrated that the expression of the trait is also more pronounced in American Indians than in Inuit.

The expressions of shovelling were divided into four categories to identify the presence of this trait. These were adapted from the original description by Hrdlička ('20) and follow closely the expressions indicated on Dahlberg's plaques for use in standardized recording of the expressions. In addition to the absence category, the expressions were recorded as trace, semi-shovel, shovel, or marked shovel. Two further categories were included that may or may not be associated with the shovel-shape trait. Peg-shaped incisors may be simply a subdivision of the smooth or absent category, and they may be an indication that a tooth did not reach its full potential of growth.

At the other extreme is the barrel-shaped incisor. This expression may be the ultimate shovel-shaped incisor. While this has been hypothesized, the present results do not seem to support this argument as there is a lack of continuity between the expressions of shovelling and the barrel shape, i. e. there are no incisors displaying marked shovelling as might be expected.

In the maxillary incisors the only teeth to evidence the extremes of expression are the lateral incisors. This lends further credence to the field concept of Butler ('37, '39, and '63) and Dahlberg ('45, '49, and '63). The central incisors appear to the more conservative of the maxillary incisors.

The males from Hall Beach and Igloolik have the same range of expressions of shovelling, with neither group demonstrating marked shovelling. Few males have a total absence of shovelling (one tooth in each group). The majority of the centrals in the males are semi-shovel in expression, while in the laterals there are nearly equal numbers of trace and semi-shovel manifestations. All of the incisors showed few expressions that could be identified as "shovel" and none in the "marked" classification. The general trend in the males is towards a larger expression of the trait in the centrals when compared with the laterals. There also appears to be a bilateral symmetry to the expression of the trait.

The females show the same narrow range of expression. Very few teeth display an absence of the trait, and none show a marked expression. The majority of the centrals of the females are "trace" or "semi-" with the Igloolik females tending towards the larger expressions. The laterals of the females show the same trends as seen in the males with smaller expressions overall than in the centrals.

The comparison of the males and females does not elucidate any major differences in the expressions of maxillary shovelling.

Mandibular Incisors (Table 3)

Males and females are remarkable for their consistent patterns of shovelling of the mandibular incisors. This is in keeping with the similarity of the morphology of the centrals and laterals. As can be seen by the table, there is only a small development of the lingual marginal ridges. No sexual dimorphism is apparent from the results.

Premolar Occlusal Tubercles (Table 4)

The occurrence of an enamel covered tubercle on the occlusal surfaces of incisors, canines, premolars, and molars has been documented by various authors (Leigh, '25; Yumikara and Yoshida, '36; Tratman, '49 and '50; Lau, '55; Oehlers, '56; Alexandersen, '70; Curzon et al., '70). The occurrence on a premolar has been termed Mongoloid premolar, oriental premolar, axial core odontome, tuberculated premolar, occlusal enamel pearl and evaginated odontome, to name a few. In the past I have referred to these as premolar occlusal tubercles but Alexandersen ('70) feels that tuberculated premolar is preferable.

The range of occurrence of this trait in Mongoloids is between 0 percent in Sadlermiut (Alexandersen, '70) to 38.1 percent in Koyukon Indians (Mayhall, unpublished data). It is appropriate to point out that in both of these cases the samples sizes are small, and the results may be skewed.

This is the single trait reported here which seems to have only present or absent categories of expression. As yet, no one has defined intermediate categories, although Kirveskari et al. ('72) have shown a bulge on the occlusal tubercles. Kirveskari is not convinced of this, however (pers. comm.). While the observation of the presence of a well-developed, unworn tubercle is relatively easy, care must be taken in ascertaining the presence of a worn or broken tubercle. In the latter case, a ring of roughened enamel and dentin will be found in the buccal triangular ridge area. It may or may not be slightly raised above the surrounding surface, but the roughness is discernible even on dental stone casts.

It is somewhat surprising to find such a low frequency of this trait in the Inuit since past studies have indicated that this is a Mongoloid trait. In a previous study (Mayhall, '69), however, the frequency of occurrence was found to be low in Alaskan Eskimos. There are no apparent differences in occurrences between the sexes, nor are there significant differences between the residents of Igloolik and Hall Beach.

Protostylid (Table 5)

As Dahlberg has noted ('50), originally any cusp that appeared on the buccal surface of maxillary or mandibular molars and premolars was considered a "paramolar cusp". The protostylid or tubercle of Bolk (DeSmet and Brabant, '69) is a paramolar structure found on the mesiobuccal cusp of mandibular molars.

Until 1950 the protostylid appeared to have escaped the scrutiny of most investigators. As Dahlberg ('50) noted, only 10 instances of the occurrence of the cusp on first molars had been reported. The subsequent studies of this trait have elucidated varying frequencies of occurrence in Mongoloid populations with Pima Indians having the highest incidence, while Old Harbor Eskimos showed 42.1 percent absence of the trait in first molars. Japanese also have a low incidence of expression on first molars (Suzuki and Sakai, '54).

The present study shows that 60 percent of males and 62 percent of females show no expression of the trait on first molars. The range of expression of the trait appears to go from absence (smooth) through intermediate manifestations which include a distal deviation of the buccal groove; a buildup of tooth material on the buccal of the mesiobuccal cusp, the latter with furrows surrounding it; and, finally, a cusp. Once again Dahlberg's standards were used for scoring these expressions.

None of the first or second molars demonstrate any expression that could be considered a cusp, but third molars occasionally show such expression. This adds credence to Bolk's report that these cusps never occurred on first permanent molars ('16). This trend has been shown graphically by Dahlberg ('45) in his important discussion of the field concept. He demonstrates that the intensity of the field increases toward the posterior of the molar series for the protostylid.

One category that has created some discussion is the inclusion in the range of variation of the pit category. Kirveskari ('74) and Mayhall ('76) have both questioned the inclusion of this feature within the range since those groups having a high incidence of the trait also have high frequencies of occurrence of terminal pits on the buccal grooves. While it is beyond the scope of this paper to discuss this problem in detail, I should like to reiterate my suspicion that the pit category is not a manifestation of the protostylid due to its somewhat distal placement in relation to the other protostylid manifestations and the fact that statistical testing indicates that it appears to operate independently of the protostylid (Mayhall, '76).

Sixth Cusp (Tuberculum Sextum) (Table 6)

The tuberculum sextum (C_6) is located on the distal marginal ridge of mandibular molars between the distal and distolingual cusps. Hellman ('28) and Dahlberg ('45) have demonstrated the high incidence of this cusp in Mongoloid populations. Dahlberg also points out that Caucasians have a very low incidence in all of the molars.

While the results of Dahlberg's study and that of Hellman would indicate a field in which C_6 is most strongly expressed in the third molar when compared to the other two, the present study shows little indication of this trend. However, this cusp does have a strong expression in all the mandibular molars, which would indicate the Mongoloid affinities of the Foxe Basin Inuit.

Hanihara's ('60) standards were used for scoring the expression of this cusp. While these standards were designed for deciduous teeth they were found to be suitable for use with the permanent dentition. In addition to the absent category, four other categories of expression were recorded: small, medium, large and cusp present but size undeterminable.

The males display a consistent pattern in both first molars, with the majority of teeth having some expression. Igloolik males had the larger percentage of molars with a large expression of the cusp, but, generally, the majority of teeth with an expression of the trait fell into the small and medium cusp categories. Females appear to have fewer large cusps than the males, but no overall sexual dimorphism is apparent.

Seventh Cusp (Tuberculum Intermedium)(Table 7)

This accessory cusp is located on the marginal border between the metaconid and the entoconid of mandibular molars. Both Dahlberg ('45) and Hellman ('28) have noted that this cusp is most prominent in first molars and diminishes as one proceeds distally in the molar series. This trend is supported by the present results. Turner ('67) feels that the absence of C_7 is characteristic of Aleuts and Eskimos, as well as most Mongoloids. He would like to include this absence as a part of the overall dental pattern of Mongoloids.

This trait was analyzed using the same methods and criteria used for the sixth cusp. The categories (after Hanihara, '60) include small, medium and large cusps, as well as an absent category. The data provide evidence that this trait is seen frequently in Canadian Inuit as the vast majority of first molars display at least a small cusp. The expressions tend to become smaller going posteriorly, and few second and third molars have any expression at all. Thus, it is difficult to support Turner's suggestion that absence of the trait should be included in the Mongoloid dental complex. There is no apparent sexual dimorphism in the occurrence or expression of this trait.

Carabelli's Trait (Table 8)

While Carabelli has been credited by many as being the "discoverer" of this acessory cusp, Korenhof ('60) points out that,in fact, the first description of it was in 1827 by Rosseau. Korenhof does credit Carabelli with the type description of "an acessory cusp, which occurs sometimes on the inside of molars, especially the inside of the first one." I have used the term "trait" to describe the manifestations found on the lingual surface of the mesiolingual cusp of maxillary nolars. Others have used Cusp of Carabelli or Carabelli's anomaly, but these terms imply that the expression is either large or very rare.

In the analysis of this trait the standards suggested by Dahlberg have been followed, with the addition of a category to describe the bulging of the mesiolingual surface. In this category it is possible to identify teeth which have appreciable extra tooth substance but do not have the furrows around this area that would delineate them as Carabelli's cusps. In addition to this category, the following expressions were included, along with the absent (smooth) category: single furrow, pit, "Y" conformation of the furrow, double furrow, small and large cusps.

First molars display the smallest percentage of teeth with an absence of the trait, followed by the second and third molars. Generally, the first molars were the teeth which displayed cusp expressions, although small cusps are represented in the second and third molars occasionally. The expressions classified as being cusps bring to the fore the question of Caucasian admixture in this population, as Pedersen ('49) has shown clearly that in Greenland those Greenlanders living in isolated settlements had almost no cusps. In contrast, the Greenlanders living in more accessible settlements where white admixture was known had much higher percentages of cusps.

The present paper is part of a larger study which also studied Thule culture skeletal material and Sadlermiut skeletal material. On first molars the Sadlermiut (extinct 1902-03) show no evidence of cusps while the Thule culture material (ca 1200 a.d.) shows an eight percent incidence. In the present study the figure is approximately fourteen percent. This six percent increase in occurrence of cusps over the Thule material from the same general area is interesting in light of recent studies of Igloolik blood factors. McAlpine and co-workers (' 75) found that about six percent of the genes of the Igloolik gene pool were Caucasoid. This admixture figure was further enchanced by extensive information from family interviews establishing a minimum of 3.17 percent Caucasoid contribution to the gene pool. The significance of the increase in the cusp frequency is yet to be determined but is the subject of ongoing work. However, I believe that again the Carabelli trait has been shown to be a powerful indicator of admixture in Mongoloid populations.

Odontometry (Tables 9-12,)

Tooth size in two dimensions was measured as previously described. The mesiodistal and buccolingual diameters were analyzed statistically for sexual differences in size. When analyzing the t-values for male-female differences one is immediately cognizant of the large number of significant differences which appear. The greatest amount of sexual dimorphism is in the buccolingual diameter. The Igloolik group shows statistically significant differences between the sexes in buccolingual diameters in all teeth except the maxillary third molars, the mandibular central incisors, and right third molars. The Hall Beach results show the same general trends.

Also tested but not reported here were the intercommunity differences. The males showed only three statistically significant differences, as did the females, of the total of 64 comparisons.

Discussion

In the foregoing, there have been few comparisons of the data with other studies of other populations. It is not the primary objective of this paper to make such comparisons, but rather to present the data in order to better characterize the morphology of the Central Arctic Inuit dentition. Further, it is difficult to draw comparisons with other studies as the standards of observation may vary considerably from those used here. With the understanding that only general comparisons are possible, the following are presented.

As mentioned earlier shovel-shaped incisors have been used as the prime example of the strengthened Mongoloid dental complex. American Indian populations studied have shown an almost universal presence of the trait with Arctic Indians showing a marked or shovel expression in 55 percent of their central incisors (Turner, ' 67). This figure climbs to 98.3 percent in Sioux Indians (Hrdlička, ' 31) and 99 percent in Pima Indian females (Dahlberg, ' 49). Eskimos generally show some expression of the trait with between 38 percent (Turner, ' 67) and 84 percent (Pedersen, ' 49) having the two larger expressions of the trait. American whites, in comparison, show a presence of the trait of between 30 and 34 percent (Hrdlička, ' 20). Thus, the present study indicates that, while few Inuit don't have shovel-shaped incisors, the larger expressions are not as common as in other North American native groups. The majority of the teeth are semi-shovel in expression.

The prevalence of premolar occlusal tubercles has been reported in Mongoloid groups as ranging up to 38 percent (Mayhall, unpublished data), but most studies indicate a range for Eskimos of about 5 to 15 percent. Alexandersen and Dahlberg (Alexandersen, ' 70) found a 5.6 percent occurrence in Kodiak Island Eskimos, and Hoffman (' 59) reported a 15 percent prevalence in Alaskan Eskimos. The range for North American Indians is between one percent (Navaho) and 11 percent (Pima) as reported by Alexandersen (' 70). There have been only occasional reports of the trait in Caucasians. The prevalence reported here is low but consistent with the other Eskimo studies.

Hanihara (' 63) has proposed that the protostylid should be included as part of the Mongoloid dental complex, but this appears to be difficult to support when 42 percent of Old Harbor Eskimos showed a complete absence of the trait, a figure higher than that for Sioux Indians (20 percent) or American Whites (26 percent) (Dahlberg, '63). Japanese also have a low incidence of expression with 81.5 percent showing a complete absence on first molars (Suzuki and Sakai, '54). Turner ('67) also noted a low incidence of the trait in the Alaskan skeletal material he studied. In the present study, the males showed no expression in 60 percent while the females showed smooth surfaces in 62 percent, figures in the same range as those of Turner.

Probably in no other area of dental morphology is there as much confusion as in the description of "accessory" cusps found on the occlusal surfaces of mandibular molars. It is practically impossible to use any of the earlier published reports to derive standards of observation for the sixth and seventh cusps. A high frequency of the sixth cusp on first molars and deciduous second molars was noted by Hanihara and coworkers ('75), but Hellman ('28) found no cusps in his small sample of Chinese. Kirveskari ('74) noted that 20 percent of Skolt Lapp men displayed a cusp on the first molar, but only two percent of the women showed the same expression. The cusp was more frequent in the pure Skolts than in the Hybrids he studied. In the present study only 28 percent of the first molars have no sixth cusp.

While the data on C_6 are confusing, those for the seventh cusp are even more so. The results presented in papers to date are contradictory, possible due to a lack of standardization. Kirveskari ('74) has suggested that much of the confusion has resulted from the lack of standards until Hanihara's. Older reports seemingly ignored small cusps, while more recent ones included much smaller manifestations. In fact, from the reported lack of C_7 on Eskimo permanent teeth (Dahlberg, '45) the figures have now expanded to include an 80 percent frequency in deciduous teeth (Hanihara, '67). The present results indicate an 88 percent frequency of occurrence on first molars.

The occurrence of the cusp of Carabelli has been shown to be present in 63 percent of white first molars (Dahlberg, '63). The figure for American Negroes is 34 percent (Kraus and Jordan, '65), while Athabaskan Indians showed a five percent frequency (Turner, '67). Pedersen ('49) found no cusps in East Greenland Eskimos. The Foxe Basin Inuit have a frequency of 14 percent as noted earlier. This figure is probably related to the admixture with whites, as the earlier populations in the area (Thule culture) had an eight percent occurrence.

The presentation of odontometric determination is one which could include many different aspects than those given here. In an earlier work (Mayhall, '76) the coefficients of variation are given for all teeth, as are detailed statistical analyses of the between community size differences. However, at that time, as in the present paper, comparisons with other groups were limited because of the possibility of interinvestigator error and because of the large amount of variation in size within the population. Because of differing criteria the Inuit material can not be compared adequately with measurements from Aleut and East Greenland studies. However, Pedersen's ('49) data on Eskimos and that of Selmer-Olsen ('49) on Swedes and Lapps have been noted with the following observations. For the maxillary mesiodistal measurements, the males and females of Igloolik exceed the Lapps in every case. They have larger lateral incisors and canines than the Swedes and Eskimos.

For the maxillary buccolingual measurements, those of Igloolik again exceed the Lapps in each tooth. The measurements are approximately the same as in the other groups except that the Inuit have larger anteriors.

The mandibular mesiodistal diameters of the Inuit are larger than the Lapps, except in the central incisors and second molars where they are essentially the same. There are no differences between the Swedes and Inuit measurements except for the larger Inuit lateral incisors and canines.

The buccolingual diameters of the mandibular anteriors are again larger than those of the comparative groups, as are those of the premolars and molars.

While the comparisons above give some indication of a slightly larger tooth size, most of the differences are quite small, and the Inuit can not be characterized as being macrodont as many people have assumed.

Summary

It should be reiterated that it is not the intention of this paper to draw detailed comparisons with other populations but, rather, to present the data that will help characterize the dentition of the Igloolik-Hall Beach Inuit. They might, therefore, be identified as having shovel-shaped incisors with moderate expressions in size, a low but significant occurrence of premolar occlusal tubercles, and a low incidence of protostylids. Over one-quarter of the first molars had no C_6 expression, and the seventh cusp was represented in a higher percentage of mandibular first molars. Few maxillary molars displayed the cusp of Carabelli. However, this latter trait was found in a higher percentage than in non-contact skeletal material from the same geographical area. Tooth size of the Inuit, while larger than that of Lapps, was not remarkably different from East Greenland or Swedish figures.

References

Alexandersen, V. 1970 Tandmorfologisk variation hos Eskimoer og andre Mongoloide populationer. Tandlaegebladet, 74: 587-602.

Biggerstaff, R. H. 1973 Heritability of the Carabelli Cusp in Twins. J. of Dent. Res., 52: 40-44.

Bolk, L. 1916 Problems of Human Dentition. Am. J. of Anat., 19: 91-148.

Butler, P. M. 1937 Studies of the Mammalian Dentition. I: The teeth of Centetes ecaudatus and its allies. Proceedings of the Zool. Soc. Lond., 107: 103-132.

——— 1939 Studies of Mammalian Dentition: Differentiation of Post-Canine Dentition. Proceedings of the Zool. Soc. Lond., 109: 1-36.

——— 1963 Tooth Morphology and Primate Evolution. In D. R. Brothwell (ed.), Dental Anthropology, 1-13. London: Pergamon.

Curzon, M. E. J., Curzon, J. A. and Poyton, H. G. 1970 Evaginated Odontomes in the Keewatin Eskimo. Brit. Dent. J., 129: 324-328.

Dahlberg, A. A. 1945 The Changing Dentition of Man. Journal of the Am. Dent. Assoc., 32: 676-690.

——— 1949 The Dentition of the American Indian. In W. S. Laughlin (ed.), Papers on the Physical Anthropology of the American Indian, 138-177. New York: Viking Fund, Inc.

——— 1950 The Evolutionary Significance of the Protostylid. Am. J. Phys. Anthrop., 8: 15-25.

——— 1963 Analysis of the American Indian Dentition. In D. R. Brothwell (ed.), Dental Anthropology, 149-177. London: Pergamon.

——— N. D. Materials for the Establishment of Standards for Classifications of Tooth Characters, Attributes and Techniques in Morphological Studies of the Dentition. Mimeo.

DeSmet, R. and Brabant, H. 1969 Observations anthropologiques sur la denture des Indiens Javagos. Bull. Soc. Roy. Belge d'Anthrop. et Préhist., 80: 97-123.

Hanihara, K. 1960 Standard Models for Classification of Crown Characters of the Human Deciduous Dentition. Mimeo.

——— 1963 Crown Characters of the Deciduous Dentition of the Japanese-American Hybrids. In D. R. Brothwell (ed.), Dental Anthropology, 105-124. London: Pergamon.

——— 1967 Racial Characteristics in the Dentition. J. Dent. Res., 46: 923-926.

Hanihara, K., Matsuda, T., Tanaka, T., and Tamada, M. 1975 Comparative Studies of Dentition. In S. Watanabe, S. Kondo and E. Matsunaga (eds.), Anthropological and Genetic Studies on the Japanese, Part III. Anthropological and Genetic Studies of the Ainu, JIBP Synthesis 2, 256-262. Tokyo: University of Tokyo Press.

Hellman, M. 1928 Racial Characters in the Human Dentition. Proceedings of the Am. Phil. Soc., 67: 157-174.

Hoffman, B. 1959 Quoted by Merrill, R.G. , 1964.

Hrabowsky, I. and Sim, J. 1971 F.D. I. Approved System for Encoding the Human Dentition. J. Can. Dent. Assoc., 37: 196-198.

Hrdlička, A. 1920 Shovel-Shaped Teeth. Am. J. Phys. Anthrop., 3: 429-465.

______ 1931 Anthropology of the Sioux. Am. J. Phys. Anthrop., 16: 123-166.

Kirveskari, P. 1974 Morphological Traits in the Permanent Dentition of Living Skolt Lapps. Ph.D. Thesis, University of Turku.

Kirveskari, P., Hedegard, B., and Dahlberg, A.A. 1972 Bulging of the Lingual Aspects of Buccal Cusps in Posterior Teeth of Skolt Lapps from Northern Finland. J. Dent. Res., 51:1513.

Korenhof, C.A.W. 1960 Morphogenetical Aspects of the Human Upper Molar. Doctoral thesis of State University of Utrecht.

Kraus, B.S. and Jordan, R.E. 1965 The Human Dentition Before Birth. Philadelphia: Lea and Febiger.

Lau, T.C. 1955 Odontomes of the Axial Core Type. Brit. Dent. J., 99: 219-225.

Leigh, R.W. 1925 Dental Pathology of the Eskimo. Dental Cosmos 67: 884-898.

Mayhall, J.T. 1969 Thule Culture Eskimo Mandibles: A Radiographic Study. Am. J. Phys. Anthrop., 31(ns): 264.

______ 1976 The Morphology of the Permanent Dentition of Prehistoric and Modern Central Arctic Eskimoid Peoples: A study of their biological relationships. Ph.D. Thesis, University of Chicago.

______ 1979 The Biological Relationships of Thule Culture and Inuit Populations: An odonotologicalinvestigation. In A.P. McCartney (ed.) Thule Eskimo Culture: An ArchaeologicalRetrospective, Archaeological Survey of Canada, No.88:488-473.

McAlpine, P.J., Chen, S.H., Cox, D.W., Dossetor, J.R., Giblett, E.R., Steinberg, A.G. and Simpson, N.E. 1975 Genetic Markers in Blood in a Canadian Eskimo Population with a Comparison of Allele Frequencies in Circumpolar Populations. International Biological Programme, Human Adaptability Project (Igloolik, N.W.T.) Report number 5, University of Toronto, Anthropological Series number 16, 123-169.

Merrill, R.G. 1964 Occlusal Anomalous Tubercles on Premolars of Alaskan Eskimos and Indians. Oral Surgery, Oral Med. and Oral Path., 17: 484-496.

Moorrees, C.F.A. 1957 The Aleut Dentition. Cambridge, Mass.: Harvard University.

Oehlers, F.A.C. 1956 The Tuberculated Premolar. Dent. Pract., 6: 144-148.

Pedersen, P.O. 1949 The East Greenland Eskimo Dentition. Meddelelser om Grønland, 142.

Selmer-Olsen, R. 1949 An Odontometrical Study of the Norwegian Lapps. Oslo: I Kommisjon Hos Jacob Dybwad.

Suzuki, M. and Sakai, T. 1954 On the Protostylid of the Japanese. Zinruigaku Zassi 63: 81-84.

Tratman, E.K. 1949 An Unrecorded Form of the Simplest Type of the Dilated Composite Odontome. Brit. Dent. J., 86: 271-275.

Tratman, E.K. 1950 A comparison of the teeth of people (Indo-European racial stock with the mongoloid racial stock). Dent. Rec., 70:31-53. 63-88.

Turner, C.G. 1967 The Dentition of Arctic People. Ph.D. Thesis, Madison: University of Wisconsin, University Microfilms.

Yumikura, S. and Yoshida, K. 1936 Abnormal Cusp on the Occlusal Surface of the Human Premolar, as cited by Merrill R.G., 1964.

TABLE 1.

Sample Selection for Odontological Study of Northern Foxe Basin Inuit

	(1968) R. C. M. P. Census	Number Examined
Igloolik	406	425
Hall Beach and F. E. C. [a]	236	168
Camps	81	b
Total	723	593

[a] Federal Electric Corporation, i. e. DEWline Inuit employees and their families

[b] These are included in the Hall Beach and Igloolik figures.

TABLE 2.

Frequency of Occurrence of Shovel-Shaped Maxillary Incisors

Community	N	Absent	Trace	Semi-shovel	Shovel	Marked	Peg	Barrel
				Tooth 11 Males				
Igloolik	134	1	39	80	14	0	0	0
Hall Beach	33	1	8	21	3	0	0	0
				Tooth 11 Females				
Igloolik	98	0	28	64	6	0	0	0
Hall Beach	32	1	14	12	5	0	0	0
				Tooth 21 Males				
Igloolik	131	1	34	83	13	0	0	0
Hall Beach	35	1	10	22	2	0	0	0
				Tooth 21 Females				
Igloolik	98	0	28	64	6	0	0	0
Hall Beach	32	1	14	13	4	0	0	0
				Tooth 12 Males				
Igloolik	114	1	56	53	4	0	3	1
Hall Beach	34	1	16	15	2	0	0	0
				Tooth 12 Females				
Igloolik	82	1	34	44	3	0	1	2
Hall Beach	31	0	17	11	3	0	1	0
				Tooth 22 Males				
Igloolik	117	1	51	60	5	0	2	2
Hall Beach	32	1	16	11	4	0	0	0
				Tooth 22 Females				
Igloolik	82	1	34	44	3	0	0	1
Hall Beach	29	1	17	9	2	0	1	0

TABLE 3.
Frequency of Occurrence of Shovel-Shaped Mandibular Incisors

Community	N	Absent	Trace	Semi-shovel	Shovel	Marked
				Tooth 31 Males		
Igloolik	112	15	95	2	0	0
Hall Beach	30	4	25	1	0	0
				Tooth 31 Females		
Igloolik	88	5	79	4	0	0
Hall Beach	31	3	28	0	0	0
				Tooth 41 Males		
Igloolik	111	13	97	1	0	0
Hall Beach	29	4	24	1	0	0
				Tooth 41 Females		
Igloolik	87	5	79	3	0	0
Hall Beach	31	2	29	0	0	0
				Tooth 32 Males		
Igloolik	116	14	100	2	0	0
Hall Beach	34	5	28	1	0	0
				Tooth 32 Females		
Igloolik	92	4	85	3	0	0
Hall Beach	32	4	27	1	0	0
				Tooth 42 Males		
Igloolik	116	15	98	3	0	0
Hall Beach	33	3	29	1	0	0
				Tooth 42 Females		
Igloolik	89	6	80	3	0	0
Hall Beach	31	4	26	1	0	0

TABLE 4.
Frequency of Occurrence of Premolar Occlusal Tubercles

	Males		Females	
Community	Present	Absent	Present	Absent
		Tooth 15		
Igloolik	0	102	4	79
Hall Beach	0	29	0	27
		Tooth 14		
Igloolik	0	111	3	80
Hall Beach	1	32	0	28
		Tooth 24		
Igloolik	0	115	4	83
Hall Beach	0	33	0	28
		Tooth 25		
Igloolik	1	97	4	75
Hall Beach	1	27	0	25
		Tooth 35		
Igloolik	1	94	1	75
Hall Beach	2	29	0	27
		Tooth 34		
Igloolik	0	104	0	82
Hall Beach	0	33	0	30
		Tooth 44		
Igloolik	0	105	0	84
Hall Beach	0	36	0	31
		Tooth 45		
Igloolik	0	93	3	75
Hall Beach	1	32	1	25

BLE 5.

Frequency of Occurrence of the Protostylid

mmunity	N	Smooth	Pit	Groove--Distal Deviation	Surface Irregularity	Surface Prominence	Prominence & Furrow	Small Cusp	Large Cusp
					Tooth 46 Males				
olik	111	74	11	5	2	17	2	0	0
l Beach	35	20	6	1	3	4	1	0	0
					Tooth 47 Males				
olik	77	35	13	7	8	10	4	0	0
l Beach	23	13	4	2	1	2	1	0	0
					Tooth 48 Males				
olik	31	9	1	1	5	2	10	3	0
l Beach	8	2	0	0	0	0	3	3	0
					Tooth 46 Females				
olik	80	52	11	6	4	6	1	0	0
l Beach	23	17	6	0	0	0	0	0	0
					Tooth 47 Females				
olik	63	36	10	7	4	5	1	0	0
l Beach	19	16	2	1	0	0	0	0	0
					Tooth 48 Females				
olik	11	4	0	1	2	1	1	1	1
l Beach	4	2	0	0	0	1	0	1	0
					Tooth 36 Males				
olik	105	60	15	17	3	8	2	0	0
l Beach	33	15	9	3	3	2	1	0	0
					Tooth 37 Males				
olik	70	35	15	9	5	2	4	0	0
l Beach	18	7	4	3	2	2	0	0	0
					Tooth 38 Males				
olik	21	4	1	0	4	1	9	2	0
l Beach	6	1	1	0	0	1	2	1	0
					Tooth 36 Females				
olik	81	49	14	10	2	3	2	1	0
l Beach	26	15	5	6	0	0	0	0	0
					Tooth 37 Females				
olik	47	27	5	11	0	3	1	0	0
l Beach	17	12	4	1	0	0	0	0	0
					Tooth 38 Females				
olik	10	3	1	0	3	1	1	1	0
l Beach	3	2	0	0	0	0	1	0	0

TABLE 6.

Frequency of Occurrence of Sixth Cusp (Tuberculum Sextum)

Community	N	Absent	Small Cusp	Medium Cusp	Large Cusp	Present [a]
				Tooth 46 Males		
Igloolik	87	18	26	29	9	69
Hall Beach	25	10	8	6	1	15
				Tooth 47 Males		
Igloolik	62	21	16	18	4	41
Hall Beach	20	12	5	2	0	8
				Tooth 48 Males		
Igloolik	17	4	4	6	3	13
Hall Beach	2	1	0	0	1	1
				Tooth 46 Females		
Igloolik	67	12	34	12	0	55
Hall Beach	24	14	6	2	1	10
				Tooth 47 Females		
Igloolik	52	12	22	13	3	40
Hall Beach	17	11	3	1	1	6
				Tooth 48 Females		
Igloolik	11	4	4	1	2	7
Hall Beach	2	2	0	0	0	0
				Tooth 36 Males		
Igloolik	75	20	28	20	7	55
Hall Beach	23	8	7	6	0	15
				Tooth 37 Males		
Igloolik	50	9	11	20	3	41
Hall Beach	14	7	1	5	1	7
				Tooth 38 Males		
Igloolik	12	2	2	5	2	12
Hall Beach	3	1	1	1	0	2
				Tooth 36 Females		
Igloolik	57	15	20	16	1	42
Hall Beach	22	9	9	4	0	13
				Tooth 37 Females		
Igloolik	42	13	9	15	2	19
Hall Beach	18	11	3	4	0	7
				Tooth 38 Females		
Igloolik	5	2	1	1	1	3
Hall Beach	1	1	0	0	0	0

[a] Includes small, medium, large cusps and trait present but size undeterminate.

TABLE 7

Frequency of Occurrence of Seventh Cusp (Tuberculum Intermedium)

Community	N	Absent	Small Cusp	Medium Cusp	Large Cusp	Present [a]
				Tooth 46 Males		
Igloolik	99	12	70	16	1	87
Hall Beach	28	7	19	2	0	21
				Tooth 47 Males		
Igloolik	77	23	50	4	0	54
Hall Beach	24	14	9	0	0	10
				Tooth 48 Males		
Igloolik	27	17	11	2	2	15
Hall Beach	7	5	2	0	0	2
				Tooth 46 Females		
Igloolik	88	5	67	12	1	83
Hall Beach	28	5	21	2	0	23
				Tooth 47 Females		
Igloolik	64	13	47	2	1	51
Hall Beach	23	9	14	0	0	14
				Tooth 48 Females		
Igloolik	15	6	9	0	0	9
Hall Beach	1	1	0	0	0	0
				Tooth 36 Males		
Igloolik	101	12	76	9	2	89
Hall Beach	25	6	17	2	0	19
				Tooth 37 Males		
Igloolik	70	23	41	5	1	47
Hall Beach	20	8	11	1	0	12
				Tooth 38 Males		
Igloolik	20	3	15	2	0	17
Hall Beach	6	1	5	0	0	5
				Tooth 36 Females		
Igloolik	88	8	66	10	1	80
Hall Beach	25	4	19	2	0	21
				Tooth 37 Females		
Igloolik	55	6	42	5	0	49
Hall Beach	16	7	9	0	0	9
				Tooth 38 Females		
Igloolik	8	2	5	1	0	6
Hall Beach	1	0	1	0	0	1

[a] Includes small, medium, large cusps and trait present but size undeterminable

TABLE 8.

Frequency of Occurrence of Carabelli's Trait

Community	N	Smooth	Single Furrow	Pit	Y	Double Furrow	Bulging of Tooth Substance	Small Cusp	Large Cusp
Tooth 16 Males									
Igaloolik	125	26	15	0	27	40	4	12	1
Hall Beach	34	3	5	0	6	14	1	4	1
Tooth 17 Males									
Igloolik	87	56	12	0	6	11	0	2	0
Hall Beach	27	18	1	0	2	5	1	0	0
Tooth 18 Males									
Igloolik	53	43	3	1	2	2	0	2	0
Hall Beach	15	13	0	0	1	1	0	0	0
Tooth 16 Females									
Igloolik	99	25	14	1	26	24	2	7	0
Hall Beach	31	8	8	0	5	6	2	2	0
Tooth 17 Females									
Igloolik	70	47	13	0	4	6	1	1	1
Hall Beach	25	19	3	1	0	1	1	0	0
Tooth 18 Females									
Igloolik	25	22	1	0	0	1	0	1	0
Hall Beach	2	2	0	0	0	0	0	0	0
Tooth 26 Males									
Igloolik	125	24	9	1	29	44	1	16	1
Hall Beach	30	1	5	1	7	12	1	3	1
Tooth 27 Males									
Igloolik	88	56	16	0	6	9	1	0	0
Hall Beach	27	13	6	0	2	6	0	0	0
Tooth 28 Males									
Igloolik	42	36	1	2	1	0	0	2	0
Hall Beach	14	10	0	0	1	2	1	0	0
Tooth 26 Females									
Igloolik	93	18	14	3	27	21	4	6	0
Hall Beach	32	11	4	0	5	7	1	4	0
Tooth 27 Females									
Igloolik	67	48	10	0	1	8	0	0	0
Hall Beach	23	16	2	1	4	0	0	0	0
Tooth 28 Females									
Igloolik	20	18	1	0	1	0	0	0	0
Hall Beach	6	6	0	0	0	0	0	0	0

Igloolik Mean Tooth Size (mm.) Mesiodistal diameters

Tooth	Males	Variance	N	Females	Variance	N	T-scores Males-Females	df	Significance
18	9.2	1.11	39	8.4	2.20	31	2.490	68	+
17	10.4	0.39	90	10.0	0.50	82	3.945	170	++
16	11.1	0.34	116	10.7	0.29	105	5.427	219	++
15	6.8	0.28	105	6.7	0.36	98	1.818	201	
14	7.3	0.24	110	7.2	0.30	100	1.826	208	
13	8.2	0.22	119	7.9	0.25	101	4.638	218	++
12	7.2	0.54	125	7.0	0.34	102	2.421	225	+
11	8.7	0.26	138	8.4	0.23	111	4.681	247	++
21	8.6	0.24	138	8.3	0.27	108	4.291	244	++
22	7.2	0.44	129	7.1	0.30	105	1.933	232	
23	8.2	0.22	118	7.9	0.22	98	5.042	214	++
24	7.3	0.20	120	7.2	0.35	106	2.398	224	+
25	6.8	0.33	107	6.7	0.37	89	2.074	194	+
26	11.2	0.30	135	10.7	0.30	104	6.661	237	++
27	10.4	0.42	91	10.0	0.43	80	3.664	169	++
28	8.8	1.75	29	8.6	2.47	27	0.503	54	
38	11.4	0.76	16	11.0	0.91	12	0.905	26	
37	11.4	0.54	75	11.0	0.55	69	3.332	142	++
36	11.8	0.41	111	11.3	0.51	97	6.082	206	++
35	7.5	1.41	113	7.1	0.87	97	2.311	206	+
34	7.3	0.28	116	7.1	0.26	97	2.689	211	++
33	7.4	0.25	120	7.0	0.16	97	7.119	215	++
32	6.3	0.22	123	6.1	0.23	104	3.463	225	++
31	5.3	0.14	115	5.2	0.21	92	0.571	205	
41	5.3	0.14	119	5.3	0.18	90	1.337	207	
42	6.4	0.20	124	6.2	0.17	99	3.456	221	++
43	7.4	0.18	117	7.0	0.15	98	8.405	213	++
44	7.2	0.18	109	7.0	0.21	101	2.680	208	++
45	7.3	0.86	103	7.0	0.69	87	2.252	188	+
46	11.7	0.87	117	11.1	0.85	100	4.312	215	++
47	11.3	0.46	83	10.8	0.51	84	4.943	165	++
48	11.5	0.54	19	10.7	0.87	10	2.487	27	+

\+ Significant at 95 per cent level of confidence.

++ Significant at 99 per cent level of confidence.

TABLE 10.
Igloolik Mean Tooth Size (mm.) Buccolingual diameters

Tooth	Males	Variance	N	Females	Variance	N	T-scores Males-Females	df	Significance
18	11.0	1.75	50	10.4	2.56	34	1.868	82	
17	11.8	0.71	104	11.3	0.45	83	4.466	185	++
16	11.8	0.56	123	11.4	0.29	110	5.480	231	++
15	9.3	0.38	109	9.1	0.47	100	2.876	207	++
14	9.5	0.37	118	9.2	0.46	107	3.429	223	++
13	8.7	0.35	105	8.3	0.23	96	5.278	199	++
12	7.2	0.66	111	6.9	0.35	95	2.807	204	++
11	7.7	0.39	129	7.5	0.36	104	2.979	231	++
21	7.7	0.40	123	7.5	0.42	103	3.094	224	++
22	7.2	0.57	115	7.0	0.27	95	2.254	208	+
23	8.6	0.49	109	8.2	0.26	95	4.004	202	++
24	9.4	0.39	127	9.1	0.44	111	3.541	236	++
25	9.3	0.44	113	9.0	0.46	92	2.696	203	++
26	11.9	0.55	141	11.5	0.30	116	4.961	255	++
27	11.8	0.66	104	11.4	0.48	90	3.769	192	++
28	10.9	1.93	41	10.7	1.72	36	0.870	75	
38	11.1	0.39	23	10.3	2.53	15	2.148	36	+
37	11.1	0.48	81	10.5	0.36	75	5.981	154	++
36	11.2	0.35	115	10.8	0.33	99	4.290	212	++
35	8.5	0.35	110	8.3	0.33	100	2.876	208	++
34	7.9	0.21	113	7.6	0.20	101	3.897	212	++
33	8.0	0.54	108	7.5	0.18	98	5.815	204	++
32	6.8	0.32	125	6.6	0.27	117	2.313	240	+
31	6.4	0.35	123	6.3	0.28	100	1.854	221	
41	6.3	0.35	115	6.2	0.22	101	1.375	214	
42	6.7	0.29	122	6.5	0.29	114	2.672	234	++
43	8.0	0.43	109	7.5	0.21	104	6.337	211	++
44	8.0	0.23	111	7.6	0.23	105	5.106	214	++
45	8.5	0.32	109	8.2	0.30	99	4.124	206	++
46	11.3	0.32	114	10.9	0.31	109	4.851	221	++
47	11.2	0.61	83	10.7	0.33	89	5.006	170	++
48	11.2	0.52	26	10.7	0.95	16	1.857	40	

+ Significant at 95 per cent level of confidence.
++ Significant at 99 per cent level of confidence.

Hall Beach Mean Tooth Size (mm.) Mesiodistal diameters

						T-scores			
Tooth	Males	Variance	N	Females	N	Males-Females		df	Significance
18	9.06	1.40	20	8.02	3.70	8	1.749	26	
17	10.26	0.27	33	9.86	0.23	28	3.116	59	++
16	11.05	0.24	33	10.30	2.15	29	2.775	60	++
15	6.73	0.24	30	6.71	0.35	28	0.107	56	
14	7.21	0.19	36	7.06	0.42	30	1.085	64	
13	7.99	0.23	36	7.64	0.23	27	2.851	61	++
12	7.21	0.25	37	6.98	0.45	31	1.636	66	
11	8.49	0.34	37	8.30	0.41	33	1.268	68	
21	8.55	0.34	38	8.37	0.37	32	1.237	68	
22	7.24	0.21	36	6.97	0.53	27	1.842	61	
23	7.96	0.19	35	7.66	0.22	28	2.650	61	+
24	7.22	0.18	36	7.14	0.45	31	0.573	65	
25	6.67	0.21	27	6.72	0.33	24	-0.367	49	
26	11.03	0.27	30	10.71	0.45	31	2.123	59	+
27	10.18	0.27	32	9.89	0.32	25	2.045	55	+
28	9.23	1.90	14	9.06	0.63	8	0.313	20	
38	10.65	0.01	2	9.82	0.31	4	1.955	4	
37	11.28	0.29	25	10.48	0.57	15	3.924	38	++
36	11.67	0.29	36	11.26	0.29	28	2.988	62	++
35	7.29	1.51	35	7.00	0.75	29	1.071	62	
34	7.18	0.23	42	7.07	0.89	31	0.666	71	
33	7.34	0.28	39	6.86	0.21	31	4.005	68	++
32	6.34	0.26	38	6.10	0.19	31	2.067	67	+
31	5.25	0.20	34	5.30	0.25	31	-0.365	63	
41	5.33	0.17	34	5.34	0.25	31	-0.052	60	
42	6.40	0.21	36	6.10	0.18	30	2.732	64	++
43	7.32	0.29	19	6.89	0.21	30	3.543	67	++
44	7.19	0.21	41	6.91	0.24	29	2.365	68	+
45	7.11	0.74	35	7.09	0.68	28	0.117	61	
46	11.70	0.34	35	11.28	0.30	30	3.027	63	+
47	11.01	1.36	23	10.60	0.59	17	1.253	38	
48	11.12	2.30	5	11.44	1.98	3	-0.297	6	

\+ Significant at the 95 per cent level of confidence.

++ Significant at the 99 per cent level of confidence.

TABLE 12.
Hall Beach Mean Tooth Size (mm.) Buccolingual diameters

Tooth	Males	Variance	N	Females	Variance	N	T-scores Males-Females	df	Significance
18	11.0	2.04	23	9.5	5.14	9	2.213	30	+
17	11.9	0.43	36	11.1	0.29	31	5.288	65	++
16	12.0	0.26	40	11.3	0.32	33	5.887	71	++
15	9.0	0.29	39	8.8	0.40	29	1.222	66	
14	9.2	0.37	41	9.0	0.46	33	0.976	72	
13	8.4	0.20	33	8.2	0.19	26	2.314	57	+
12	7.2	0.32	35	6.9	0.35	26	2.018	59	+
11	7.7	0.41	33	7.4	0.15	33	1.615	62	
21	7.7	0.41	33	7.4	0.19	25	2.007	56	+
22	7.3	0.28	36	6.7	0.44	27	4.447	61	++
23	8.4	0.29	35	8.0	0.18	26	2.622	59	+
24	9.2	0.42	40	8.9	0.46	33	1.433	71	
25	9.0	0.23	35	9.0	0.35	29	0.460	62	
26	11.9	0.22	39	11.3	0.26	38	5.965	75	++
27	11.7	0.93	34	11.0	0.38	27	2.976	59	++
28	11.1	2.37	20	10.5	0.51	8	1.105	26	
38	10.7	0.79	9	10.3	0.18	4	0.914	11	
37	10.9	0.35	28	10.1	0.18	21	5.060	47	++
36	11.0	0.28	45	10.5	0.18	31	4.316	74	++
35	8.4	0.25	45	8.1	0.36	36	2.386	79	+
34	7.8	0.15	44	7.5	0.26	34	2.532	76	+
33	7.9	0.48	36	7.3	0.18	34	3.982	68	++
32	6.8	0.41	43	6.4	0.17	37	3.023	77	++
31	6.4	0.38	36	6.2	0.16	33	1.556	67	
41	6.4	0.63	37	6.2	0.19	32	1.486	67	
42	6.9	0.27	42	6.4	0.17	37	4.290	77	++
43	7.8	0.55	36	7.3	0.22	32	3.210	66	++
44	7.8	0.20	44	7.5	0.24	35	2.751	77	++
45	8.4	0.24	44	8.0	0.42	35	2.945	77	++
46	11.2	0.17	40	10.8	0.31	32	3.724	70	++
47	11.1	0.17	27	10.4	0.23	21	4.829	46	++
48	11.1	0.66	10	10.1	0.02	4	2.300	12	+

+ Significant at 95 per cent level of confidence.
++ Significant at 99 per cent level of confidence.

A comparative study on craniofacial morphology of North American Caucasian and Japanese children

FUJIO MIURA

OSSA

Racial differences concerning cephalometric angular and linear measurements and the mode of growth changes between North American Caucasian and Japanese children are described.

Materials consisted of serial cephalograms taken from Japanese children, 7 to 15 years of age, 26 boys and 24 girls. Comparative data from North American children was made available from the atlas edited by the Center for Human Growth and Development, The University of Michigan. None of the children had received orthodontic treatment.

The characteristic racial differences were as follows:

(1) A longer anterior cranial base and nasal floor were found among North American children.

(2) The development of prognathism was found among Japanese children.

(3) A backward rotation and a relatively small mandibular body was found among Japanese children.

(4) The most marked difference was recognized in the growth change of the mandibular symphysis.

Keywords: Morphology - Cranio-facial - N. American, Caucasian and Japanese Children.

В статье описаны расовые различия, касающиеся цефалометрических угловых и линейных измерений и характера возрастных изменений у детей кавказской расы из Северной Америки и у японских детей.

Материал состоял из серии цефалограмм, сделанных у японских детей, в возрасте от 7 до 15 лет, 26 мальчиков и 24 девочек. Сравнительные данные о североамериканских детях взяты из атласа, изданного Центром человеческого роста и развития Мичиганского Университета. Никто из детей не получал ортодонтического ухода.

Были отмечены следующие характерные расовые различия:

1/ у детей кавказской расы из Северной Америки были замечены более удлиненные переднее основание черепа и основание носа;

2/ у японских детей найдено развитие прогнатизма;

3/ обратная ротация и относительно небольшое тело нижней челюсти также отмечено у японских детей;

4/ наиболее заметное отличие обнаружено в изменении нижнечелюстного симфизиса в процессе роста.

Ключевые слова: морфология, лицевой череп, североамериканские дети кавказской расы и японские дети.

Fujio Miura, Department of Orthodontics, School of Dentistry, Tokyo Medical and Dental University, , 1-5-45 Yushima, Bunkyo-ku, Tokyo, Japan.

Vol. 6, pp. 219-228, Lund. ISSN 0345-8865.

Introduction

Professor Shinjiro Takahashi was a pioneer of the orthodontic field in Japan. He recognized that malocclusion in Japan was fairly different from malocclusion found among Caucasians and he thought that orthodontics should be researched on the basis of dental anthropology. He went to the United States in 1928 as the first Japanese exchange professor to receive Fulbright funds in dentistry. He was aware that Dr. Dahlberg had researched the dentition of the American Indian. The two men became well known to each other in their private and scientific lives. The author, as one of Dr. Takahashi's staff, first assisted Dr. Dahlberg in his research from 1960 to 1961. Within the ten years which followed, many of my friends and staff have been able to work with Dr. Dahlberg and to gain knowledge from him. Through Dr. Dahlberg we started cooperative research with Dr. Moyers, who had researched growth and development of maxillo-facial anatomy of Caucasoid people in the United States. Dr. Moyers and I presented some of our research at the VIIIth International Congress of Anthropological and Ethnological Sciences in Tokyo, 1968. In this paper the author will introduce a part of our current research in Japan, comparing it with Dr. Moyers's research in the States, in honor of this celebration.

Racial differences in craniofacial morphology and growth have been frequently reported (Björk, '47; Altemus, '60; Miura et al., '58; Miura et al., '60). Many size and form differences as well as the growth timing among several ethnic groups have been noticed (Altemus, '60; Miura and Moyers, '68; Moyers and Miura, '68; Kuroda, '70). However, most of the papers dealt only with a two stage comparison, between younger and older ages. Therefore, it is difficult to define the differences in the mode of growth changes.

In orthodontics, findings from these comparative studies include a number of important suggestions for diagnosis, treatment planning and also the retention of malocclusion (Miura et al., '65; Iwasawa et al., '77).

The purpose of this paper is to study and identify the racial differences in cephalometric angular and linear measurements and also in the mode of growth changes between North American Caucasian and Japanese children.

Materials and Methods

Serial lateral cephalograms were taken at annual intervals of Japanese children without any orthodontic treatment. They were selected at random from the growth study file in the Department of Orthodontics, Tokyo Medical and Dental University. Materials used in this study comprised records available at every age from 7 to 15 years of 26 boys and 24 girls. Comparative data for North American children was made available from "An atlas of craniofacial growth" edited by the Center for Human Growth and Development, The University of Michigan (Riolo, et al., '74). These samples consisted of 47 males and 36 females selected from university school children who had not been treated orthodontically during or previous to the dates of the data collection.

Corrections were made for the effect of cephalometric enlargement.

Individual cephalometric tracing sets of Japanese children were sent to the computing system for digitization and disc storage. Cephalometric data for computer analysis used in the present study consisted of 12 linear and 10 angular measurements commonly taken in cephalometrics.

The mean value and standard deviation of measurements of each sample were calculated and compared with those of North American data at the 5% level of significance.

Measurements are as follows:

1. Angular measurements
    - A) Anterior cranial base/Nasomaxillary complex
        - i) Sella-Nasion-Anterior Nasal Spine (SN-ANS)
        - ii) Sella-Nasion-Point A (SNA)

- iii) Angle of Convexity (NA/A-Pg)
- iv) Sella-Nasion/Nasal floor (SN/ANS-PNS)

B) Anterior cranial base/mandible
- i) Sella-Nasion-Pogonion (SNPg)
- ii) Sella-Nasion-Point B (SNB)
- iii) Sella-Nasion/Gonion-Menton (SN/GoMe)
- iv) Sella-Nasion/Posterior border of ramus (GZN)

C) Nasomaxillary complex/mandible
- i) A-B plane angle (N-Pg/A-B plane)
- ii) Occlusal plane angle (SN/Occl.)

2\. Linear measurements

A) Anterior cranial base
- i) Sella to Nasion (SN)

B) Anterior cranial base/Nasomaxillary complex
- i) Nasion to Anterior Nasal Spine (N-ANS)
- ii) Nasal floor (ANS-PNS)
- iii) Anterior Nasal Spine to Upper incisor (ANS-Ul)
- iv) Upper incisor to Nasion-Pogonion (N-Pg to Ul)

C) Anterior cranial base/mandible
- i) Nasion to Menton (N-Me)
- ii) Sella to Menton (S-Me)
- iii) Lower incisor to Nasion-Point B (N-Pgp to L1)
- iv) Pogonion to Nasion-Point B (NB to Pg)
- v) Menton to Lower incisor (Me-L1)
- vi) Menton to Gonion (Me-Go)
- vii) Gonion to Articulare (Go-Ar)

Results

All the calculated data for Japanese children and the published data for North American Caucasian children are given in tables 1 and 2.

The graphic illustrations of growth curves are shown in figures 1 and 2.

Comparative results between the two races are summarized in table 3.

Discussion

The results of this study confirmed the findings reported previously by many authors.

It is a well known fact that Japanese have a brachycephalic head form. As shown in the linear measurements of anterior cranial base (SN) and nasal floor (ANS-PNS), North American children have longer dimensions. These longer dimensions have a direct influence on the difference in cephalic index between the races.

In the development of prognathism, Japanese children showed a marked tendency of protrusion in the anterior part of the nasomaxillary complex (SN-ANS, SNA, Angle of Convexity) and the horizontal positioning of the upper incisor (N-Pg/U1) as well as the horizontal positioning of the lower incisor (N-Pg/L1).

Another interesting difference between the races was found in the facial rotation. The nasal floor angle of North American children shows a tendency to open slightly during the growth period. On the other hand, Japanese showed a backward rotation of the mandible (SN/GoMe, GZN). No significant differences, however, were observed in the angular measurements of the anterior mandible (SNPg, SNB) or in the anterior facial heights (ANS-U1, N-Me, Me-L1), except in the length from the Sella to the Menton. Posterior facial height (Go-Ar) showed no particular difference in size and in its growth changes. Interpretations of these findings should take into consideration the size differences of the mandibular body length (Me-Go) which were clearly demonstrated by Miura and Moyers (' 68).

Angular measurement

		Japanese				North American White			
		Male		Female		Male		Female	
		mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
A-i SN-ANS	7	85.6	3.0	84.9	4.1	85.9	3.0	86.7	3.5
	8	85.2	3.1	85.0	3.6	86.1	3.4	86.5	3.6
	9	85.5	3.1	85.3	3.5	86.2	3.2	85.9	3.0
	10	85.8	2.9	85.0	3.6	86.5	3.3	85.9	3.8
	11	86.0	3.1	84.5	3.5	86.5	3.2	86.3	4.4
	12	86.3	3.3	85.5	2.8	86.8	3.7	86.4	3.7
	13	87.2	3.7	85.7	3.1	86.9	3.6	86.1	4.0
	14	87.6	3.6	85.9	3.4	86.6	3.7	86.7	4.2
	15	87.7	3.3	86.3	3.4	86.7.	3.5	87.3	3.6
A-ii SNA	7	81.7	3.0	81.5	3.8	80.7	3.0	81.9	3.0
	8	81.5	3.1	80.8	3.6	81.0	3.1	81.2	3.3
	9	81.4	3.2	81.0	3.3	80.6	3.0	80.5	3.2
	10	81.9	3.1	80.9	3.3	80.8	3.1	80.7	3.7
	11	82.2	3.2	80.7	3.2	80.8	3.0	81.1	3.8
	12	82.5	3.4	81.6	2.7	81.2	3.3	81.4	3.6
	13	83.1	3.7	81.6	3.0	81.2	3.4	81.0	3.8
	14	83.4	3.6	81.7	3.5	80.7	3.4	81.3	3.5
	15	83.2	3.7	81.8	3.0	80.9	3.2	81.8	3.5
A-iii Convexity	7	12.2	4.8	13.3	4.3	10.9	4.9	12.0	5.4
	8	11.2	5.4	11.9	3.6	9.3	5.1	9.0	5.2
	9	10.2	5.6	11.0	4.0	8.0	4.5	7.6	5.6
	10	10.1	5.7	10.2	4.2	7.9	4.9	7.2	5.7
	11	9.7	6.0	9.3	4.4	7.5	4.5	6.6	4.5
	12	9.4	6.3	8.9	4.9	6.7	4.8	6.4	5.5
	13	9.4	6.5	8.2	4.4	6.1	4.8	5.4	5.3
	14	8.2	6.6	7.7	5.0	5.2	4.8	5.3	5.9
	15	7.1	6.1	7.2	4.9	4.9	5.1	4.1	5.9
A-iv SN-NF	7	7.8	2.0	8.3	3.3	5.9	2.8	6.6	2.3
	8	8.0	1.5	8.8	3.2	5.9	2.6	7.0	2.5
	9	8.3	2.0	8.5	3.2	6.4	2.3	7.7	2.3
	10	8.4	1.7	8.6	3.4	6.1	2.6	7.5	2.8
	11	8.2	1.9	8.8	3.8	6.5	3.0	7.7	2.7
	12	8.4	2.1	8.7	3.6	6.5	3.0	8.3	2.4
	13	8.2	2.3	8.4	3.5	7.1	3.2	8.2	2.9
	14	8.1	2.4	8.3	4.0	7.3	3.5	8.1	1.8
	15	7.9	2.3	8.4	3.6	6.9	3.4	7.8	2.4
B-i SN-Pg	7	75.5	2.8	74.7	3.6	75.4	2.6	75.9	3.1
	8	76.0	2.8	74.8	3.7	76.4	2.7	76.8	3.3
	9	76.4	2.9	75.5	3.6	76.7	2.5	76.7	3.3
	10	77.0	2.8	75.9	3.6	76.9	2.4	77.2	3.5
	11	77.4	2.8	76.1	3.8	77.1	2.5	77.9	3.9
	12	77.6	2.9	77.2	3.5	77.9	2.6	78.4	3.4
	13	78.6	3.1	77.6	3.7	78.2	2.8	78.4	4.0
	14	79.3	3.1	77,9	4.0	78.2	3.0	78.8	4.1
	15	79.6	3.0	78,2	3.6	78.5	3.1	79.8	4.1

		Japanese				North American White			
		Male		Female		Male		Female	
		mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
B-ii SNB	7	76.7	3.0	76.0	3.3	75.7	2.8	76.3	3.1
	8	76.8	2.8	75.8	3.6	76.3	2.8	76.7	3.3
	9	77.2	2.9	76.5	3.4	76.4	2.5	76.5	3.4
	10	77.7	2.9	76.7	3.4	76.5	2.5	76.7	3.5
	11	78.1	2.9	76.7	3.6	76.5	2.6	77.3	3.9
	12	78.2	2.8	77.7	3.3	77.3	2.7	77.7	3.4
	13	78.9	3.0	77.7	3.6	77.5	3.0	77.5	3.9
	14	79.5	3.1	78.1	3.9	77.3	3.1	77.9	3.8
	15	79.6	3.0	78.4	3.5	77.6	3.0	78.9	3.9
B-iii SN/MeGo	7	39.3	3.7	41.1	4.0	36.0	4.9	36.7	4.9
	8	39.2	3.7	41.6	4.1	35.1	4.5	35.4	5.0
	9	39.1	3.4	41.0	4.2	34.7	4.6	35.3	5.3
	10	38.5	3.9	41.0	4.3	34.7	4.7	35.3	5.1
	11	38.1	4.1	40.2	4.2	34.7	4.7	34.8	5.6
	12	38.1	4.4	39.3	4.1	33.8	4.9	34.1	5.3
	13	36.8	4.6	38.8	4.8	33.2	5.0	34.3	5.8
	14	36.0	4.4	38.6	5.0	33.2	5.1	33.7	6.2
	15	35.6	4.7	38.6	5.2	33.2	5.2	32.4	5.8
B-iv GZN	7	87.4	4.1	89.5	4.9	85.5	4.2	86.7	4.4
	8	87.8	4.1	89.9	4.0	85.6	4.2	86.8	4.5
	9	87.6	3.9	89.6	4.3	86.2	4.0	88.0	4.9
	10	87.7	4.5	89.5	4.6	86.8	3.6	87.9	4.7
	11	87.8	4.2	89.8	4.6	87.5	4.4	87.8	5.1
	12	88.2	4.6	89.6	4.7	87.3	3.9	87.9	4.4
	13	88.3	4.7	90.4	4.5	87.4	4.2	88.2	5.2
	14	88.2	4.6	90.7	5.1	89.1	4.3	88.7	5.5
	15	88.4	5.1	90.4	4.6	89.4	4.6	88.3	6.3
C-i A-B pl.	7	-5.5	3.2	-5.9	2.3	-6.5	3.3	-6.9	3.5
	8	-5.9	3.3	-5.9	2.3	-6.3	2.9	-6.1	3.1
	9	-5.4	3.5	-5.4	2.5	-5.9	2.5	-5.6	3.7
	10	-5.5	3.3	-5.1	2.9	-6.3	2.7	-5.9	3.7
	11	-5.4	3.4	-5.2	2.9	-6.6	2.6	-5.9	3.2
	12	-5.9	3.8	-5.5	3.2	-6.1	2.7	-5.9	3.6
	13	-6.0	3.7	-5.5	3.0	-6.0	2.7	-5.7	3.4
	14	-5.6	3.6	-5.1	3.5	-5.9	2.9	-5.7	3.5
	15	-5.2	3.1	-4.7	3.4	-5.8	2.9	-5.1	3.9
C-ii SN/Occl.pl.	7	19.2	5.4	21.3	5.1	19.2	4.4	19.3	3.9
	8	19.7	3.5	21.8	3.9	18.1	3.4	17.7	3.5
	9	19.3	3.8	20.7	3.7	17.6	3.3	17.6	3.1
	10	18.5	3.8	20.4	3.5	17.5	3.2	17.3	3.5
	11	17.6	3.4	19.7	3.5	17.0	3.8	16.5	3.6
	12	17.6	3.8	19.0	4.0	16.2	3.7	16.3	3.3
	13	16.2	3.8	18.2	3.7	15.6	3.8	15.0	4.0
	14	15.3	4.0	17.6	3.6	15.4	3.9	15.7	4.0
	15	14.7	3.8	18.1	3.9	14.3	3.8	14.7	3.8

		Japanese				North American White			
		Male		Female		Male		Female	
		mean	S. D.	mean	S. D.	mean	S. D.	mean	S. D.
A-i S-N	7	63.8	3.4	62.2	2.4	73.9	3.1	70.6	2.6
	8	64.8	3.3	63.1	2.2	75.2	3.0	72.3	2.9
	9	65.9	3.3	64.2	2.4	75.9	3.3	72.6	2.7
	10	66.4	3.3	64.8	2.6	76.8	3.2	73.9	2.8
	11	67.2	3.6	66.0	2.7	78.2	2.9	74.3	3.0
	12	68.2	4.0	66.3	2.8	78.3	3.3	74.9	3.0
	13	69.6	4.5	67.4	2.8	79.5	3.8	75.5	3.1
	14	70.5	4.4	67.7	3.0	80.5	4.1	76.0	2.9
	15	71.8	4.5	67.6	3.0	81.3	4.0	76.9	2.8
B-i N-ANS	7	47.9	2.3	47.5	2.3	47.9	3.2	47.1	2.9
	8	49.5	2.2	49.5	2.3	49.5	2.8	48.6	3.0
	9	51.2	2.7	50.9	2.3	51.0	3.0	50.4	3.1
	10	52.5	2.5	52.3	2.3	52.3	3.1	52.1	3.7
	11	54.0	2.8	54.1	2.4	53.8	3.4	52.7	3.3
	12	55.5	3.1	55.0	2.5	54.6	3.6	54.0	3.7
	13	57.5	3.3	56.0	2.4	56.8	3.7	54.7	3.3
	14	59.1	3.2	56.4	2.5	58.2	4.1	55.3	2.7
	15	60.2	2.9	56.6	2.5	59.0	4.0	55.3	3.2
B-ii ANS-PNS	7	44.8	1.9	43.8	2.3	51.4	2.5	50.5	2.9
	8	45.4	1.9	45.5	2.1	52.1	2.9	51.2	2.5
	9	46.9	2.2	46.5	2.4	53.3	2.9	51.2	3.2
	10	47.5	2.2	47.3	2.8	54.4	2.6	53.1	3.1
	11	48.6	2.4	47.8	2.9	56.0	2.4	53.9	4.0
	12	49.7	3.2	49.1	2.6	56.7	3.1	54.1	3.2
	13	51.3	2.9	49.6	3.1	57.8	3.1	55.3	3.0
	14	52.9	3.0	50.6	2.5	58.7	3.6	56.7	2.9
	15	53.8	3.2	51.1	3,2	59.6	3.6	57.1	2.7
B-iii ANS-Ul	7	21.2	5.4	21.1	4.9	27.1	2.4	24.9	3.3
	8	26.1	3.1	26.2	3.4	27.9	2.2	25.3	2.8
	9	27.9	1.9	27.8	2.9	28.9	2.4	26.3	2.7
	10	28.0	2.0	28.7	2.5	29.9	2.2	27.2	2.8
	11	29.0	1.9	29.2	2.7	30.7	2.0	27.8	2.8
	12	29.4	2.3	29.9	2.5	31.1	2.2	27.9	2.7
	13	30.1	2.3	30.6	2.4	31.1	2.4	28.6	2.7
	14	30.6	2.4	31.0	2.5	31.7	2.3	29.3	3.0
	15	31.1	2.5	31.6	2.4	32.4	2.8	29.4	3.2
B-iv N-Pg′Ul	7	6.3	3.9	6.8	3.7	7.8	3.5	7.3	3.1
	8	9.3	3.6	9.4	3.3	8.6	4.1	7.8	3.8
	9	10.5	3.8	10.0	3.3	9.2	3.5	8.9	3.9
	10	11.3	3.7	10.5	2.9	10.0	3.8	8.7	3.6
	11	11.8	4.2	10.6	3.3	10.2	3.6	8.4	3.6
	12	11.9	4.5	10.5	3.4	9.2	3.6	8.7	3.9
	13	12.1	4.8	10.7	3.7	8.9	4.2	8.0	3.5
	14	11.8	4.9	10.6	3.5	8.2	4.8	7.9	3.7
	15	11.4	5.0	10.9	3.8	8.0	3.9	6.9	3.9
C-i N-Me	7	106.7	4.6	106.2	3.6	110.7	5.8	107.8	5.3
	8	109.5	4.7	109.3	4.1	113.6	5.6	109.5	5.4
	9	112.4	5.0	112.0	4.5	115.9	5.4	112.1	5.7
	10	114.7	5.2	115.1	4.4	118.7	5.7	115.1	6.7
	11	117.7	5.3	118.1	5.2	121.5	6.0	116.2	6.4
	12	120.6	6.3	120.8	5.5	123.3	6.3	118.3	6.0
	13	125.1	6.8	123.7	5.4	126.6	7.0	120.7	5.8
	14	129.1	6.7	125.4	5.5	130.3	7.9	122.3	5.9
	15	132.1	6.4	126.4	5.7	133.8	7.8	122.7	6.4
C-ii S-Me	7	104.8	5.0	103.3	4.0	111.9	4.9	108.9	5.1
	8	106.9	5.3	106.3	4.7	115.8	4.5	112.0	5.1
	9	111.2	5.5	109.7	5.2	118.4	4.5	114.2	4.9
	10	113.9	5.9	112.9	5.3	121.3	4.8	117.6	5.3
	11	117.4	5.8	116.0	6.3	124.2	5.3	119.5	5.0
	12	120.4	6.6	119.7	6.4	126.9	5.4	122.1	5.1
	13	125.9	7.1	123.1	6.2	130.5	6.7	124.4	4.8
	14	130.6	7.1	125.0	6.3	133.7	6.7	126.6	5.3
	15	134.1	6.2	126.3	6.3	137.5	6.7	128.5	5.8
C-iii N-Pg′Ll	7	5.0	3.1	6.1	2.8	3.2	3.0	3.3	2.5
	8	6.4	3.2	6.9	2.7	3.9	3.1	3.3	2.7
	9	6.9	3.2	7.3	2.8	4.2	3.0	3.9	3.0
	10	7.2	3.6	7.5	2.8	4.6	3.1	3.8	2.5
	11	7.8	3.6	7.3	2.8	4.6	3.2	3.6	2.7
	12	7.9	4.1	7.1	3.0	4.3	3.4	4.1	3.1
	13	8.2	4.4	7.0	3.2	4.3	3.7	3.4	3.0
	14	8.1	4.4	6.9	3.5	3.6	3.3	3.5	3.4
	15	7.8	4.4	7.2	3.4	3.6	3.4	2.5	3.3
C-iv N-B′Pg	7	2.3	1.6	2.4	1.3	-0.5	1.5	-0.6	1.3
	8	2.1	1.3	2.0	1.1	0.2	1.4	0.2	1.3
	9	1.9	1.3	1.9	1.2	0.5	1.3	0.5	1.6
	10	1.8	1.2	1.8	1.2	0.8	1.6	0.9	1.1
	11	2.1	1.3	1.6	1.1	1.2	1.5	1.2	1.2
	12	2.2	1.4	1.4	1.1	1.3	1.6	1.3	1.5
	13	2.2	1.4	1.2	0.9	1.5	1.8	1.7	1.3
	14	2.2	1.4	1.2	0.8	1.9	1.6	1.7	1.6
	15	2.4	1.5	1.4	0.9	2.1	1.8	1.9	1.4
C-v Me-Ll	7	35.2	5.6	34.9	5.1	38.3	2.5	36.7	2.2
	8	39.3	2.7	38.1	3.5	39.6	2.4	37.8	2.2
	9	40.6	2.4	39.9	2.7	40.7	2.4	38.9	2.5
	10	41.1	2.6	40.7	2.8	41.9	2.4	40.0	2.6
	11	42.5	2.6	40.6	3.1	42.9	2.7	40.5	2.6
	12	43.5	3.0	42.6	3.3	43.3	2.7	41.1	2.2
	13	45.0	3.1	43.7	3.4	44.2	3.1	42.0	2.6
	14	46.4	3.2	44.3	3.4	45.6	3.6	42.1	2.6
	15	47.3	3.1	44.8	3.4	46.6	3.4	42.0	3.2
C-vi Go-Me	7	56.5	3.4	56.8	3.2	63.3	3.0	62.7	4.0
	8	59.0	3.4	59.1	3.2	65.7	3.1	65.7	4.3
	9	61.1	3.4	61.1	3.5	67.7	3.1	66.5	4.4
	10	62.9	3.5	62.9	3.2	69.6	3.0	69.0	4.2
	11	65.2	3.3	64.8	3.8	71.5	3.3	70.6	3.9
	12	67.0	3.9	66.9	3.6	73.1	3.5	71.5	4.0
	13	70.3	4.4	69.9	3.6	75.3	3.8	73.4	4.4
	14	72.7	4.4	70.8	3.9	77.4	3.9	74.8	4.4
	15	74.6	3.7	71.4	3.9	79.4	4.0	75.9	4.4
C-vii Ar-Go	7	38.8	3.0	37.7	2.7	40.5	3.3	38.9	3.4
	8	39.9	3.4	38.0	2.8	42.2	3.4	40.2	3.2
	9	40.6	3.4	39.4	2.6	43.4	3.3	41.2	3.5
	10	41.4	3.8	40.4	3.1	44.2	3.4	41.6	3.2
	11	42.7	4.3	41.9	3.0	45.0	3.9	42.3	3.1
	12	43.8	4.4	43.5	3.0	46.7	3.8	44.9	3.9
	13	46.5	4.5	44.7	3.7	48.0	3.6	44.7	3.8
	14	48.9	4.9	46.0	3.7	49.8	4.6	46.4	4.6
	15	50.6	5.0	46.7	3.7	51.4	4.6	48.1	4.1

Table 2. List of linear measurements

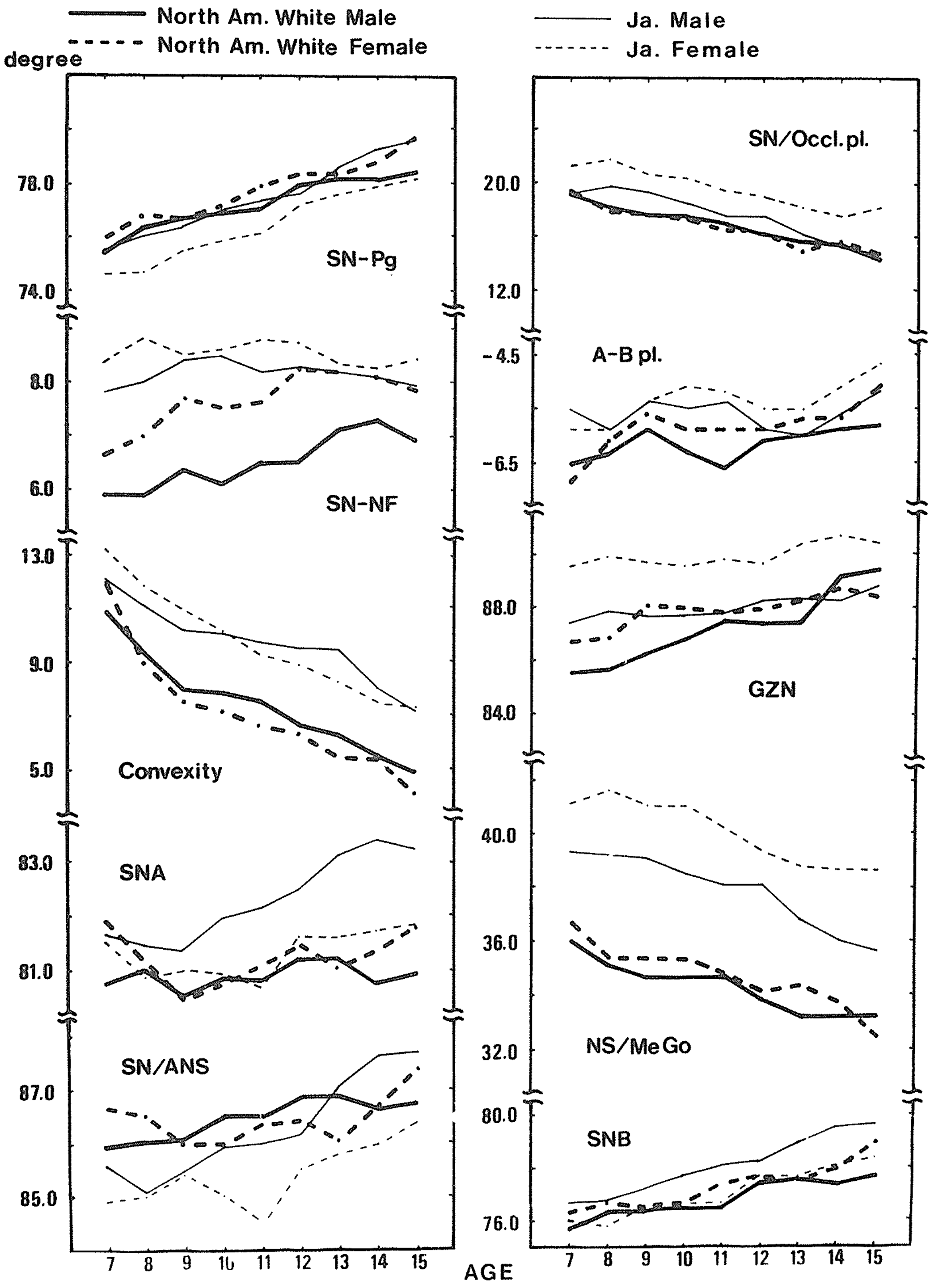


Fig. 1. Angular measurements

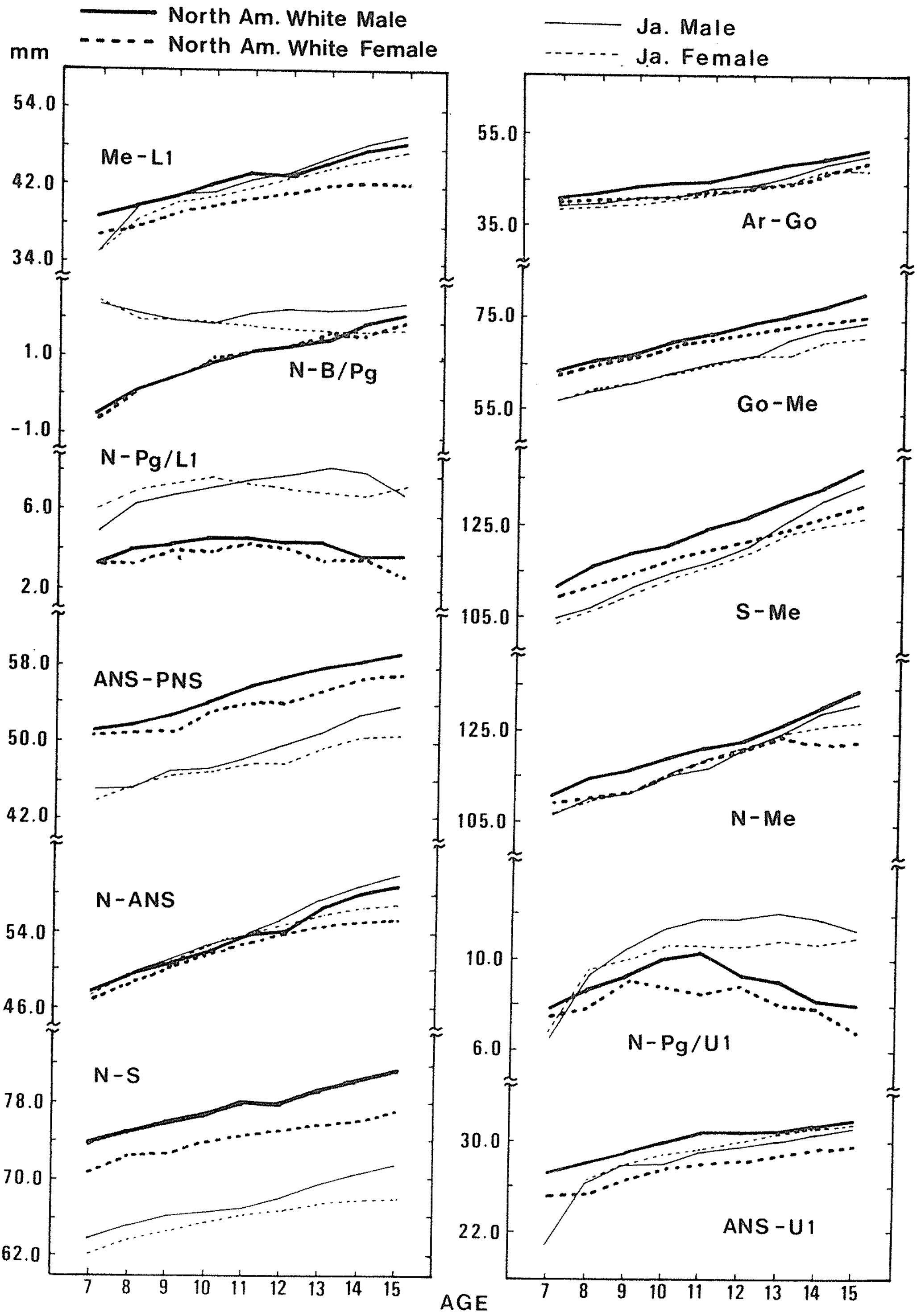


Fig. 2. Linear measurements

		SN/ANS	SNA	NA/A-Pg	SN/NF	SNPg	SNB
Angular Measurement	A	+	+	+	+	-	+
	G	-	+	-	+	-	-
		SN/GoMe	GZN	N-Pg/A-B	SN/Occl.		
	A	+	+	+	+		
	G	-	+	-	-		
Linear Measurement		SN	N-ANS	ANS-PNS	ANS-U1	N-Pg to U1	N-Me
	A	+	-	+	-	+	-
	G	-	-	-	-	+	-
		S-Me	N-Pg to L1	NB to Pg	Me-L1	Me-Go	Go-Ar
	A	+	+	+	-	+	-
	G	-	-	+	-	-	-

Table 3 Comparative results between two races
A: Amount of Growth +: significant diff.
G: Growth Trend -: no significant diff.

The most striking differences between the races were found in the protrusion of the Pogonion and its growth changes. It is a generally accepted opinion that Caucasians have a well developed symphysis compared to other ethnic groups. The results of this study support this opinion very well.

From the view points above, we can summarize the character of craniofacial form and growth changes in Japanese children as the shortening of the anterior cranial base, the smaller size of the mandibular body, a more backward mandibular rotation and a less prominent mandibular symphysis.

It is very interesting and meaningful to evaluate the facial form and its growth changes among several ethnic groups. Morphological variations in different races is not only found in size and shape but also in the growth timing. These differences definitely affect the planning of orthodontic treatment.

Summary and Conclusion

Racial differences in the craniofacial form and growth changes have been studied by using serial cephalometric data of Japanese and North American Caucasian children. Comparisons have been made of each age in dimensional and angular differences of measurements.

Several racial differences were identified:

(1) North American children had a longer anterior cranial base and nasal floor.

(2) The development of prognathism was observed among Japanese children.

(3) A backward mandibular rotation and relatively small mandibular body were found among Japanese children.

(4) The most typical differences were recognized in the growth change of the mandibular symphysis.

References

Altemus, L. A. 1960 A comparison of cephalofacial relationships. Angle Orthodont., 30:223.

Björk, A. 1947 The face in profile. Svenska tand.-tidsk., 40: No. 5B (supp.)

Iwasawa, T., T. Moro and K. Nakamura 1977 Tweed triangle and soft-tissue consideration of Japanese with normal occlusion and good facial profile. Am. J. Orthod., 72: 119-127.

Kuroda, T. 1970 A longitudinal cephalometric study on the craniofacial development in Japanese children. Paper presented at the I. A. D. R., New York, March.

Miura, F., Sakamoto, T., Irie, M. and Yano, Y. 1958 Analysis of class II, division 1 malocclusion in Japanese by Henry's method. J. Jap. Orthod. Soc., 17:201-209.

Miura, F., Irie, M., Kuwabara, M., Inoue, N. and Yano, Y. 1960 The facial analysis in Japanese female adults by Coben's method. J. Jap. Orthod. Soc., 19: 40-56.

Miura, F., Inoue, N. and Suzuki, K. 1965 Cephalometric standards for Japanese according to the Steiner analysis. Am. J. Orthod., 51: 288-295.

Miura, F. and Moyers, R. E. 1968 The use of serial cephalograms to study racial differences in development, I. VIIIth Congress of Anthropological and Ethnological Sciences, Tokyo, 284-290.

Miura, F. and Moyers, R. E. 1968 The use of serial cephalograms to study racial differences in development, II. VIIIth Congress of Anthropological and Ethnological Sciences, Tokyo, 290-296.

Riolo, M. L., Moyers, R. E., McNamara, Jr. J. A. and Hunter, S. W. 1974 An atlas of craniofacial growth The Center for Human Growth and Development, Univ of Michigan, 25-216.

The Dentition of King Christian the Third

Dental Disease and Oral Hygiene Habits of a Sixteenth Century King of Denmark and Norway

P. O. PEDERSEN

OSSA

King Christian the Third of Denmark and Norway was born in 1503 and died in 1559. Recently, his skeletal remains were examined by J. Balslev Jørgensen and the present author the latter being responsible for the dental aspects. The dental findings include loss of several molars intra vitam, severe buccal and approximal carious lesions in the cementum of molars and premolars, and moderately severe attrition of most teeth. The location of calculus indicates a course of the gingival margin with little recession, and there is only slight recession of the alveolar margin except opposite the facial surfaces of the roots of the upper anterior teeth and premolars where marginal bone recession is considerable. The facial surfaces of the upper anterior tooth crowns exhibit very pronounced abrasion of enamel with exposure of islands of dentine gingivally. These surfaces show fine microscopic scratches in the main running transversally. This loss of tooth substance seems to have been caused by frequent cleansing with a fine abrasive a procedure also responsible for the gum recession. The same tooth crowns exhibit loss of approximal contours and microscopic tracks caused by the use of metal tooth-picks. Periapical bone destruction is found around three teeth and the temporo-mandibular joints show osteoarthritic changes.

Keywords: Sixteenth Century King, Dental Disease of - Oral Hygiene Habits of -.

Король Дании и Норвегии, Кристиан III, родился в 1503 г. и умер в 1559 г. Исследованием его скелетных останков занимался недавно Й.Балслев Йоргенсен. Зубы были изучены автором настоящей статьи. Обнаружено, что потеря нескольких коренных зубов произошла еще при жизни; наблюдались тяжелые кариесные буккальные и апроксимальные поражения цемента больших и малых коренных зубов, а также умеренное изнашивание большинства зубов. Отложение зубного камня указывает место прохождения края десны, снабженного небольшим углублением. Отмечается лишь незначительное углубление альвеолярного края, за исключением противоположных лицевых поверхностей корней верхних передних зубов и малых коренных зубов. Наблюдалось значительное углубление у края кости. Лицевые поверхности коронок верхних передних зубов демонстрируют резко выраженное стирание эмали, причем разрушению подвергались участки дентина в самой десне. Эти поверхности выявляют тонкие микроскопические царапины, проходящие, главным образом, в поперечном направлении. Отмеченная потеря зубной субстанции могла быть вызвана часто проводимой чисткой зубов с помощью специальной шлифовки. Та же самая процедура могла вызвать углубление в десне. Коронки тех же зубов обнаруживают потерю апроксимальных контуров и микроскопические следы, возникшие благодаря употреблению металлических зубочисток. Разрушение периапикальной кости найдено у трех зубов. Челюстно-височные суставы указывают на костноартритические изменения.

Ключевые слова: король из XVI столетия, зубные болезни, обычаи зубной гигиены.

P. O. Pedersen, Grønnevej 255, ^{12}, DK-2830 Virum, Denmark.

Vol. 6, pp. 229-242, Lund. ISSN 0345-8865.

Introduction

Christian the Third was born in 1503. He ascended the Throne as King of Denmark and Norway in 1534 after a long period of internal and external wars. Having carried through the Reformation in his countries he died on New Year's day in 1559 aged 55. Over the years he suffered from several spells of serious illness and died from one associated with severe inflammation in one of his legs.

The coffins of Christian the Third and his Queen Dorothea are kept in a chamber under a magnificent sepulchral monument in a Royal Chapel of the Cathedral of Roskilde, Denmark. Recent repair necessitating opening of the coffins offered an opportunity of anthropological and odontological examinations of the two skeletons. The present report deals with the results of the examination of the King's dentition. Data on the Queen's dentition will be published later as will a joint report by J. Balslev Jørgensen and the present author on the entire study.

Methods

The skull is well proportioned (Figs. 3-6). It is well preserved except for a few patches of brushite. The facial bones and the teeth carried a certain amount of dry soft tissue debris which, however, could easily be removed by the use of a wet soft brush.

The teeth were inspected and measured and all changes of the dental hard tissues recorded in great detail. Deposits of calculus and the course of the alveolar margin were recorded on periodontal diagrams. The distances from the alveolar limbus to the cemento-enamel junction were measured opposite each tooth. A large number of photos were taken. The roentgenological examination included photos of the skull (Figs. 5-6) for cephalometric analysis and dental films of jaws and teeth. Finally, a special study was made of the microscopic structure of the facial and approximal surfaces of the anterior teeth using metal-shadowed collodion replicas for light microscopy (see Pedersen & Scott, 1951). All surfaces of C sup. dext. and I_2 sup. dext. were also studied by means of scanning electron microscopy (see Hayat, 1978).

The dentition

The following dental situation was found,

$$\begin{array}{c} \text{sup.} \\ \text{dext.}\ \begin{array}{cccccccc|cccccccc} M_3 & M_2 & & & P_1 & C & I_2 & I_1 & & I_2 & C & P_1 & P_2 & & & M_3 \\ \hline M_3 & & & P_2 & P_1 & C & I_2 & I_1 & I_1 & I_2 & C & P_1 & P_2 & & & \end{array}\ \text{sin.} \\ \text{inf.} \end{array}$$

M_1 sup. dext., P_2 sup. dext., M_1 sup. sin., M_2 inf. dext., M_1 inf. dext. and M_2 inf. sin., i.e. six posterior teeth were lost years before death their sockets having healed completely. Two further molars (M_2 sup. sin. and M_3 inf. sin.) were either present at death as carious stumps or were lost shortly before death (traces of sockets left). Though clearly present at death two teeth (I_1 sup. sin. and M_1 inf. sin.) could not be found.

All teeth present were well developed and showed no enamel hypoplasia. Their dimensions fall within the ranges reported for medieval Danes by Lunt (1969) and medieval Swedes by Sagne (1976).

Fig. 1.
King Christian III painted by Jost Verheiden.

Fig. 2.
The corpse of King Christian III painted by Jost Verheiden.

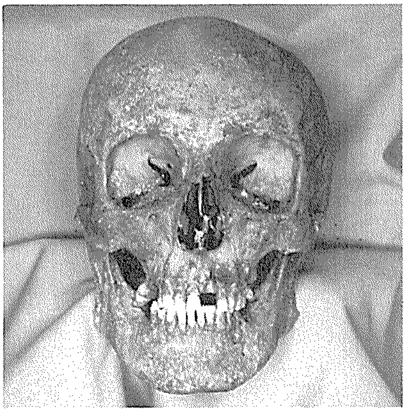


Fig. 3.
Norma frontalis of skull.

Fig. 4.
Norma lateralis of skull.

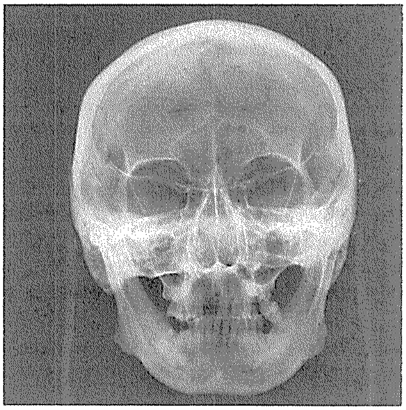


Fig. 5.
Postero-anterior head film.

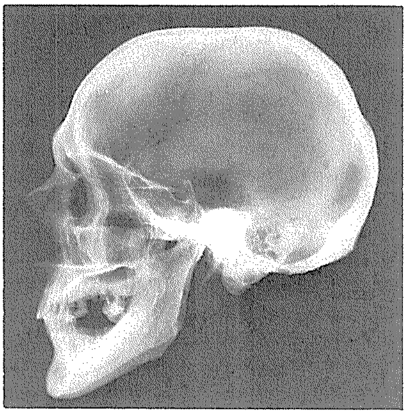


Fig. 6.
Lateral head film.

Attrition

All teeth are worn. While the elongated P_2 inf. dext. only shows slight occlusal attrition due to early loss of P_2 sup. dext. all other teeth exhibit pronounced wear their dentine being exposed partially (molars and premolars) or totally (canines and incisors). The exposed dentinal surfaces of the anterior teeth are hollowed out more so than usually found in contemporary dentitions. There is pulp exposure in one tooth, viz. P_1 inf. sin. The resulting pulp necrosis and infection caused the periapical bone destruction seen in Figs. 11-12.

Abrasion

The maxillary canines and incisors as well as P_1 sup. dext. exhibit considerable loss of facial enamel attaining a maximum in their gingival thirds. In C sup. dext. a smooth rather deep gingival defect is located both in the dentine and the cementum (Fig. 13). Mesio-gingivally in I_2 sup. dext. and disto-gingivally in I_1 sup. dext. (Fig. 14) large islands of dentine are exposed. There are minor changes of the same type in the gingival parts of the facial surfaces of I_2 sup. sin. and C sup. sin. as well as the mandibular central incisors.

Studies of the areas mentioned above by means of a stereomicroscope, metal-shadowed collodion replicas for light microscopy and SEM revealed multiple very fine scratches running in all directions though mainly transversally across the tooth crowns. The exposed dentine (Figs. 18-19) and cementum showed deeper scratches with a similar main course. The enamel surfaces did not show the typical honeycomb pattern due to influence by acids. It is reasonable to assume that the loss of facial enamel, dentine, and cementum was brought about by rubbing the teeth with a very fine abrasive applied by means of a piece of cloth or possibly with a brush.

The close study of the surfaces of the upper anterior teeth disclosed a further kind of loss of enamel, viz. on the approximal surfaces which had lost their convex contours. They appeared flattened and in places were transversed by straight or curved furrows clearly seen microscopically (Fig. 20). This particular loss of proximal enamel is likely to have been caused by the use of metal toothpicks.

Dental caries

There is every reason to believe that the teeth lost intra vitam were lost due to caries. Carious lesions were found in 12 teeth out of 22 teeth present. Ultimate stages of carious destruction were found in M_2 sup. dext. (Fig. 10) and in P_2 inf. sin.(Fig. 11). Rampant lesions were seen in several other molar and premolar teeth. At least two of these lesions (in M_3 sup. dext. and P_1 sup. sin.) showed manifestations of pulp involvement. With the exception of a small carious cavity in the enamel mesially in C sup. dext. all cavities were located in the cementum buccally (Fig. 10) or approximally (Fig. 11). The early stages involved the cementum only while the advanced stages transgressed the cemento-enamel junction undermining the enamel (Fig. 10). This type of dental caries is predominant in mature medieval Scandinavian skulls studied by the present author and others (Mellquist & Sandberg, 1939; Brinch, 1952; Møller-Christensen, 1958 and Swärdstedt, 1966). By clinical standards ten of King Christian the Third's anterior teeth (five upper and five lower) were caries-free. Upon stereomicroscopic scrutiny, however, superficial brown lesions were seen in the approximal enamel of several upper anterior teeth.

Calculus

Calculus was present on all teeth. Most calculus deposits formed rims on the crowns parallel to the gum margin and indicating the course of the latter (Figs. 15-17). Where recession of the gingivae occurred, the calculus rims were situated on the root surfaces. This applied especially to the facial aspects of the upper anterior teeth and premolars on the right side and the buccal aspects of the three third molars.

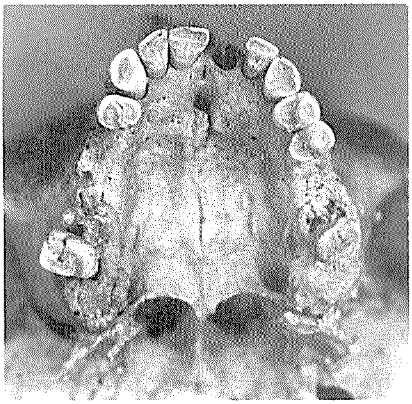


Fig. 7.
Occlusal aspect of maxillary dental arch.

Fig. 8.
Occlusal aspect of mandibular dental arch.

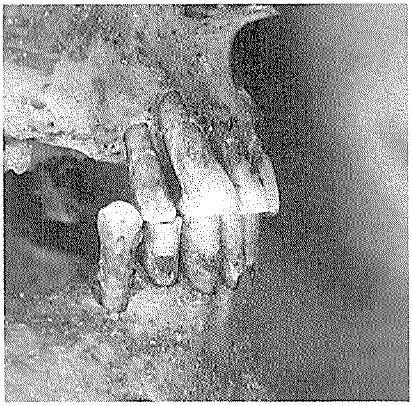


Fig. 9.
View of right dental arches. Elongation of P_2 inf. dext. Slight distal occlusion. Faciogingival caries in P_1 inf. dext. Note location of calculus deposit rim and pronounced recession of facial alveolar limbus at P_2 inf. as well as P_1 and C sup.

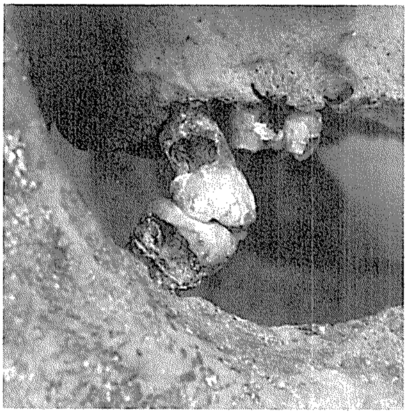


Fig. 10.
Right side of jaws. Third molars occluding. Severe carious cavities in both M_3s. Decayed roots of M_2 sup. dext. visible.

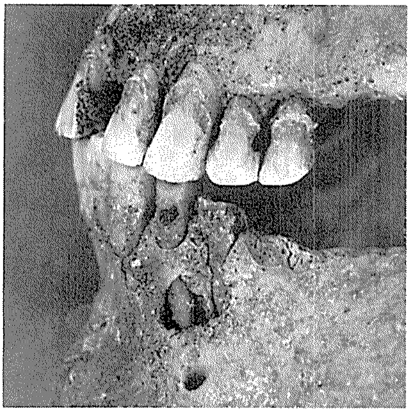


Fig. 11.
View of left dental arches. Gingivo-approximal carious cavities in both upper premolars. Facio-gingival carious lesion in the cementum of P_1 inf. sin. and total carious destruction of P_2 inf. sin. The bone cavity around the root of P_1 is caused by pulp exposure due to attrition. There is much less recession of the facial alveolar limbus at the upper teeth than on the right side of the jaws.

Fig. 12.
Roentgenogram of the same region as Fig. 11. Note periapical bone cavities and insignificant marginal loss of interdental septa.

Periodontal disease

As mentioned previously considerable recession of the gingival margin occurred facially/buccally opposite many upper and some lower teeth (Figs. 9 and 13). In addition, moderate pocket formation probably added to loss of attachment. It is remarkable, however, that in the entire dentition the alveolar margin seemed almost unaffected lingually (Figs. 16-17). The marginal alveolar limbus and the interdental septa were well preserved except in the aforementioned areas showing considerable gum recession. In these areas there was both recession of the facial alveolar walls, of the summits of the interdental septa, and of the facial aspects of the latter which looked somewhat eroded and porous (Figs. 9 and 13). In view of the age of King Christian the Third at death (55 years) and his abundant dental disease likely to have caused discomfort, malfunction and poor oral hygiene his periodontal situation was surprisingly good.

Fractures

Four incisors (two upper and two lower) presented small fractures of their incisal enamel (Figs. 14 and 15).

Hypercementosis

One tooth, viz. the elongated P_2 inf. sin. exhibited moderate hypercementosis.

Occlusion

The occlusion of the anterior dental arches in the mesiodistal direction was distal on the right side (Fig. 9) and neutral on the left side (Fig. 11). There was slight maxillary overjet and overbite. P_2 inf. dext. was elongated. M_3 sup. dext. and M_3 inf. dext. were the only occluding molars (Fig. 10).

Jaws and temporomandibular joints

The surfaces of the jaw bones were very rough in places. The mandible in particular carried pronounced and irregular muscle insertion areas.

The periapical bone was the site of chronic inflammation around four teeth, viz. P_1 inf. sin. (attrition exposing pulp) and M_2 sup. dext., P_2 inf. sin. and P_1 sup. sin. (caries).

The examination of the skeleton as a whole revealed a great deal of severe pathological changes of joints the temporomandibular joints being no exception. The mandibular condyles as well as the temporal components of the TMJ showed worn porous areas. The latter also exhibited small osteophytes. These osteoarthritic changes may have a general background. It is likely, however, that loss of posterior teeth and the ensuing masticatory dysfunction may be responsible, at least in part, for the changes observed (cfr. Wedel et al., 1978 and Bergmann & Hansson, 1979).

Discussion

The state at death of the dentition of King Christian the Third indicates that he suffered from lifelong oral ailments likely to have caused pain and malfunction. It is known that his daughter Anna suffered from frequent and tormenting toothache (Lübbers, 1902) but there seems to be no written accounts of His Majesty's oral hardships.

According to Troels Lund (1883) his Court consumed 550 kilograms of sugar in one year, and additional amounts of sugar were eaten in many forms. King Christian's rampant caries may thus be explained in terms of current concepts of caries etiology. His periodontal resistance on the other hand, was remarkable.

While the King was given no other dental treatment than extractions he performed meticulous oral hygiene measures to no small extent, viz. in the form of rubbing his

Fig. 13.
P_1, C and I_2 sup. dext. showing facial abrasion exposing dentine and/or cementum. Recession of facial wall of sockets and erosion of facial surfaces of interdental septa.

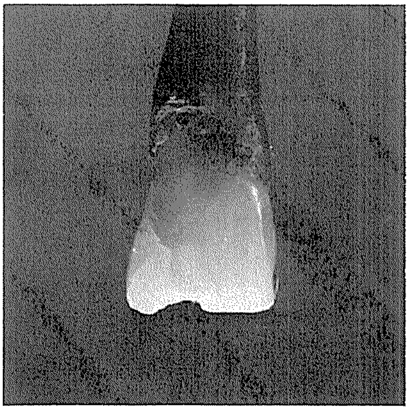


Fig. 14.
I_1 sup. dext. Severe abrasion of facial surface exposing dentine disto-gingivally. Incisal fracture.

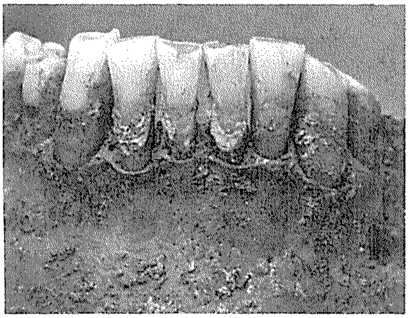


Fig. 15.
Facial aspect of lower anterior teeth. Calculus on all teeth. Moderate recession of alveolar limbal bone. Eroded appearance of facial surfaces of interdental septa.

Fig. 16.
Lingual aspects of the teeth shown in Fig. 15. Much less calculus than facially and almost intact alveolar limbus.

Fig. 17.
I_2, C, P_1 and P_2 sup. sin. Rim of calculus deposits. Palatal aspects of alveolar limbus and interdental septa almost intact.

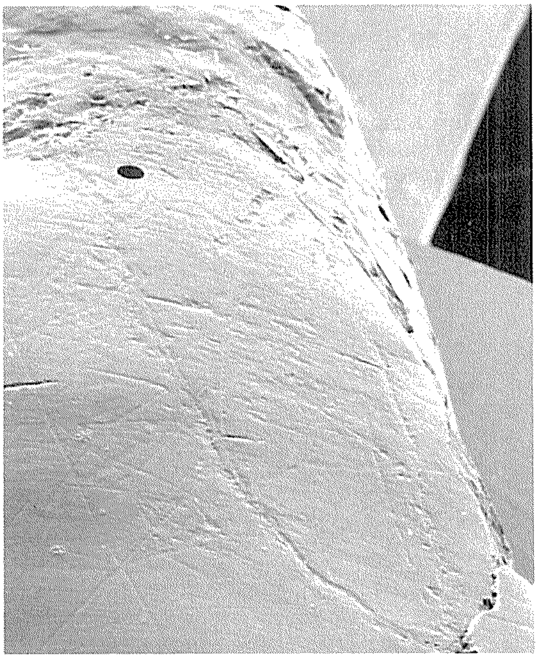


Fig. 18.
Scanning electron micrograph (SEM) of mesio-gingival part of facial surface of I_2 sup. dext. Large oval-shaped area of exposed dentine seen to the right. Scratches are in the main transversal and are deeper in the dentine.
x 20.

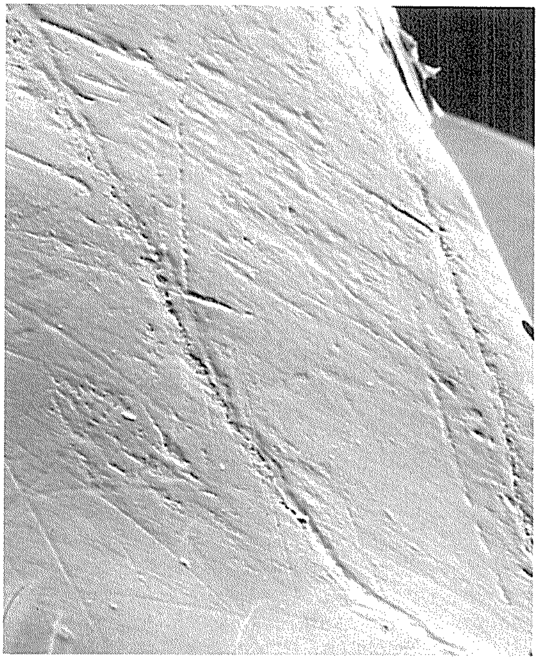
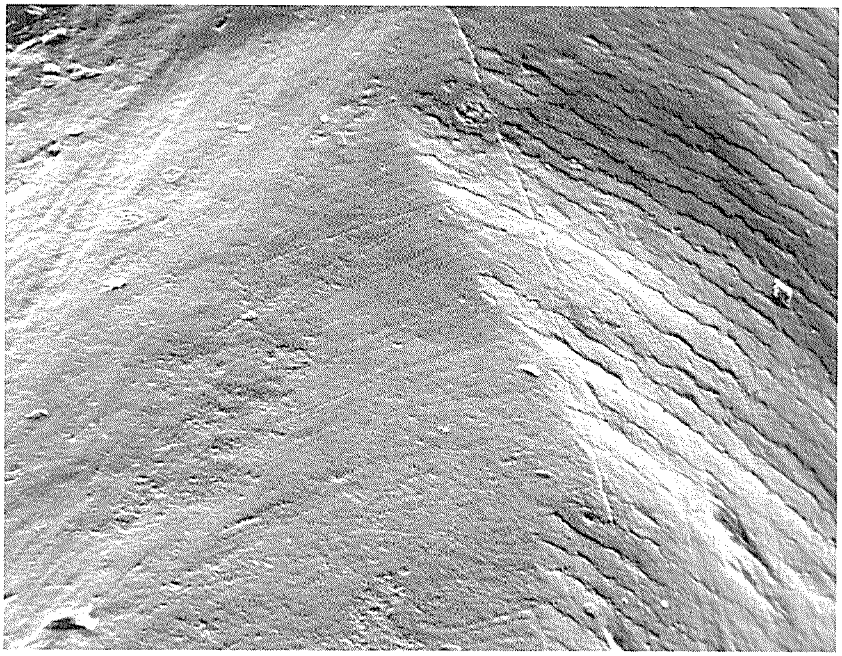


Fig. 19.
SEM of same exposed dentine (right) and enamel (left) areas as seen in Fig. 18. x 40.

Fig. 20.
SEM. Left: abraded flattened mesial enamel surface with nearly parallel scratches (metal toothpick). Right: perikymata on unworn palatal surface. x 80.



facial tooth surfaces with a very fine abrasive applied with a cloth or brush. Also he made use of metal toothpicks between his upper anterior teeth. Figs. 13-14 and 18-20 show the undesired effects of these measures. As for powders and remedies used for oral hygiene purposes in the 14th-16th centuries a wide variety are on record (Aas, 1925 and 1929, Boers, 1954) and it is impossible to tell which ones, if any, King Christian preferred. Metal toothpicks, common in Europe at the time, are known to have been used by the upper classes in Denmark in the sixteenth century. A beautifully decorated scimitar-shaped specimen made of gold was found near Viborg. It was described by Lindahl (1962). Medieval metal toothpicks were also dealt with at some length by Sachs (1967), Witt & Proskauer (1962) and others.

King Christian' s miserable dental situation was by no means unique among sixteenth century European Royalty. King Christian the Second of Denmark and Norway had only one (defective) tooth left, when he died in 1559 aged 77. While afflicted with less dental caries, the Swedish kings Gustav Vasa (1496-1560, king 1523-1560) and Erik the Fourteenth (1533-1577, king 1560-1568) had rather advanced marginal periodontal disease (Ingelmark, 1956, Lysell, 1958, Hjortsjö, 1962). Queen Elizabeth I who ruled England 1558-1603 suffered from frequent heavy toothache. She is known to have cleansed her teeth by rubbing them with a cloth and to have used gold toothpicks (Lavine, 1967).

Acknowledgements

This study was conducted in collaboration with Dr. J. Balslev Jørgensen to whom the present author extends his thanks. The author is also grateful to the following members of the staff of the Royal Dental College, Copenhagen: Professor Tor Zelander for expert advice, Dr. Ib Sewerin and Bente Friederichsen for taking the roentgen photos, Bente Kudahl for extensive photographic service and Lise Fredebo for performing the SEM laboratory work.

References

Beckett, F. 1932 Renæssancens Portrætmaleri. 28 pp. + 47 plates. Gads Forlag, København. (In Danish.)

Bergmann, L.-E. & Hansson, T. 1979 Hard tissue changes of the temporomandibular joint in an archaeo-osteological material from the 11th century. Swed. Dent. J. 3, 149-155.

Boers, H. 1954 Folketro om tænder, tandmidler og tandbehandling hos almuen i Danmark. 183 pp. Dansk Videnskabs Forlag, København. (In Danish.)

Brinch, O. 1952 Investigations into the occurrence of dental caries in Denmark in the Middle Ages. Brit. Dent. J. 93, 88-92.

Gejvall, N.-G. 1960 Westerhus. Medieval population and church in the light of skeletal remains. 144 pp. + numerous plates. Håkan Ohlsons boktryckeri, Lund.

Hammarlund-Essler, E. 1952 Histologisk undersökning av tänder och käkben från medeltidsskelett. Svensk Tandl. Tidskr. 45, 275-290. (In Swedish with English summary.)

Hayat, M.A. 1978 Introduction to biological scanning electron microscopy. 323 pp. University Park Press, Baltimore, London, Tokyo.

Hjortsjö, C.-H. 1962 Erik XIV. En historisk, kulturhistorisk och medicinsk-antropologisk undersökning i samband med gravöppningen 1958 i Västerås domkyrka. (In Swedish with English summary.)

Ingelmark, B.-E. 1956 Medicinska och antropologiska undersökningar. Chapters 21-24 in Olsson, M. (ed.): Vasagraven i Uppsala domkyrka. Stockholm. (In Swedish with English summary.)

Isager, K. 1938 Zahnkaries und Zahnverlust an 374 Kranien aus dem dänischen Mittelalter. Tandlægebladet 42, 787-804.

Klafstad, J. 1979 Odontopathology of a Norwegian medieval population - a pilot study. Ossa 5, 43-55.

Lavine, B.H. 1967 Elizabethan toothache: a case history. J. Amer. Dent. Assoc. 74, 1286-1290.

Lindahl, F. 1962 Tandstikkere fra Christian IVs tid. Nationalmuseets Arbejdsmark 5-17. (In Danish.)

Lund, Troels 1883 Danmarks og Norges Historie i Slutningen af det 16de Aarhundrede. Femte Bog. Dagligt Liv: Fødemidler. 445 pp. C.A. Reitzel, Kjøbenhavn. (In Danish.)

Lunt, D.A. 1969 An odontometric study of mediaeval Danes. Acta odont. Scand. 27, suppl. 55, 173 pp.

Lübbers, A. 1902 De oldenborgske Kongers og deres nærmeste Families Sygdom og Død. Christian III. Ugeskr. f. Læger Nr. 15, 338-346. (In Danish.)

Lysell, L. 1958 An odontological examination of the remains of Erik XIV. Trans. Roy. Schools Dent. Stockh. and Umeå 1, 22-35.

Mellquist, C. & Sandberg, T. 1939 Odontological studies of about 140 mediaeval skulls from Halland and Scania in Sweden and from the Norse colony in Greenland, and a contribution to the knowledge of their anthropology. Odont. Tidskr. 47, Suppl. 3 B, 1-83.

Mohlin, B., Sagne, S. & Thilander, B. 1979 The frequency of malocclusion and the craniofacial morphology in a medieval population in Southern Sweden. Ossa 5, 57-84.

Møller-Christensen, V. 1958 Bogen om Æbelholt kloster. 284 pp. Dansk Videnskabs Forlag, København. (In Danish.)

Pedersen, P.O. 1955 Tænder og tandsygdomme hos nogle historiske personer. Tandlægebladet 59, 197-221. (In Danish with a summary in English.)

Pedersen, P.O. & Scott, D.B. 1951 Replica studies of teeth from Alaskan eskimo, West Greeland natives and American whites. Acta odont. Scand. 9, 262-292.

Sachs, H. 1967 Der Zahnstocher und seine Geschichte. 52 pp. Georg Olms Verlagsbuchhandlung, Hildesheim.

Sagne, S. 1976 The jaws and teeth of a medieval population in Southern Sweden. Ossa 3, suppl. 1, 131 pp.

Swärdstedt, T. 1966 Odontological aspects of a medieval population in the province of Jämtland/Mid-Sweden. 120 pp. Tiden-Barnängen, Stockholm.

Wedel, A., Carlsson, G.E. & Sagne, S. 1978 Temporomandibular joint morphology in a medieval skull material. Swed. Dent. J. 2, 177-187.

Witt, F.H. & Proskauer, C. 1962 Bildgeschichte der Zahnheilkunde. 221 pp. Verlage M. DuMont Schauberg, Köln.

Aas, I. 1925 Tannmidlene i de nordiske lægebøger fra middelalderen. Oslo. (In Norwegian.)

______ 1929 Den nordiske tannmedisin i middelalderen. Oslo. (In Norwegian.)

Regional diversity in epipaleolithic populations

PATRICIA SMITH

OSSA

Human skeletal remains from Epipaleolithic sites in Israel (Natufians), North Africa, and Nubia were compared. Although contemporary to one another, the Natufians were incipient agriculturalists, while the other two groups were large-game hunters. The specimens from Israel (Natufian Culture) were small-boned with high-vaulted, mesocephalic crania, short faces, small jaws and teeth, whereas those from North Africa and Nubia were tall and robust with long low-vaulted crania, large teeth and jaws. These populations thus fall into two distinct morphological categories, the first characteristic of Neolithic agricultural populations, the second characteristic of Upper Paleolithic hunting and gathering populations. Some of the skeletal differences found between the Natufians and their contemporaries, as well as resemblances between them and Neolithic populations in other areas, may then reflect the influence of dietary and behavioral variables on the phenotype rather than basic differences in genetic relationships. Further investigations need to be made to determine the susceptability of various skeletal parameters to such environmental variables. Only then can statistical techniques be confidently applied to the examination of evolutionary pathways or racial relationships.

Running Headline: Epipaleolithic Populations.

Сравнивали человеческие скелетные останки из эпипалеолитических стоянок в Израиле /натуфийцы, натуфийская культура/, Северной Африки и Нубии. Хотя они и жили в одно и то же время, натуфийцы были зарождавшимися земледельцами, тогда как две другие группы охотились на крупную дичь. Натуфийцы были мелкокостными, с мезоцефалическими черепами, обладавшими высокими сводами, с короткими лицами, некрупными челюстями и зубами, тогда как люди из Северной Африки и Нубии были высокими и крепкими, с длинными черепами, обладавшими низкими сводами, с крупными зубами и челюстями. Таким образом, эти популяции принадлежали к двум различным морфологическим категориям. Первая из них характеризует неолитические земледельческие популяции, тогда как вторая характеризует верхне-палеолитические охотничьи популяции. Некоторые скелетные различия, найденные между натуфийцами и их современниками, а также сходства между ними и неолитическими популяциями в других областях, могут отражать влияние на фенотип менявшихся условий питания и поведения. Последнее более вероятно, чем возможные различия в генетическом родстве. Дальнейшие исследования необходимы для того, чтобы установить чувствительность различных скелетных параметров к таким изменениям окружающей среды. В данном случае только статистические методы могут быть с уверенностью применены для изучения путей эволюции или расовых взаимоотношений.

Ключевые слова: эпипалеолитические популяции.

Patricia Smith, Hebrew University - Hadassah School of Dental Medicine, P.O.Box 1172, Jerusalem, Israel.

Vol. 6, pp. 243-250, Lund. ISSN 0345-8865.

Introduction

The end of the Pleistocene is characterised by marked climatic change, which caused drastic alterations in the distribution of fauna and flora and was associated with the disappearance of many genera and reduction in size of others. Human populations associated with this period and the immediate Post Pleistocene, also seem to have undergone rapid change, as shown by the differences found between skeletal remains from sites closely related both geographically and temporally.

While some alteration in selective pressures undoubtedly took place as a direct consequence of climatic change, these, as well as the more indirect effects mediated through alterations in food resources, were further modified by technological and cultural innovations.

Upper Paleolithic and Epipaleolithic sites are characterized by the diversity of ecological niches utilized, while artifacts, plant, and animal remains are indicative of marked differences in the choice, methods of acquisition, and utilisation of raw resources (Coles and Higgs, '69). In many regions this led to the intensive exploitation of one particular resource and culminated in the development of an agricultural or herding economy.

Such difference in patterns of interaction with the environmental niches utilized, extend the range of environmentally mediated differences in selective pressures, and may contribute to the interpopulation variability and acceleration in rates of change found at this time. With this concept in mind I have compared three Epipaleolithic populations showing different dietary adaptations: Natufians from Israel, North Africans from Taforalt and Afalou Abou Rhummel, and Nubians from the Wadi Halfa region.

These sites have been dated at 1200-9000 B. P. (Henry and Servello, '74; Roche, '76; and Wendorf, '68) and the associated artifacts and faunal remains point to important differences in environment and diets utilized; one group, the Natufians, were already incipient agriculturalists while the other two groups were mainly big-game hunters, although fish, shellfish and molluscs were also eaten in large quantities.

Material Examined

The Natufians are known from numerous sites in Israel and have been studied by Keith ('31, '34), McCown ('39), Vallois ('36), Smith ('70) Bar-Yosef, Arensburg and Smith ('71), Ferembach ('61, '77), Soliveres ('76) and Crognier and Dupouy-Madre ('74). Located in the wooded Mediterranean zone within the area of naturally occurring emmer wheat (Zohary, '69), the sites span some 4000 years. The archeological findings include sickle blades, mortars and pestles, and storage pits and are considered presumptive evidence of intensive collection and use of wild emmer by the Natufians (Garrod, '57; Perrot, '68; and Bar Yosef et al., '71).

The dental findings support this assumption. The teeth and jaws show sizeable deposits of dental calculus and a moderate caries rate, which is suggestive of a cereal based diet (Smith, '70).

The North African sites, Taforalt in Morocco (Ferembach, '62) and Afalou Abou Rhummel in Algeria (Arambourg et al., '34; Briggs, '55; Chamla, '70, '76), lie in the coastal region, in what was even then dry, open country with desert to the south and east (Coles and Higgs, '69). In addition to hunting Hartebeeste, gnu, equids, bear and deer, shellfish and molluscs were collected and eaten in large quantities.

The Nubian sites from the Wadi Halfa region in Southern Egypt and the Northern Sudan (Anderson, '68; Greene and Armelagos,' 72) lie in the Nile Valley, with the marshy region along the river contrasting sharply with the surrounding desert. The faunal remains were mainly of bovids and hippopotami, fish and shellfish. Grinding stones were found, and were initially thought to have been used for grinding seeds. However no wild grasses have been found in this region and the stones are paint-stained. It seems therefore that the grinding stone were probably used for grinding pigments (Butzer, '64) and that cereals were not exploited at this time.

Results

Table 1 lists the mean values of skeletal parameters in males of the three groups. The Natufians were gracile and of short to medium stature. The mean value for males was 165 cm with a maximum of 168 cms, except for 5 individuals from Eynan who reached 173 cm (Soliveres, '76). The cranial index ranged from meso-space to dolicho-cranic, the vault was high and rounded with mastoid processes and nuchal crests slight to moderate. The face was low and broad and the mandibles short with low ascending rami. In all these parameters the Natufians show some important differences from both the Taforalt-Afalou and Nubia groups. These, although showing some minor intra-group differences, were all tall (178 cm males) and robust, with large, long, low-vaulted crania and large, broad mandibles. The Nubians were the most robust of those examined with longer heads, lower cranial vaults and shorter, narrower faces than the North Africans. Of these, the Afalou crania were most divergent with some specimens meso- or even brachy-cranic.

These differences in cranial dimensions are reflected in tooth size. The mean values calculated for mesiodistal and buccolingual diameters of the teeth are given in Table 2. Teeth were smallest in the Natufians and largest in the Nubians with the North African group in between. Differences in tooth size were most pronounced in the maxilla, and were especially large in the molar and premolar region. Tooth area calculated as length multiplied by breadth shows statistically significant differences between the Nubians and North Africans for all maxillary teeth from M3 to I2 ($p > 0.5$). The Nubians, the most robust population with the largest jaws, had the largest teeth.

Discussion

Many of the morphological features characteristic of the Nubia-North African groups are common to European Upper Paleolithic groups, as well as to Near Eastern Middle Paleolithic remains. Such features include the tall stature, overall robusticity, large, long, low-vaulted crania and large jaws and teeth. These resemblances have been commented upon by Ferembach ('76, '77), Chamla ('76), Anderson ('68) and Greene and Armelagos ('72) who see them as possible indications of genetic relationship between Upper Paleolithic populations in Europe and North Africa. However, they may reflect nothing more than functional adaptation to a common life style, the salient features of which include a nomadic pattern of existence, large-game hunting and a diet high in animal protein, necessitating prolonged, vigorous chewing. The Natufian morphology on the other hand, with its more rounded gracile cranium, small jaws and teeth, resembles the general pattern of Mesolithic and Neolithic populations from Iraq through Europe and North Africa such as Zawi Chemi Shanidar (Ferembach, '70), Columnata (Chamla, '70), Nubia (Nielsen, '70), Morbihan (Pequart, Boule and Vallois, '37), while contrasting markedly from that of their presumed Middle Paleolithic predecessors from Skhul and Quafzeh (Smith, '70; Ferembach, '77). The functional implications of these changes in craniofacial dimensions has been reviewed by Carlson ('76) and Carlson and van Gerven ('77). Carlson compared craniofacial dimensions in Nubians of different periods from the Paleolithic to the present. He found that the main evolutionary trends were shortening and rounding of the cranial vault, reduction of the face and bony areas of attachment of the masticatory muscles and reduction of the jaws and teeth. In a later article, Carlson and van Gerven ('77) suggested that these changes were primarily related to reduction of the masticatory complex, consequent to change in masticatory function, with dental changes secondary (or in their terms, tertiary) to reduction in the size of the jaws. They attributed these changes to behavioral changes associated with transition from a hunting and gathering to an agricultural subsistence pattern. This hypothesis could account for the differences found in the present study. This implies more than just functional changes in the masticatory complex associated with cereal eating. Activity and energy expenditure associated with collecting as opposed to a hunting life style, the altered nutritional content of a cereal based diet, and probable increase in endemic diseases associated with accompanying sedentisation, all affect skeletal morphology (Newman, '75). Some of the skeletal differences found between the Natufians and their contemporaries as well as resemblances between them and Neolithic populations in other areas, may then reflect the influence of dietary and behavioral variables on the phenotype rather than basic differences in genetic relationships. Further investigations need to be made to determine the susceptibility of various skeletal parameters to such environmental variables. Only then can statistical techniques be confidently applied to the examination of evolutionary pathways or racial relationships.

References

Anderson, J. E. 1968 Late Paleolithic skeletal remains from Nubia. pp 996-1040,in Wendorf F. Prehistory in Nubia, 1968. Dallas, Texas.

Arambourg, C., M. Boule, H. Vallois, and R. Verneau 1934 Les grottes paléolithiques des Beni Segouel (Algerie). Arch. de l'institut de Paléont. Humaine. Mém. 13. Masson et cie Paris.

Bar-Yosef, O., B. Arensburg, and P. Smith 1971 Algunas notas acera de la cultura y antropologia natufienses. Ampurias, 33: 111-152.

Briggs, L. C. 1955 The Stone Age Races of Northwest Africa. Bull. 18. Am. School of Prehis. Res. Harvard University.

Butzer, K. W. 1964 Environment and Archaeology: an introduction to Pleistocene geography. Aldine Publishing Co. Chicago, Illionois.

Carlson, D. S. 1976 Temporal variation in prehistoric Nubian crania. Am. J. Phys. Anthrop. 45: 467-484.

Carlson, D. S. and D. P. van Gerven 1977 Masticatory function and Post-Pleistocene evolution in Nubia. Am. J. Phys. Anthrop. 46: 495-506.

Chamla, M. C. 1970 Les hommes épipaléolithiques de Columnata. Mem. du centre de recherches anthropologiques, prehistoriques et ethnographiques. Arts & Metiers Graphiques. Paris.

______ 1976 Les hommes Cromagnoides d'Afrique du Nord et le problème de leur extension pp. 144-152 in Chronologie et synchronisme dans la préhistoire circum-Méditerranéene. Reprint IXth Congres ISPP Nice 1976.

Coles, J. M. & E. S. Higgs 1969 The archeology of early man. Faber & Faber, London.

Crognier, E. & M. Dupouy-Madre 1974 Les Natufians du Nahal Oren. Paleorient 2: 103-121.

Ferembach, D. 1961 Squelettes du Natoufien d'Israel. Etude anthropologique. L'Anthropologie 65: 46-66.

______ 1962 La Nécropole Epipaléolithique de Taforalt (Maroc oriental). Publie avec le concours du centre national de la recherche scientifique. Rabat.

______ 1970 Étude anthropologique des ossements humains proto-néolithiques de Zawi Chemi Shanidar (Irak) Sumer 26: 21-65.

______ 1976 Les Cromagnoides Circum-Mediterraneéns (particulièrement en Orient) et les origines des types Mediterraneéns. pp 128-143, in Chronologie et synchronisme dans la préhistoire circum-Méditerraneénne. ed. G. Camps. preprint Nice France.

Ferembach, P. 1977 Les Natoufiens de Palestine 240-251, in Eretz-Israel vol. XIII. 1977 ed. B. Arensburg, O. Bar-Yosef, Israel Exploration Society Central Press J'lem.

Garrod, D. A. E. 1957 The Natufian Culture: The life and economy of a Mesolithic people in the Near East. Proc. the Brit Acad 43: 211-227.

Greene, D. L. and G. J. Armelagos 1972 The Wadi Halfa Mesolithic population. Dept. of Anthropology, U. of Mass. Research Report #II.

Greene, D. L., G. H. Ewing, and G. Armelagos 1967 Dentition of a Mesolithic population from Wadi Halfa, Sudan. Am. J. Phys. Anthrop. 27:41-55.

Henry, D. O. & A. F. Servello 1974 Compendium of carbon-14 determinations derived from Near Eastern prehistoric deposits. Paleorient 2: 87-102.

Keith, A. 1931 New discoveries relating to the antiquity of man. W. W. Norton & Co., New York.

______ 1934 The Late Paleolithic inhabitants of Palestine. In: Proc 1st Internat'l Cong Prehist. & Protohist. Sci London pp. 46-47.

McCown, T. D. 1939 The Natufian crania from Mt. Carmel, U. of California. Unpublished dissertation.

Newman, M. T. 1975 Nutritional adaptation in man. pp. 210-259, in Damon A. Physiological Anthropology (1975). Oxford University Press, London, Toronto.

Nielsen, O. V. 1970 The Nubian skeleton through 4000 years. Andelsbogtrykkeriet i Odense Copenhagen.

Péquart, M. et St. J., Boule M., H.V. Vallois, 1937 Téviec. Station nécropole mésolithique du Morbihan. Arch. institut. Paléont. Humaine Mém. 18. Masson et Cie Paris.

Perrot, J. 1968 Préhistoire Palestinienne. Supplément au Dictionnaire de la Bible. 8: 286-446.

Roche, J. 1976 Cadre chronologique de l' epipaleolithique marocain pp. 153-167 in Chronologie et synchronisme dans la préhistoire circum-Mediteraneénne. pre-print for IXth Congress. ISPP. Nice 1976.

Soliveres, O. 1976 Les Natufiens de Mallaha (Israel). Dissertation, University of Paris.

Smith, Patricia 1970 Dental Morphology and pathology in the Natufians: the dental evidence for dietary specializations. U. of Chicago. Unpublished dissertation.

Vallois, H.V. 1936 Les ossements Natoufiens d' Erq-elAhmar. L' Anthropologie 46: 36-539.

Wendorf, F. 1968 Site 117: A Nubian Final Paleolithic graveyard near Gebel Sahaba, Sudan. p. 954-995, in Wendorf, F. The Prehistory of Nubia vol. 2. S.M.U. Press, Dallas, Texas.

Zohary, D. 1969 The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. In: The domestication and exploitation of plants and animals. P. Ucko and G.W. Dimbleby ed. London G. Duckworth and Co. Ltd. pp. 47-66.

Trotter, M. and G.C. Gleser 1958 A re-evaluation of estimation of stature taken during life and of long bones after death. Am. J. Phys. Anthrop. 16: 79-123.

TABLE 1.

Mean values of Craniofacial Measurements and Stature Calculated for Males (mm)

	Nubia		North Africa		Israel	North Africa	Nubia
	#61336[1]	#117[2]	Taforalt[3]	Afalou[4]	Natufian[5]	Columnata[6]	A group[7]
Cranial length	195	195	195	195	188	188	186
Cranial breadth	141	137	146	145	137	143	136
Basion-bregma height	135	132	144	144	139	135	134
Minimum frontal breadth	103	102	94	98	98	91	96
Bizygomatic diameter	138	142	147	141	136	---	126
Upper facial height	66	71	69	70	67	---	68
Total facial height	119	121	---	121	---	---	109
Nasal height	47	47	54	53	50	---	48
Nasal breadth	26	28	28	28	26	---	26
Bigonial diameter	105	110	114	111	99	115	91
Symphysis height	36	40	40	40	35	33	34
Ramus height	66	64	68	65	59	68	55
Ramus breadth	41	43	40	34	38	37	34
Mandibular length	114	112	114	109	104	107	---
Bicondylar diameter	118	128	129	124	121	124	---
Stature	1726	1769	1740	1780	1650	1719	1780

Footnote

[1] Green and Armelagos, '72
[2] Anderson, '68
[3] Ferembach, '62
[4] Briggs, '55
[5] Bar Yosef, Arensburg, and Smith, '71-'72
[6] Chamla, '70
[7] Nielson, '70

TABLE 2.

Tooth measurements of epipaleolithic populations

			M3			M2			M1			Pm2		
		Site	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
MAXILLA	MD	Wadi Halfa	10	9.4		9	11.10		8	11.30		8	7.40	
		J. Sahaba	12	9.07	0.7	14	10.90	0.8	13	11.21	.4	12	7.08	0.3
		Taforalt [2]	10	9.27	0.7	9	10.15	0.8	12	10.50	.5	13	6.71	0.5
		Afalou [2]	23	8.99	0.6	14	10.40	0.7	20	10.56	.5	20	7.11	0.9
		Natufian	49	8.88	0.7	66	9.74	0.5	75	10.44	.8	74	6.97	1.0
	BL	Wadi Halfa	10	11.80		9	12.30		8	12.30		8	10.00	
		J. Sahaba	12	11.62	1.0	14	12.75	0.6	13	12.64	.4	12	10.21	0.6
		Taforalt	10	11.90	0.8	9	12.33	0.8	13	11.86	.5	13	9.87	0.6
		Afalou	23	11.99	0.7	23	12.47	0.7	21	12.32	.4	21	10.43	0.6
		Natufian	46	11.19	1.0	65	12.16	0.7	72	12.22	.7	70	9.83	0.6
MANDIBLE	MD	Wadi Halfa	6	11.80		8	11.80		9	12.10		5	7.70	
		J. Sahaba	11	11.27	0.6	15	11.34	0.6	15	11.95	.5	15	7.43	0.4
		Taforalt	11	11.63	0.8	12	11.37	1.0	11	11.53	.6	11	7.14	0.5
		Afalou	15	10.86	0.9	16	11.22	0.5	17	11.20	.5	17	7.26	0.6
		Natufian	73	10.50	0.6	97	10.83	0.6	96	11.40	.6	90	7.71	1.3
	BL	Wadi Halfa	6	11.50		8	11.50		9	11.50		5	9.20	
		J. Sahaba	11	11.08	0.6	14	11.14	0.7	15	11.40	.5	15	8.85	0.6
		Taforalt	11	11.53	0.8	12	11.49	1.0	11	11.35	.7	11	9.13	0.8
		Afalou	15	11.10	0.8	16	11.30	0.4	17	11.26	.4	17	9.16	0.4
		Natufian	69	10.39	0.6	96	10.67	0.6	92	11.04	.5	88	8.42	0.7

---

[1] After Greene, Ewing and Armelagos, '67

[2] Computed from measurements supplied by D. Freyer

TABLE 2 cont.

			Pm1			C			I 2			I 1		
		Site	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
MAXILLA	MD	Wadi Halfa	9	7.60	-	4	7.60	-	5	7.60	-	5	9.80	-
		J. Sahaba	12	7.79	.3	12	8.20	.4	11	7.48	.4	11	9.67	.5
		Taforalt	9	7.22	.5	9	7.82	.5	10	7.23	.7	2	9.10	.1
		Afalou	17	7.25	.5	14	7.98	.4	13	7.20	.5	-	-	-
		Natufian	69	7.08	.5	59	7.69	.6	47	6.83	.7	31	9.06	.7
	BL	Wadi Halfa	9	9.70	-	4	8.50	-	5	6.80	-	5	7.30	-
		J. Sahaba	12	10.29	.4	12	8.85	.6	11	7.08	.5	11	7.70	.3
		Taforalt	10	9.82	.7	9	9.00	.7	10	6.64	.4	2	7.60	.4
		Afalou	18	10.17	.4	14	9.14	.7	13	7.23	.4	--	--	--
		Natufian	68	9.67	.7	56	8.66	.5	45	6.61	.5	28	7.30	.4
MANDIBLE	MD	Wadi Halfa	5	7.60	-	4	7.40	-	3	6.20	-	4	5.70	-
		J. Sahaba	15	7.50	.4	15	7.38	.3	13	6.43	.4	11	5.89	.3
		Taforalt	11	7.07	.5	11	7.19	.5	9	6.00	.2	10	5.71	.4
		Afalou	15	7.15	.5	15	7.34	.5	13	6.21	.5	13	5.76	.3
		Natufian	82	7.18	.7	63	6.89	.5	56	6.03	.6	46	5.32	.4
	BL	Wadi Halfa	5	8.90	-	4	8.10	-	6	6.60	-	4	6.30	-
		J. Sahaba	15	8.69	.7	13	8.61	.6	13	7.02	.5	11	6.51	.4
		Taforalt	11	8.53	.5	11	8.40	.5	9	6.98	.4	10	6.50	.4
		Afalou	15	8.71	.5	15	8.00	.5	13	6.64	.3	13	6.14	.3
		Natufian	77	8.08	.5	51	7.80	.7	52	6.54	.4	43	6.13	.4

Asymmetrical tooth forms in human monozygotic twins

ROBERT N. STALEY

OSSA

The purpose of this paper is to report unusual asymmetrical tooth forms observed in three monozygotic twin pairs, and to review possible explanations for such occurrences.

A t-shaped maxillary lateral incisor, having a large ridge along the entirety of the lingual surface, was found unilaterally in one member of a pair of female monozygotic twins. The father of the twins was reported by the mother to also have a unilateral t-shaped maxillary lateral incisor. A triangular-shaped, three-rooted mandibular deciduous first molar was observed unilaterally in one member of a male monozygotic twin pair. An odd-shaped maxillary deciduous second molar was observed unilaterally in one member of a female twin pair. A brother of the twins had two maxillary deciduous second molars which resembled the odd tooth in the twin pair.

Several genetic and environmental processes could possibly explain such asymmetries: somatic crossing over, somatic mutation, chromosomal alterations arising from mitotic mishaps, Lyon hypothesis, gene penetrance and expressivity, cytoplasmic inheritance, epigenetic and environmental influences. The plausibility of these explanations is discussed.

Keywords: Twins - Dentition - Asymmetry.

Целью данной статьи является сообщение о необычной асимметрической форме зуба, наблюдавшейся у трех пар однояйцевых близнецов, и предлагает возможные объяснения этого явления.

Имеющий t-форму верхнечелюстной боковой резец, несущий большую складку вдоль всей поверхности, обращенной к языку, был найден на одной стороне у одного из женских однояйцевых близнецов. По сообщению матери, отец близнецов также обладал верхнечелюстным боковым резцом t-формы. Трехкорневой нижнечелюстной первый молочный большой коренной зуб, имеющий треугольную форму, наблюдался с одной стороны у одного из мужских близнецов. Второй верхнечелюстной молочный большой коренной зуб неправильной формы наблюдался с одной стороны у одного из женских близнецов. Брат этих близнецов имел два верхнечелюстных молочных больших коренных зуба, которые были похожи на неправильный зуб у близнеца.

Различные генетические процессы и процессы, происходящие в окружающей среде, могут, возможно, объяснить такую асимметрию: соматический кроссинг-овер, соматическая мутация, хромосомные изменения, возникающие в результате ошибок во время митоза, гипотеза Лиона, генное пенетрирование и выражение наследственного признака, цитоплазматическая наследственность, влияние механизма развития и окружающей среды. Обсуждается правдоподобность этих объяснений.

Ключевые слова: близнецы, зубы, асимметрия.

Robert N. Staley, Department of Orthodontics College of Dentistry, The University of Iowa, Iowa City, 52242 U.S.A.

Vol. 6, pp. 251-260, Lund. ISSN 0345-8865.

The purpose of this paper is to report unusual asymmetrical tooth forms observed in three monozygotic twin pairs, and to review the thoughts of several investigators who have been concerned with differences found between monozygotic twins.

Materials and methods

The twins were participants in the Twin Growth Study at the State University of New York at Buffalo. They were caucasian residents of western New York State. Zygosity was determined serologically, using six blood factors: ABO, Rh, MNSs, P, Kell, and Duffy. Discordance in any one factor was considered evidence of dizygotic origin. Facial appearance and anthropometric measurements of the pairs supported their serolog diagnoses.

Observations of the teeth of the twins were taken from plaster models derived from alginate impressions.

Findings

T-shaped Maxillary Lateral Incisor. A maxillary left permanent lateral incisor with a large median ridge extending from the cingulum to the incisal edge on the lingual surface was observed in one member of a female monozygotic twin pair (Figure 1, B). The other teeth of the twins were quite similar in size and shape.

The mother of the twins and two other daughters in the family were reported by their dentists to have maxillary permanent lateral incisors of normal shape. According to the mother, the father of the twins had an unusual maxillary right permanent lateral incisor, apparently similar in shape to the T-shaped incisor of the twin. Observation of the incisors of the father by the author was not possible.

Triangular Shaped Mandibular Deciduous First Molar. A triangular shaped mandibular right deciduous first molar was observed unilaterally in one of the twins of a male monozygotic twin pair (Figure 2, B). The triangular shaped molar had four cusps, the protoconid, hypoconid, metaconid, and entoconid. The metaconid and entoconid (mesiolingual and distolingual cusps) were essentially fused together; however, the tips of these cusps were both retained. The other three mandibular deciduous first molars of the twin pair were of normal shape with five cusps (Figure 2, A, C, D). The triangular shaped molar had three roots (Figure 3, A). The other teeth of the twins were very similar in size and shape.

A younger brother of the twins had normally shaped mandibular deciduous first molars with five cusps.

Maxillary Deciduous Second Molar. A maxillary left deciduous second molar in one of the twins of a female monozygotic twin pair differed in form from the other three deciduous second molars of the pair (Figure 4, B). The occlusal surface of the odd-shaped molar was square in outline, whereas, the occlusal surfaces of the other molars were rhomboidal in outline (Figure 4, A, B, C, D). The odd-shaped molar had a smaller hypocone and larger cusp of Carabelli than the other three molars of the twin pair. The odd-shaped molar had a well developed groove which passed from an anterior fossa on the occlusal surface through the marginal ridge onto the mesiolingual surface. The other three molars had no such groove. The odd-shaped molar was larger mesiodistally and buccolingually than the other molars of the pair. The other teeth of the twins were very similar in size and shape.

The maxillary deciduous second molars of a sister of the twins (Figure 4, E, F) were similar in form to the three molars of the twins which were alike (Figure 4, A, C, D).

The maxillary deciduous second molars of a brother of the twins (Figure 4, G, H) resembled the odd-shaped molar of the twin pair (Figure 4, B). The occlusal surface outlines, the small hypocones, and the occlusal groove system of the brother's molars resembled the odd tooth observed in the twins. An interesting difference was observed

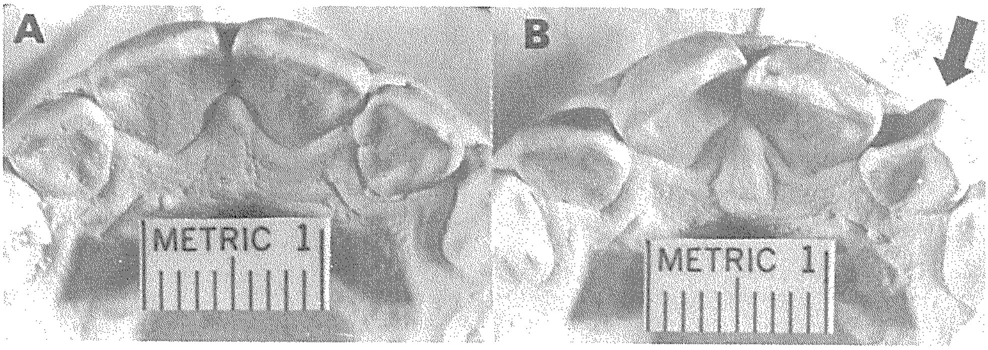


Fig. 1. An asymmetrical maxillary left permanent lateral incisor (B, arrow) observed in a female monozygotic twin pair (first twin A, second twin B). Scale length equals 1 cm.

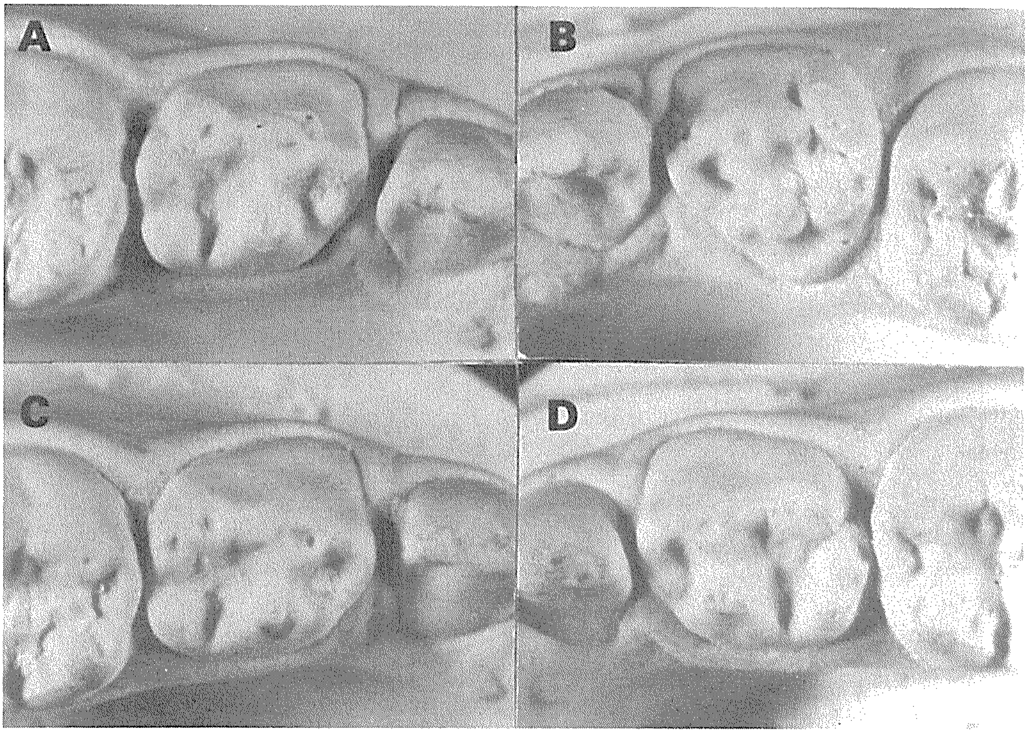


Fig. 2. An asymmetrical triangular shaped mandibular right deciduous first molar (B) observed in a male monozygotic twin pair (first twin A and B; second twin C and D).

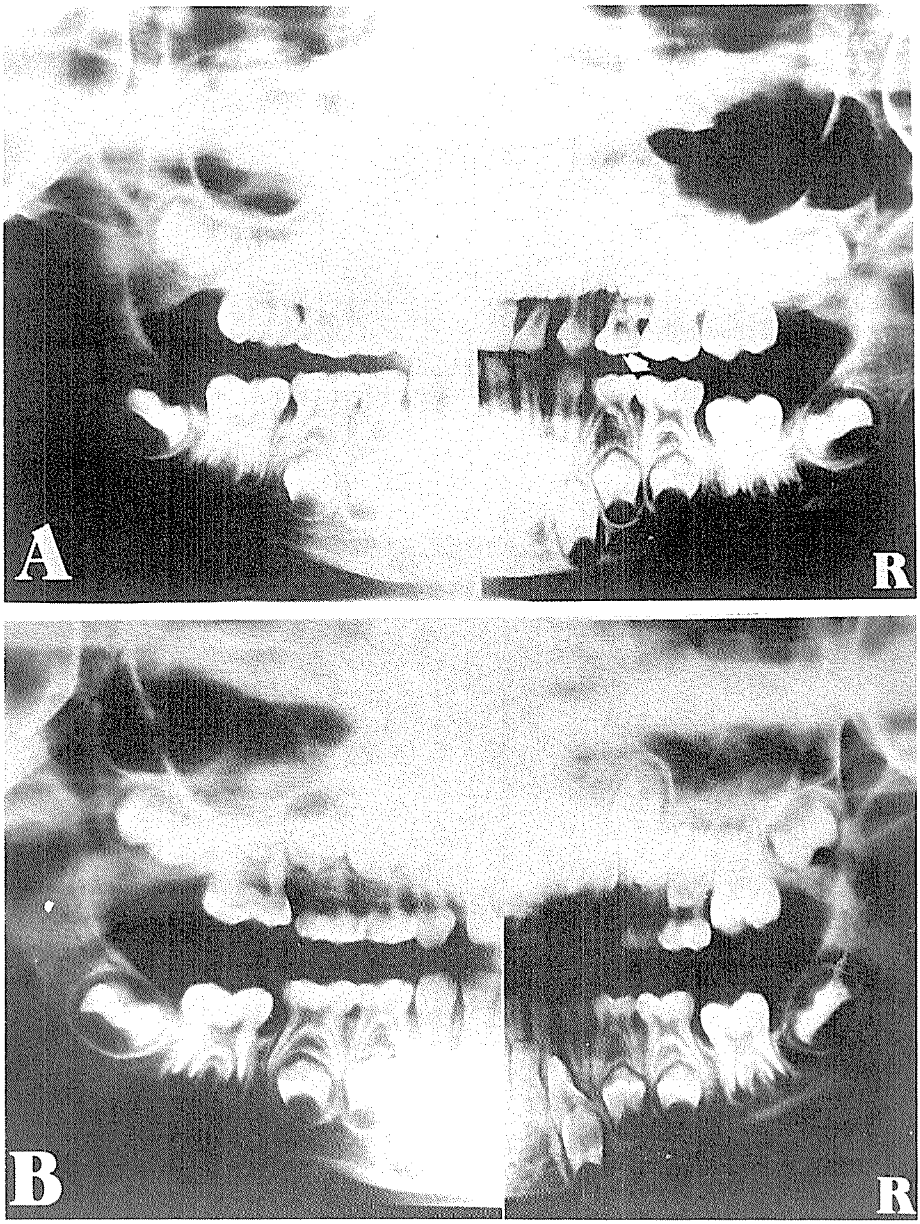


Fig. 3. The three rooted mandibular right deciduous first molar is illustrated in a panorex x-ray (A, arrow). The panorex of the twin brother is also shown (B).

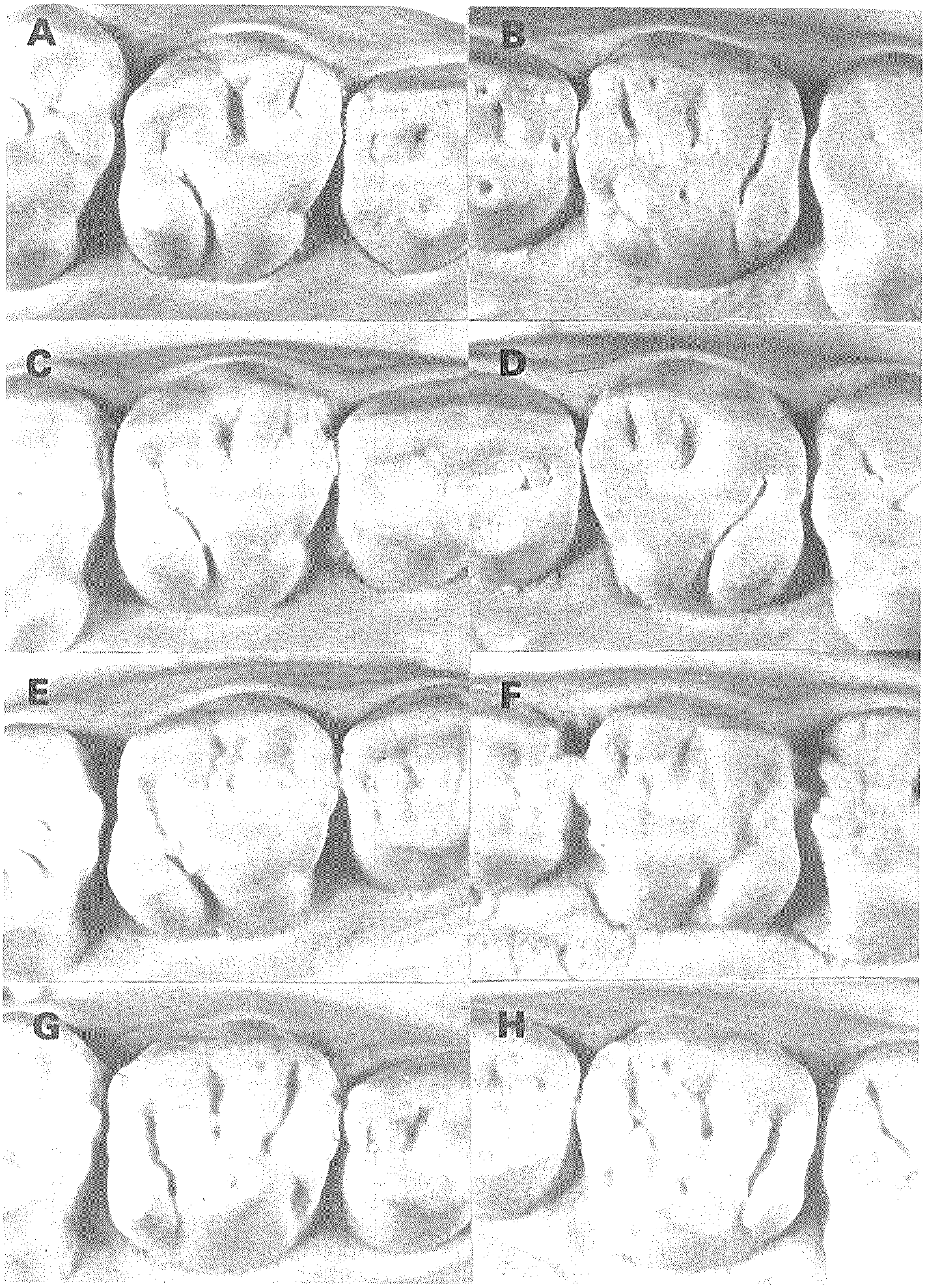


Fig. 4. An asymmetrical maxillary left deciduous second molar (B) observed in a female monozygotic twin pair (first twin A and B; second twin C and D). The maxillary deciduous second molars of a sister (E and F) and brother (G and H) of the twins. Note the similarity between the asymmetrical tooth of the twin (B) and the teeth of her brother (G and H).

between the odd-shaped molar of the twin and the molars of the brother; the cusp of Carabelli, which was well developed on the odd twin tooth, was only minimally developed on the molars of the brother.

The twin having the unusual shaped deciduous second molar also had a bifed small toe on the right foot which was not observed in her twin sister. The father of these twins also had a bifed small toe on his right foot.

Discussion

Two of the asymmetrical tooth forms reported here have been observed by others. Dahlberg ('57) illustrated a Mongoloid dentition having a unilaterally occurring maxillary permanent lateral incisor with an enlarged median ridge on the lingual surface, similar to the tooth illustrated in Figure 1, B.

Jørgensen ('56) described a triangular form of the mandibular deciduous first molar in an examination of the deciduous teeth of medieval Danes and modern Danes and Dutchmen. In the medieval material, he reported that the triangular forms occurred in 3.1% of the observed teeth (5 teeth out of 160). The triangular forms had a tendency to occur asymmetrically; however, one instance of bilateral development of the form was observed in the medieval sample. Some of the triangular deciduous first molars had a third (distolingual) root.

The illustrations of the occlusal surfaces of two of these triangular forms (Jørgensen, '56, figure 27) indicate that the tooth reported in the twin pair is intermediate between the form having a separation of the metaconid and entoconid and the form having a fusion of the metaconid and entoconid. The tooth of the twin has a deep groove on the buccal surface between the protoconid and hypoconid not seen in the teeth illustrated by Jørgensen.

Many interesting differences between the individuals of a monozygotic twin pair have been observed. The differences have been ascribed to genetic, developmental, and environmental factors.

Newman ('17) studied scute doubling and band doubling in 140 armadillo mother-monozygotic quadruplet sets and found a pattern of discordance of these anomalies among the quadruplets which strongly suggested a genetic origin, however, the pattern did not agree with typical Mendelian theory. He stated ('17, pages 149-150):

> "That band and scute doubling are definitely heritable is proved by the fact that doubling is always present in some form in the offspring of mothers that show doubling. The real problem is to find a mechanism to explain why it so often happens that some of the fetuses derived from a single egg exhibit the character and others do not. In monozygotic quadruplets we should expect the same genetic constitution in each individual unless there exists some segregative mechanism resulting during early ontogeny in an irregular distribution of the factors responsible for doubling. It has been suggested that the real differentiating factors are environmental; but the only environmental differences conceivable for monochorial quadruplets are nutritional differences due to more or less extensive placentation. It can be shown, however, that nutritional differences, so great as to have a pronounced effect on size and stage of development of different individuals of a set, have no effect on the inheritance of doubling. There are several quadruplets in which the various individuals are pronouncedly different in size, but are practically identical in the character and incidence of doubling. The differentiating factors therefore, must be within the embryo itself. It seems logical to look to the cleavage mechanism as the probable seat of the irregular distribution to different areas of the blastoderm of the factors of doubling. Presumably, with an ideally accurate cleavage mechanism there would result an exactly identical set. That identity in doubling is not realized argues strongly for unequal distribution

> *(or somatic segregation) of factors during cleavage*. Moreover, since doubling is evidently as strongly inherited from father as from mother, it seems probable that nuclear elements are chiefly involved, for the cytoplasm of the sperm cell is so small in amount as to be negligible."

Newman ('17) further reasoned that the mechanisms which produce bilateral asymmetry in paired structures of the individual are closely related to, or are identical to, those mechanisms which produce differences between monozygotic twins.

Many genetic mechanisms could produce the somatic segregation which Newman felt was responsible for the asymmetries he observed in armadillo quadruplets. Somatic (mitotic) crossing over, somatic mutation, chromosomal disparities arising from mitotic mishaps, single X-chromosome inactivation in females, and cytoplasmic (extra nuclear) inheritance are all mechanisms which could possibly produce differences between monozygotic twins and bilateral asymmetries in individual monozygotic twins.

The timing of the onset of these genetic mechanisms during ontogenetic development can have an important impact on the effect produced in the tissues of the organism. The action of one of these mechanisms prior to or at the division of a zygote into two monozygotic twins, could produce genetic differences between the twins. The action of one of these mechanisms early in the development of each individual monozygotic twin, could produce bilateral asymmetries, in one or both twins, or large scale mosaicism in cells of the blood, for example. Finally, the action of these mechanisms late in development could produce cells of unlike genetic composition adjacent to one another in a local region of tissue resulting in a localized mosaicism or twin spot formation.

Somatic or mitotic crossing over is known to occur in Drosophila (Stern, '36), and molds (Pontecorvo, '58). The effect of mitotic crossing over is to produce from a heterozygous nucleus two daughter nuclei each of which is homozygous for that part of the chromosome, affected by the crossing over, which was heterozygous in the parent cell nucleus. Somatic crossing over has been diagrammatically illustrated by Stern ('73, page 576).

Pontecorvo ('58) reported that mitotic crossing over is a rather rare event in molds. He reasoned that mitotic crossing over must be a rare event in higher organisms because of its disrupting production of mosaic soma ('58, page 113):

> "And now I would like to offer some evolutionary speculation. In organisms in which the life cycle is practically all in the diploid stage, mitotic crossing over has to be kept in check because it leads to mosaic soma. We can assume that in higher organisms there are mechanisms keeping its rate as low as possible. Perhaps these mechanisms have developed pari passu with the evolution of the diploid stage.
>
> Examples of organisms in which crossing over is suppressed at meiosis are known and not uncommon: for instance it is prevented at gametogenesis in the Drosophila male and in the silkworm female. Furthermore, meiotic crossing over is variable under a series of genetic and environmental factors. It is conceivable that similar mechanisms are available for preventing crossing over at mitosis.
>
> All this brings us back to the speculations outlined in the last chapter: crossing over is a primitive feature, perhaps inevitably connected with the physical chemistry of chromosome duplication, and therefore occurring perhaps between sister chromatids in haploids. To lead to genetically relevant results it must occur between homologues, i.e., it requires a diploid stage no matter how transient. In the evolution of the diploid stage it has first been utilized for recombination, perhaps in transient diploids as found in phages and bacteria today, and finally, as the differentiation between soma and germ tract became sharper, it has been prevented in the soma but not in gametogenesis where its timing and correlation with haploidisation have become quite precise."

It is likely that somatic crossing over occurs at least rarely in man and could possibly cause discordances in monozygotic twin pairs.

Somatic mutation is a process which could lead to differences between monozygotic twins. If the mutation rate for somatic cells is similar to the probable rate for gametes, many somatic mutations would occur during the course of human development. Some mutations would probably result in unviable cells, others might not produce detectable changes. It is probable that every human is mosaic to some extent as a consequence of somatic mutation.

Mishaps at mitosis which involve the chromosomes have been suggested as probable causes of marked dissimilarities observed in rare instances between monozygotic twins. Monozygotic twin pairs consisting of a normal male with a Turner's syndrome sister and a normal female with a Turner's syndrome sister have been reported (Turpin and Lejeune, '69). The elimination of a lagging chromosome in an early post-zygotic mitosis is the probable explanation for these occurrences. A monozygotic twin pair has been observed discordant for trisomy 21 (Turpin and Lejeune, '69). Various mishaps in mitosis, including chromosome elimination, have been offered to explain this unusual discordance.

A number of mechanisms such as chromosome breakage, chromosome non-disjunction, and haploidization acting in somatic cells will produce daughter cells of different chromosomal constitution. The sequential action of two or more of the previously mentioned genetic mechanisms in the same cell lineage, although less likely to occur, could also produce chromosomal differences between somatic cells.

Stern ('68) reviewed various interesting processes which have or are theorized to have produced unusual genetic mosaics among animals. Proof of the occurrence of these processes in man is a difficult and largely unsolved problem at present. Our understanding of the genetics of dental morphology in man may well be considerably advanced by a better understanding of the genetic processes discussed by Stern.

Factors which affect gene function in somatic cells could cause discordance in twins. In these instances, the genetic constitution of the affected somatic cells remains identical, but the activity of the genes differs in the involved cells. The Lyon hypothesis, gene penetrance, gene expressivity, position effect variegation, and codominance, are processes which have been invoked to explain variability in gene function.

The Lyon hypothesis (Lyon, '62) may be considered as a possible explanation for differences occurring between female monozygotic twins. A random and irreversible inactivation of the maternal and paternal X-chromosomes at an early stage of development could produce differing patterns of genetic activity in the somatic cells of monozygotic twins. Questions remain concerning the onset of X-chromosome inactivation, the completeness of inactivation, and the irreversibility of the inactivation. In any event, this hypothesis can only account for discordances in females, and can only involve information contained on X-chromosomes.

Penetrance and expressivity of genes are mechanisms which could also explain discordances in monozygotic twins. Penetrance describes the presence or absence of a gene in the form or function of a phenotype. Expressivity refers to variableness in the expression of a gene in the form or function of a phenotype. Lundström ('63) concluded that discordances he observed in tooth cusp formation in two pairs of monozygotic twins were probably caused by variation in gene expressivity.

Position effect variegation, a phenomen studied in Drosophila, involves a change in gene function related to rearrangement of genes brought about by breakage and abnormal reunion of chromosomes. Little is known about the occurrence of this phenomenon in man.

Codominance of the alleles of a gene and their interaction during differentiation could produce discordance in twins. Grüneberg ('66) described the effects of the sex linked gene tabby on the dentition of heterozygous female mice. Some of the molars of an individual mouse were of normal morphology, some were of tabby morphology, and some teeth showed a mixture of tabby and normal characteristics. Bilateral asymmetry in normal and tabby features was observed. The gene crinkled, an autosomal mimic of the tabby gene, produced a similar heterozygous manifestation in the molar morphology of mice. Grüneberg explained the heterozygous manifestation of these genes as the result of co-dominance. The association between heterozygosity and bilateral asymmetries has interested several earlier investigators (Sumner and Huestis, '21; Bond, '32; and Landauer, '48).

Cytoplasmic or extranuclear inheritance has been proposed as a cause of discordance between monozygotic twins. Dahlberg ('43) introduced the term genotypical asymmetry to describe differences between monozygotic twins which appeared to be of genetic origin. He proposed that a particular gene caused an unequal distribution of a cytoplasmic inclusion at a determinative cell division which would lead to a genotypical asymmetry. Storr and Williams ('68) speculated that the differences they observed between armadillo quadruplets in organ size and weight and in endocrine amounts in organs were due to extrachromosomal factors acting during the process of cell differentiation.

The numerous genes and cells involved in tooth morphogenesis are undoubtedly involved in a complexity of intracellular and intercellular interactions during differentiation which affect the final production of tooth form. Threshold and pattern effects contribute to the complexity of differentiation. Environmental effects could either initiate a genetic mechanism or exert a direct affect altering the course of tooth morphogenesis. An explanation for the type of discordances described in the dentitions of the twins in this paper must await further advances in our understanding of human genetics.

Acknowledgements

The author wishes to thank Drs. John J. Cunat and Larry J. Green of the Department of Orthodontics at the State University of New York at Buffalo, who provided the encouragement, materials, and facilities which made the publication of this paper possible.

This study was supported in part by USPHS Grant DE-02713 and a General Research Support Grant 5S01FR0330 from the National Institute of Dental Research, National Institutes of Health, Bethesda, Maryland.

Literature cited

Bond, C.J. 1932 On certain aspects of human biology. Lecture I. On the genetic significance of hemilateral asymmetry in the vertebrate organism. William Withering Lectures, The University of Birmingham Faculty of Medicine. 1-38.

Dahlberg, A.A. 1957 Criteria of individuality in the teeth. J. Forensic Sciences, 2: 389-401.

Dahlberg, G. 1943 Genotypic asymmetries. Proceedings Royal Soc. Edinburg, 62: 20-31.

Grüneberg, H. 1966 The molars of the tabby mouse, and a test of the 'single-active X-chromosome' hypothesis. J. Embryol. Exp. Morph., 15: 223-244.

Jørgensen, K.D. 1956 The deciduous dentition. Acta Odont. Scand., 14 (Suppl. 20): 1-202.

Landauer, W. 1948 The phenotypic modification of hereditary polydactylism of fowl by selection and by insulin. Genetics, 33: 133-157.

Lundström, A. 1963 Tooth morphology as a basis for distinguishing monozygotic and dizygotic twins. Am. J. Hum. Genet., 15: 34-43.

Lyon, M.F. 1962 Sex chromatin and gene action in mammalian X-chromosomes. Am: J. Hum. Genet., 14-135-148.

Newman, H.H. 1917 The Biology of Twins. Univ. of Chicago Press, Chicago. Chap. VII, 149-150.

Pontecorvo, G. 1958 Trends in Genetic Analysis. Columbia Univ. Press, New York. Chap. V, 113.

Stern, C. 1936 Somatic crossing over and segregation in Drosophila melanogaster. Genetics 21: 625-730.

______ 1968 Genetic Mosaics and Other Essays. Harvard University Press, Cambridge. Chap. 2, 27-129.

______ 1973 Principles of Human Genetics 3rd ed., W. H. Freeman and Co., San Francisco. Chap. 22, 576.

Storr, E. E. and R. J. Williams 1968 A study of monozygous quadruplet armadillos in relation to mammalian inheritance. Proceed. Nat. Acad. Sciences, 60: 910-914.

Sumner, F. B. and R. R. Huestis 1921 Bilateral asymmetry and its relation to certain problems of genetics. Genetics, 6: 445-485.

Turpin, R. and J. Lejeune 1969 Human Afflictions and Chromosomal Aberrations. Pergamon Press, Oxford. Chap. 13, 248-261.

The incidence of underbite occlusion in leaf-eating monkeys

DARIS R. SWINDLER

OSSA

This investigation is concerned with the range and magnitude of underbite occlusion variability in leaf-eating monkeys and the degree of sexual dimorphism of this trait within these species. The high incidence of underbite is confirmed in this study of five genera and ten species of leaf-eating monkeys. The underbite was more prevalent in females than males in the majority of species studied. The hypothesis that mandibular incisors are relatively wider than the maxillary incisors in leaf-eating monkeys versus nonleaf-eating monkeys is not supported by this investigation. The antiquity of underbite occlusion is documented by a two million year old colobine skull from Leadu, Ethiopia.

Исследование посвящено изучению диапазона и размеров окклюзионной изменчивости у обезьян, питающихся листьями, и степени полового диморфизма данной черты у этих видов. Высокая распространенность прогнатизма сравнивается в этой работе у пяти родов и десяти видов обезьян. Прогнатизм преобладал у самок по сравнению с самцами у большинства изученных видов. Это исследование не подтвердило гипотезы о том, что нижнечелюстные резцы относительно шире, чем верхнечелюстные у обезьян, питающихся листьями, по сравнению с обезьянами, не питающимися листьями. Древность прогнатической окклюзии документирована черепом колобуса, сохранившимся два миллиона лет, найденным в Леду /Эфиопия/.

Ключевые слова: зубы; обезьяны, питающиеся листьями.

Daris R. Swindler, Department of Anthropology, University of Washington, Seattle, Washington, 98195 U.S.A.

Vol. 6, pp. 261-272, Lund. ISSN 0345-8865.

Introduction

The normal occlusion of the incisor teeth in both Old and New World monkeys is edge-to-edge, i.e., the incisal ridges of the maxillary and mandibular incisors come together in even contact so that the labial surfaces are level with one another (Fig. 1b). A notable exception is found among the predominately leaf-eating taxa where a high incidence of underbite, mandibular protrusion, occurs (Fig. 1a). Colyer ('36) was one of the earliest odontologists to identify the underbite and document its high frequency among leaf-eating monkeys. Some years later, Serra ('51) noted the presence of underbite among various species of *Alouatta*, while Schultz ('58 and '60) investigated this malocclusion in both *Alouatta* and *Colobus* species. However, it was Zingeser ('68 and '70) who finally suggested that the underbite occlusion displayed by these geographically and taxonomically divergent monkeys was an herbivorous adaptation.

The present investigation is concerned with two problems: one, is the range and magnitude of underbite variability obtaining in different species and, two, the degree of underbite sexual dimorphism in these same species.

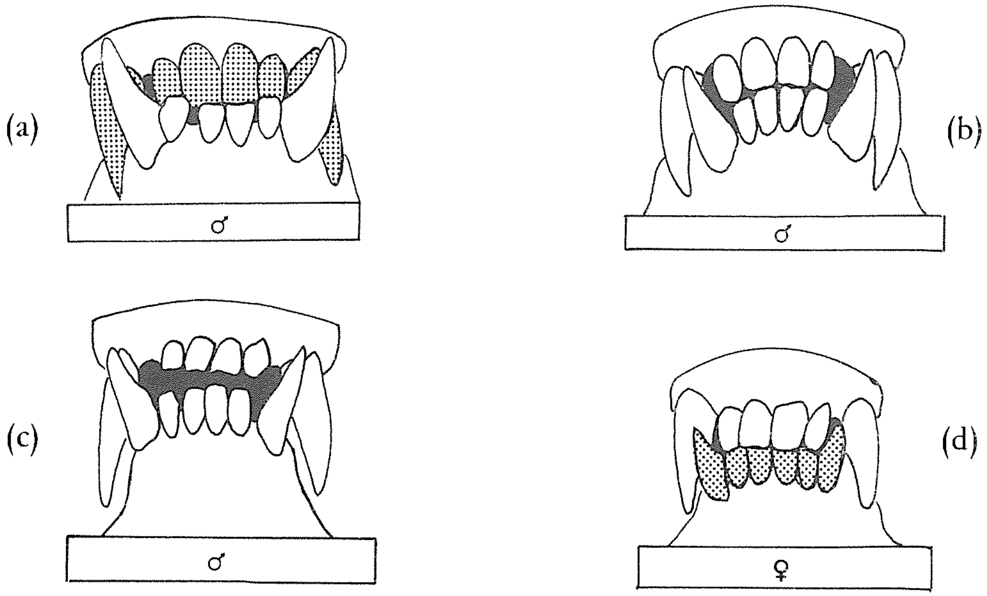


Fig. 1. *Colobus polykomos*. Frontal view showing (a) underbite (b) edge-to-edge (c) openbite and (d) overbite.

Materials and methods

The basic material presented in this paper consists of observations and measurements made on dental casts of skulls of leaf-eating monkeys. The casts were made with alginate impression compound and a dental stone for the models. The casts were poured within minutes after the impressions were made which minimizes the possibility of dimensional changes (Swindler, et al., '63).

Observations were made on articulated dental models for each sex and on both juvenile and adult monkeys. The juvenile category included animals with complete deciduous and mixed dentitions. Animals with any or all third molars erupted were considered adult. A total of 460 animals were examined from five genera and ten species. The taxa, sex and sample sizes appear in Table 1 and 2.

The chi-square statistic was performed to test the null hypothesis of equal underbite distribution between sexes.

Results and discussion

Zoogeography

The genera *Colobus*, *Presbytis*, *Nasalis* and *Rhinopithecus* belong to the subfamily Colobinae and for the most part are arboreal, leaf-eating Old World monkeys. This subfamily has been separated from the other subfamily of Old World monkeys, the Cercopithecinae, since the Miocene (Pilbeam and Walker, '68). They are distinguised anatomically by the absence of cheek pouches, reduced thumbs and the presence of an elaborated sacculated stomach and intestinal tract. *Colobus* represents the only African member of the subfamily. The other genera are distributed through Malaysia, portions of China and the southern slopes of the Himalayas. They are usually considered to be semibrachiators and most species spend the majority of their time in the trees.

Colobus polykomos inhabits the middle closed canopy montane forests from Senegal in the west to Ehiopia in the east and as far south as Tanzania. The diet is almost exclusively leaves, as ascertained by field observations and stomach examinations. Indeed, Booth (' 56) did not find a particle of fruit or animal matter in the stomaches of 41 *C. polykomos. C. badius* is also found widely distributed throughout the tropical forests of Africa. In contrast to *C. polykomos, C. badius* occupies the high open canopy and rarely descends to lower levels. Although an inveterate leaf-eater, it will on occasion consume various amounts of fruit (Kuhn, ' 64).

Nasalis larvatus, the probiscus monkey, is exclusively insular, being restricted to Borneo where it can be found inhabiting the mangrove swamps by day and retreating to the high pedade trees for protection from predators at night (Kern, ' 64).

The genus *Presbytis* enjoys a wide geographic range from India through Malaysia to Java, Borneo and many other offshore islands. All species of the genus are essentially arboreal and some species, e.g., *P. pileatus,* rarely if ever come to the ground (Pocock, ' 39). Langurs eat leaves but they also have been observed eating bark, young shoots and buds.

Rhinopithecus roxellanae lives in western China among the confireous forests and bamboo jungles (Napier and Napier, ' 67). As most leaf-eating monkeys, they are arboreal, only coming to the ground for water. The diet consists of leaves, buds, fruit and tender bamboo shoots.

The New World monkey *Alouatta* belongs to the Cebidae and is found in both Central and South America. It is arboreal and seems to prefer the middle and upper canopy of primary rain forests (Napier and Napier, ' 67). All species are leaf-eating, although flowers, buds and fruits are also consumed.

In summary, studies of stomach contents, as well as field investigations, suggest that all of these monkeys are predominately leaf-eaters. Leaf consumption may, and probably does, vary daily as well as seasonally; however, leaves still remain the preferred food.

Incisor Occlusal Variability

The underbite relationship of the upper and lower permanent incisors varies not only between genera but between different species of the same genus (Table 1). For example, adult *C. polykomos* have a higher incidence of underbite than *C. badius,* a condition also reported by Schultz (' 58). The greatest interspecific variability of underbite in the present study was found among the Asian langur *Presbytis* . Of the three species studied, female *P. aygula* had a frequency of 95.5% underbite while male *P. cristatus* has only 13.6%. Zingeser (' 70) reported a 100% incidence of underbite for both male and female *P. aygula* (= *P. melalophus)* while noting a low frequency of the trait in *P. cristatus* . Although not as extreme, the incidence of underbite for the leaf-eating New World monkey *Alouatta* ranges from 44 to 87% (Table 1). Schultz (' 60) also found a high frequency of underbite in *Alouatta*, particularly *A. villosa.*

The edge-to-edge bite was well represented in the present sample and always had either the highest or second highest frequency (Table 1 and Fig. 1b). Overbite, which is found in such high frequency in human populations, was extremely rare among the species studied (Table 1 and Fig. 1d). Indeed, this condition was found in only three genera and always in low frequency.

The fourth type of incisor occlusal relationship represented was openbite (Table 1 and Fig. 1c). This condition is rare in all nonhuman primates living in natural conditions and the present sample is no exception. It is, however, found occasionally in laboratory monkeys (Benjamin, ' 62; Swindler and Sassouni, ' 62; and Moore, et al., ' 72). In all reported cases, the monkeys were thumb suckers and the incisor malformation was attributed to this aberrant extra-oral behavior. In the present sample, the highest incidence of openbite appeared in *Alouatta seniculus* (Table 1). Unfortunately, we have no way of knowing if any of these monkeys were ever thumb suckers.

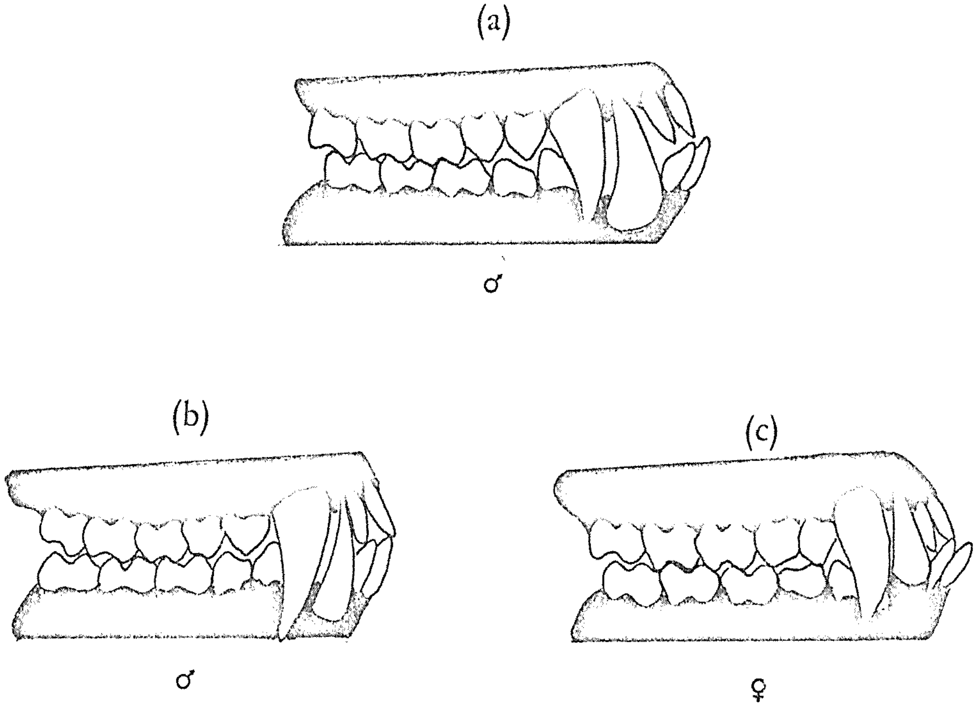


Fig. 2. *Colobus polykomos.* Lateral view showing the molar and incisor occlusion in (a) openbite, (b) edge-to-edge and (c) underbite.

In all examples of incisor occlusal variability, the basic cusp interdigitations between the maxillary and mandibular premolars and molars were normal (Fig. 2). In the author's experience, post incisor malocclusions, particularly those involving the molars, are extremely rare in nonhuman primates.

The underbite condition was also present in juvenile monkeys as shown in Table 2. The monkeys recorded in Table 2 had a complete deciduous dentition only (no permanent teeth were present); thus, their age was between six months and a year and a half. This age estimate, of course, assumes that wild monkeys erupt their deciduous teeth at approximately the same time as laboratory animals. Schultz ('58, '60) reported underbite in juvenile *Colobus* and *Alouatta* monkeys. It should be noted that the deciduous molars are in normal occlusion as was mentioned in the discussion of adult dentitions with underbite. It appears, then, that monkeys with underbite may develop the condition early and maintain it as adults. Unfortunately, this observation was based on cross-sectional rather than longitudinal data.

Underbite Sexual Dimorphism

It is apparent from Table 1 that in the majority of the species studied, epharmosis had a higher incidence among females than males. The only exceptions were *Alouatta belzebul* and *Alouatta seniculus*, both New World monkeys. Schulz ('58, '60), in his study of *Colobus*, noted that sex differences were neither uniform nor consistent in this taxon, while, in *Alouatta,* underbite was more frequent in males than females. Although Zingeser ('70) did not discuss underbite sexual dimorphism, it was recorded in his Table 1.

To estimate the degree of significance in underbite sexual dimorphism, a chi-square statistic was performed which tested the null hypothesis of equal trait distribution between the sexes. The results appear in Table 3. In one species, *Presbytis cristatus*, the sex difference of the trait was significant at $P<0.01$, while in *Presbytis pileatus* and *Nasalis larvatus*, underbite was significant at $P<0.05$. At present, we have no explanation for this sex difference. That females should be better adapted for leaf-eating, assuming underbite is indeed such an adaptation, is difficult to account for in selection terms. Both sexes live and presumably eat the same varieties of leaves, suggesting that little differential selection pressure is operating on the trait. Why, therefore, one sex should have a higher frequency of underbite than the other remains an enigma.

Underbite and Tooth Size

The incisors of leaf-eating primates are generally smaller than the incisors of nonleaf-eating forms which feed on large tough food objects such as fruits (Jolly, '70; Hylander, '75; Swindler and Sirianni, '75). The adaptive importance of this finding is probably correlated with differential tooth function. Thus, extensive incisal preparation of small food particles such as leaves, grasses, seeds, etc., is not essential before masticating with the postcanine teeth, but is a very important activity when preparing large, tough-skinned fruits for ingestion. Commensurate with small incisors is relatively large postcanine teeth (Swindler and Sirianni, '75). However, in a relative sense, are mandibular incisors larger than maxillary incisors in folivorous species, and, if so, how is this feature related to underbite?

Several years ago, Zingeser ('70) addressed this question when he suggested that underbite, at least in langurs, was "attributable to relatively wider mandibular incisors and it appears to be a leaf-eating adaptation". He compared the mean widths of maxillary and mandibular incisors (I_{1-2}/I^{1-2}) in two langur species, *Presbytis aygula* (= *P. malalophus*) and *Presbytis cristatus*, and found that the former taxon had a higher incidence of underbite and possessed relatively larger lower incisors than *P. cristatus*. The present data confirm Zingeser's findings regarding these two groups of langur (Table 1 and 4). However, when we examine a number of leaf-eating as well as nonleaf-eating monkeys regarding this characteristic, no clear-cut pattern emerges (Tables 4 and 5). In both groups, the percentages range from approximately 72 to 83, with a mean of 77.8 for leaf-eating and 76.1 for nonleaf-eating species. It is also interesting to note that in several taxa where the females had a higher incidence of underbite than the males, e.g., *P. cristatus* and *N. Larvatus* (Tables 1 and 3), the males had relatively larger mandibular incisors (Table 4). This finding is contrary to the wider mandibular incisor hypothesis for leaf-eating monkeys as enunciated by Zingeser ('70). In sum, the mosaic nature of the present findings suggests that the dimensional (functional) primacy of the mandibular incisors as a causative factor in underbite is dubious as well as its being a phyllophagus adaptation.

Underbite and Facial Dimensions

In a sample of *Colobus badius*, Colyer ('40) reported an underbite frequency of 40% for 67 skulls. He did not mention a sex difference.

A craniometric study of the skulls revealed the following information. The specimens with underbite had longer mandibles in relation to the basion-prosthion dimension, and the palate in relation to the mandible was shorter than in the specimens with an edge-to-edge bite. Colyer thus believed the explanation for underbite was to be sought in the processes of maxillary and mandibular growth. To our knowledge, no other craniometric studies have been undertaken since Colyer's initial work. Unfortunately, the present data cannot confirm or deny his findings.

Finally, underbite occurred in the present sample in the presence or absence of a maxillary diastemata between the canine and lateral incisor. A similar condition was reported in *Alouatta palliata* by Schultz ('60).

Fig. 3. Lateral view of a two million year old colobine skull from Leadu, Ethiopia, exhibiting underbite occlusion.

Underbite and Paleontology

In 1972, a skull was collected in Ethiopia at a site known as Leadu by members of an expedition under the direction of Donald Johanson. The skull is approximately 2 million years old (personal communication). The specimen is definitely colobine, although it has not yet received an official taxonomic name. Fortunately the skull and mandible were articulated and held together by matrix when discovered, allowing a diagnosis of its occlusion. The specimen had an underbite with normal molar occlusion (Fig. 3). Thus, underbite is at least 2 million years old and would appear to represent a well entrenched dental complex in colobine monkeys.

Conclusions

The data presented here confirm the high incidence of underbite in leaf-eating monkeys as reported by earlier authors. In five genera and ten species of leaf-eating monkeys studied the frequency of underbite ranged from 13.6% in male *Presbytis cristatus* to 95.5% in female *Presbytis aygula* .. In most groups examined, underbite was more prevalent in females than males and in three taxa, underbite sexual dimorphism was significantly higher in females (*P. cristatus* P 0.01, *P. pileatus* $P<0.05$ and *N. larvatus* $P<0.05$).

The size relationship between mandibular and maxillary incisors (I_{1-2}/I^{1-2}) was investigated in a large number of leaf-eating and nonleaf-eating monkeys. The hypothesis that the mandibular incisors are relatively wider than the maxillary incisors in leaf-eating monkeys when compared with nonleaf-eating taxa is not supported by the present data.

Acknowledgements

The author wishes to thank Mr. Keith Smith for preparing Figures 1 and 2, and Dr. Donald Johanson for permission to use the Leadu Colobine fossil (Fig. 3). This research was supported in part by National Institute of Health grant DE-02231, Bethesda, Maryland.

Literature cited

Benjamin, L.S. 1962 Nonnutritive sucking and dental malocclusion in the deciduous and permanent teeth of the Rhesus monkey. Child Dev. 33:29-40.

Booth, A.H. 1956 The distribution of primates on the Gold Coast, J. West. Af. Sci. Assoc. 2:122-133.

Colyer, F. 1936 Variations and diseases of the teeth of animals. John Bale, Sons and Danielsson, London.

______ 1940. Variation of the teeth of Preuss's colobus. Proc. Royal Soc. Med. 33: 63-74.

Hylander, W.L. 1975 Incisor size and diet in anthropoids with special reference to Cercopithecidae. Sci. 189: 1095-1098.

Johanson, D.C. 1978 (Personal Communication)

Jolly, C.J. 1970 The seed-eaters: A new model of hominid differentiation based on a baboon analogy. Man. 5:5-26.

Kern, J.A. 1964 Observations on the habits of the probiscus monkey, *Nasalis larvatus* (Wurmb), made in Brunei Bay area, Borneo. Zoologica 49: 183-191.

Kuhn, H.J. 1964 Zur Kenntnis von Bau und Funktion des Magens der Schlankaffen (Colobinae) Folia primat. 2: 193-221.

Moore, G.J. R.W. McNeill and J.A. D'anna 1972 The effects of digit sucking on facial growth. J. Am. Dent. Assoc. 84:592-599.

Napier, J.R. and P.H. Napier 1967 A Handbook of Living Primates. Academic Press, London-New York.

Pilbeam, D. and A. Walker 1968 Fossil monkeys from the Miocene of Napak, north-east Uganda. Nature 220: 657-660.

Pocock, R.I. 1939 The Fauna of British India, Mammalia Vol. 1, Taylor and Francis, Ltd., London.

Schultz, A.H. 1958 Cranial and dental variability in Colobus monkeys. Proc. Zool. Soc. Lond. 130:79-105.

______ 1960 Age changes and variability in the skulls and teeth of the central American monkeys *Alouatta*, *Cebus* and *Ateles* . Proc. Zool. Soc. Lond. 133: 337-390.

Serra, O.D. 1951 Variazones do articulado dos dentes incisivos nos macacos do género *Alouatta*. Lac. 1799. Papéis Avul. Dep. Zool. San Paulo 10: 139-145.

Swindler, D.R. and V. Sassouni 1962 Open bite and thumb sucking in Rhesus monkeys. Angle Orthodont. 32: 27-37.

Swindler, D.R., J.A. Gavan and W.M. Turner 1963 Molar tooth size variability in African monkeys. Hum. Biol. 35: 104-122.

Swindler, D.R. and J.E. Sirianni 1975 Dental size and dietary habits of Primates. Yearbook Phys. Anthrop. 19: 166-182.

Swindler, D.R. 1976 Dentition of Living Primates. Academic Press, London-New York.

Zingeser, M.R. 1968 Characteristics of the masticatory system. In: Biology of the Howler Monkey. M.R. Malinow, ed. Basel: S. Karger, 141-150.

______ 1970 The morphological basis of the underbite trait in langurs (*P. melalophus T. cristatus*.) with an analysis of adaptive and evolutionary implications. Am. J. Phys. Anthrop. 32: 179-186.

TABLE 1.

Percentage frequencies of incisor occlusal variability in adult leaf-eating monkeys

Taxon	Sex	N	Under-bite	Edge to Edge	Over-bite	Open-bite
Colobus polykomos	M	61	29.5	54.1	9.8	6.6
Colobus polykomos	F	33	51.5	42.4	6.1	
Colobus badius	M	36	41.7	52.7	5.6	
Colobus badius	F	34	47.1	50.0		2.9
Presbytis aygula	M	14	92.9	7.1		
Presbytis aygula	F	18	95.5	5.5		
Presbytis cristatus	M	22	13.6	81.8		4.6
Presbytis cristatus	F	32	56.3	40.6		3.1
Presbytis pileatus	M	24	41.7	58.3		
Presbytis pileatus	F	14	78.6	21.4		
Nasalis larvatus	M	26	53.8	46.2		
Nasalis larvatus	F	18	83.3	11.1	5.6	
Rhinopithecus roxellanae	M	4	25.0	75.0		
Rhinopithecus roxellanae	F	11	45.5	54.5		
Alouatta villosa	M	18	66.7	27.8	5.5	
Alouatta viloosa	F	41	87.8	12.2		
Alouatta belzebul	M	9	77.8	22.2		
Alouatta belzebul	F	3	66.7	33.3		
Alouatta seniculus	M	24	54.2	33.3	4.2	8.3
Alouatta seniculus	F	18	44.4	33.3	5.6	16.7

TABLE 2.

Percentage frequencies of incisor occlusal variability in juvenile leaf-eating monkeys

Taxon	Sex	N	Under-bite	Edge to edge	Over-bite
Colobus polykomos	M	10	50.0	40.0	10.0
Colobus polykomos	F	11	27.3	72.7	
Colobus badius	M	6	33.3	66.7	
Colobus badius	F	9	66.7	33.3	
Presbytis aygula	M	2	50.0	50.0	
Presbytis aygula	F	9	77.8	22.2	
Presbytis cristatus	M	1		100.0	
Presbytis cristatus	F	2		100.0	
Presbytis pileatus	M	3	66.7	33.3	
Presbytis pileatus	F	4	100.0		
Nasalis larvatus	M	1	100.0		
Nasalis larvatus	F	3	100.0		
Rhinopithecus roxellanae	M				
Rhinopithecus roxellanae	F	5		100.0	
Alouatta villosa	M	9	100.0		
Alouatta villosa	F	7	85.7	14.3	

TABLE 3.

Underbite sexual dimorphism in adult leaf-eating monkeys

Taxon		Chi-square tests 0.01	 0.05	 N.S.
Colobus polykomos	M:F			3.01
Colobus badius	M:F			0.13
Presbytis aygula	M:F			0.03
Presbytis cristatus	M:F	9.10		
Presbytis pileatus	M:F		4.90	
Nasalis larvatus	M:F		5.40	
Rhinopithecus roxellanae	M:F			0.51
Alouatta villosa	M:F			2.50
Alouatta belzebul	M:F			0.15
Alouatta seniculus	M:F			0.08

TABLE 4.

I_{1-2} breadths / I^{1-2} breadths in leaf-eating monkeys $^{+}$

Taxon	Sex	N	Percentage
Colobus polykomos	M	61	77.3
Colobus polykomos	F	33	79.6
Colobus badius	M	36	76.0
Colobus badius	F	34	78.8
Presbytis aygula	M	14	80.5
Presbytis aygula	F	18	81.7
Presbytis cristatus	M	22	75.3
Presbytis cristatus	F	32	74.1
Presbytis pileatus	M	24	72.2
Presbytis pileatus	F	14	77.8
Nasalis larvatus	M	26	82.0
Nasalis larvatus	F	18	78.9
Rhinopithecus roxellanae	M	4	78.8
Rhinopithecus roxellanae	F	11	82.2
Alouatta villosa	M	18	74.7
Alouatta villosa	F	41	74.3
Alouatta seniculus	M	24	78.3
Alouatta seniculus	F	18	77.3

$^{+}$ Data from Swindler, 1976

TABLE 5.

I_{1-2} breadths / I^{1-2} breadths in nonleaf-eating monkeys [+]

Taxon	Sex	N	Percentage
Cercopithecus cephus	M	8	76.8
Cercopithecus cephus	F	12	72.0
Cercopithecus nictitans	M	11	75.5
Cercopithecus nictitans	F	7	73.4
Cercopithecus mona	M	21	75.0
Cercopithecus mona	F	13	73.8
Cercopithecus mitis	M	30	76.0
Cercopithecus mitis	F	20	72.9
Cercopithecus neglectus	M	12	76.1
Cercopithecus neglectus	F	6	73.3
Cercopithecus ascanius	M	18	75.9
Cercopithecus ascanius	F	12	76.8
Cercopithecus aethiops	M	26	76.4
Cercopithecus aethiops	F	20	76.2
Cercocebus albigena	M	28	75.2
Cercocebus albigena	F	29	76.6
Cercocebus torquatus	M	12	76.9
Cercocebus torquatus	F	10	76.7
Cercocebus galeritus	M	9	78.7
Cercocebus galeritus	F	10	76.2
Macaca nemestrina	M	17	80.2
Macaca nemestrina	F	9	82.9
Macaca mulatta	M	91	76.8
Macaca fascicularis	M	55	76.6
Macaca fascicularis	F	49	77.9
Papio cynocephalus	M	37	79.3
Papio cynocephalus	F	37	79.3
Ateles geoffroyi	M	12	78.0
Ateles geoffroyi	F	14	80.0
Cebus apella	M	34	73.0
Cebus apella	F	20	74.4
Saimiri sciurens	M	14	73.5
Saimiri sciurens	F	6	70.0

[+] Data from Swindler, 1976

Dr. Dahlberg, Dental anthropology and physical anthropology at the University of Chicago, 1932–1978

RUSSELL H. TUTTLE

OSSA

Running Headline: Dr. Dahlberg at the University of Chicago.

Russell H. Tuttle, Department of Anthropology, 1126 East 59th Street, The University of Chicago, Chicago, Illinois 60637 U.S.A.

Vol. 6, pp. 273-276, Lund. ISSN 0345-8865.

Dr. Dahlberg's career at the University of Chicago has overlapped virtually all major phases in the development of physical and dental anthropology which are centered in its Department of Anthropology.

When he came to the University of Chicago Clinics as a young intern in 1932, the Department of Anthropology was barely three years old. Professor Fay-Cooper Cole was single-handedly in charge of physical anthropology in addition to teaching and supervising research on aspects of archeology. Anthropology was listed with four subfields -- (1) physical anthropology, (2) archaeology, (3) ethnology and (4) linguistics. The Ph. D. was granted after successful completion of a thesis, an oral examination over it and the field in which it lay, and a written examination covering general fields in which the student had specialized. Candidates for the Ph. D. were also expected to complete statistical work and to have reading knowledge of French and German certified by the end of the first year of study for the degree.

Dr. Dahlberg's publications during the 1930s largely reflect his intensive involvement in the Clinics though a paper titled "Inherited congenital absence of six incisors, deciduous and permanent" harbingered his anthropological career.

In 1938, Wilton Marion Krogman returned to the University of Chicago, where he had received Ph. D. (1926), M. A. (1927) and Ph. D. (1929) degrees and had served as an Instructor of physical anthropology (1929-30). Professor Cole was Chairman of the Department of Anthropology and continued to teach archeology. Professor Krogman took over Anthropology 203, The Evolution of Man, which considered theories and principles of organic evolution, primate origins and kinship, early types of man, the biological classification of races, and their present distribution. He also offered advanced physical anthropology courses on human variation, growth and development, and methods. Toward the end of Krogman's term at the University of Chicago (1938-47), Dr. Dahlberg's publications became decidedly anthropological, especially after 1946 as he inaugurated classic field studies of Native Americans in the southwestern United States.

In 1947, Sherwood L. Washburn accepted an appointment as Associate Professor in Anthropology. Always a man of boundless energy and extensive scientific curiosity and imagination, Professor Washburn taught the evolutionary and other physical anthropological components of the year-long general core course titled Human Origins and a course on methods in physical anthropology. He also directed individual research projects, and organized an innovative seminar on problems of primate evolution, classification and the relation of form to behavior.

Dr. Dahlberg was appointed as a Research Associate in the Department of Anthropology in 1949. Professor Fred Eggan, an expert on Native American cultures, was Chairman (1948-52). The Ph. D. in Anthropology was conferred on persons who passed "with a superior grade" comprehensive examinations about aspects of the major subfields of general anthropology, established reading knowledge of one foreign language, gave evidence of research capacity usually in the form of an M. A. thesis, showed command of statistical procedure, passed written examinations over their special program of training and research, completed a Ph. D. thesis, and passed an oral examination over the Ph. D. thesis and the field in which it lay.

Dr. Dahlberg conjointly taught courses on methods in physical anthropology, fossil man and human variation with Sherwood Washburn and Robert Braidwood. Bryan Patterson and Dwight Davis, members of a new Interdivisional Program in Paleozoölogy chaired by Everett Olson, also taught in the Department of Anthropology. These must have been very good times indeed. The most notable physical anthropologist to be trained during this period was F. Clark Howell, who earned his Ph. B., M. A. and Ph. D. degrees at the University of Chicago between 1947 and 1953.

Subsequent to his appointment in the Department of Anthropology, Dr. Dahlberg's publications were predominantly, though not exclusively, evolutionary and anthropological rather than clinical. He also contributed to the standardization of terminology and techniques in odontological studies. He and his wife, Thelma, often traveled to Arizona to collect additional ontogenetic and comparative data from Native American subjects.

In 1952, Sherwood Washburn became Chairman of the Department and established a special program of research in physical anthropology with the assistance of the Wenner-Gren Foundation for Anthropological Research, Inc. An Evolution Laboratory was set up in Walker Museum under the auspices of the Committee on Paleozoölogy and the Department of Anthropology. It provided facilities for research in human and primate evolution and in the experimental study of biological change.

F. Clark Howell returned to the University of Chicago in 1955 as an Assistant Professor in Anthropology. Course listings soon swelled to include Washburn's Comparative Human Anatomy (dissection of man and monkey) and Primate Social Behavior and Howell's Pleistocene Ecology and Fossil Man. In 1956, Dr. Dahlberg and Sherwood Washburn taught a new course titled The Face - a detailed comparative and experimental approach to the understanding of the face and dentition. Then Dr. Dahlberg added The Human Dentition - a comparative and genetic approach to the understanding of the dentition of man. These underpinned the graduate training programs in anthropological primatology, paleoanthropology and dental anthropology for which the University of Chicago was to become world renowned.

In 1958, Sherwood Washburn left the University of Chicago. Dr. Dahlberg and Clark Howell sustained the physical anthropology program with the assistance of Ernst Goldschmidt (1959-1963), who added courses in Human Biology and the Ecology of Human Populations. Dr. Dahlberg established a unique special M. A. Program in dental anthropology for persons who already had advanced degrees in dental science. He was well on his way to international recognition as the doyen of dental anthropology.

During the 1960s, Dr. Dahlberg not only continued to collect data on Native Americans in Arizona but also established research bases in Alaska and joined the Iranian Prehistoric Archaeological Expedition which was directed by his long-term colleague, Robert Braidwood. His diverse authoritative publications covered a broad range of anthropological topics, including results of his own research on Native American dentitions, Olduvai Hominid 3 (BK II), the dentitions of later Pleistocene peoples and early agriculturalists, and dental and cranio-facial growth. He was eagerly sought as a lecturer, visiting professor and consultant by major institutions in North America, England, continental Europe and Japan. Dr. Dahlberg often organized and graciously chaired symposia for national and international anthropological, dental and other scientific societies. But somehow he always had time to interact patiently with students and other colleagues.

In 1964, Charles Merbs and I received junior appointments to the University of Chicago. Soon thereafter Dr. Dahlberg secured a generous training grant. This coincided with an influx of excellent graduate students into the Department of Anthropology. Dr. Dahlberg and Mr. Merbs took students to Alaska and northern Canada to study living and burial populations of Eskimos, Aleuts and Canadian Indians. Mr. Merbs established a series of courses on human osteology, paleopathology and other aspects of human variation. I taught the departmental graduate level core courses on the human career with F. Clark Howell and developed a series of courses on primate comparative morphology, evolution, locomotion and naturalistic behavior. With the partial assistance of federal agencies and the Marian and Adolph Lichtstern Fund of the University of Chicago, Laboratories for Dental Anthropology, Osteology and Human Variation, Primatology, and Paleoanthropology were set up in Walker Museum.

This was a very exciting and productive period for all of us. Clark Howell made important discoveries about the hunting behavior of Middle Pleistocene peoples in Spain. Then, while serving as Chairman of the Department (1966-69), he directed fruitful paleoanthropological expeditions in the Omo Basin of southern Ethiopia. I recall one snowy evening which Dr. & Mrs. Dahlberg, my wife Marlene, and I spent at the Howells' home in Flossmoor, Illinois. Clark brought out numerous excellently preserved and fragmentary teeth from the Omo deposits in order to check his provisional identifications of them against Dr. Dahlberg's expertise. It was fascinating to watch Dr. Dahlberg skillfully orient them and to explain meticulously why each was probably permanent or deciduous, left or right, upper or lower, etc. As might be expected considering his long association with such a master, most of Clark Howell's diagnoses were confirmed.

By the early 1970s, with a cast of hundreds and thousands of casts, Dr. Dahlberg had produced an epic collection for detailed genetic, comparative, functional, medical and ontogenetic studies on Native American dentitions. He also collected an extensive series of cephalic X-rays on Native Alaskan peoples. Thus, his laboratory provided unparalleled opportunities for student research and regularly attracted many interesting visitors from overseas. The publications of Dr. Dahlberg, his students and associates testify to the richness and scientific importance of these carefully collected materials. We anticipate many additional contributions from them in the future.

Clark Howell left the University of Chicago in 1970 and Charles Merbs departed in 1973. The addition of Richard Klein in 1973 and occasional visiting professors have helped to sustain the program in physical anthropology despite current budgetary constraints under which universities must operate. Now we are looking forward to an addition of faculty and a move to new laboratories and offices in Haskell Hall which was the original home of the Oriental Institute of the University of Chicago.

Dr. Dahlberg's productivity in the Department of Anthropology is all the more remarkable in light of the fact that concurrently he established and personally maintained one of the most distinguished private dental practices in the city of Chicago. He regularly serves on University committees, was Acting Director of the Zoller Memorial Dental Clinic (1967-68), and is a founding member in the Committee on Evolutionary Biology of the University of Chicago.

Dr. Dahlberg is one of the most civil, judicious and humane individuals whom I know. He keeps constructively busy with his own projects or eagerly helps students and other colleagues to develop the best scientific and personal talents in themselves. It is no wonder then that he is a pillar in the Department of Anthropology and a tresured international professional.

Sources and acknowledgements

This commentary is based primarily on information contained in the Announcements for The University of Chicago and its Division of the Social Sciences. The research was conducted in the Special Collections (Archives) section of the Joseph Regenstein Library of The University of Chicago. I thank Mr. A. Tannler and his staff for their assistance. Also I greatly appreciate the comments of F. Clark Howell, Sol Tax and Marlene Tuttle who read the paper and Mrs. K. Barnes and Carol Lin-Bodien for clerical help. The project was supported by the Marian and Adolph Lichtstern Fund of the University of Chicago.

The adaptive significance of pongid lip mobility

PHILLIP L. WALKER

OSSA

A series of 29 captive great apes was studied to determine intergeneric differences in use of the lips, hands and teeth during feeding. Contrasts between gorillas and the other pongids indicate that the remarkably mobile, prehensile lips of orang-utans and chimpanzees adapt these animals for arboreal feeding. Use of the lower lip to express the nutrients from food items may reflect an additional feeding function of the lips since it apparently facilitates the efficient exploitation of fibrous foods with a relatively low nutritional value.

Keywords: Lip mobility - Pongid - Feeding behavior.

Была изучена серия 29 содержащихся в неволе крупных обезьян, чтобы определить межродовые различия в использовании губ, рук и зубов в процессе питания. Контрасты между гориллами и другими человекообразными обезьянами показывают, что необыкновенно подвижные, цепкие губы орангутангов и шимпанзе помогли приспособить этих животных к питанию на деревьях. Использование нижней губы для высасывания питательных веществ из кусков пищи может отражать добавочную функцию губ во время употребления пищи, поскольку это, по-видимому, помогает эффективно использовать волокнистую пищу с относительно низкой питательной ценностью.

Ключевые слова: подвижность губ, человекообразная обезьяна, поведение во время кормления.

Phillip Walker, Department of Anthropology, University of California, Santa Barbara, California 93106 U.S.A.

Vol. 6, pp. 277-284, Lund. ISSN 0345-8865.

Humans differ from other hominoids in that their habitually bipedal mode of locomotion frees the hands to function almost totally as manipulatory organs. The hands of great apes, in contrast, are a morphological compromise between the demands placed on them in their roles as manipulatory, locomotor, and suspensory organs. The purpose of this paper is to present behavioral data which indicates that the mobile, prehensile lips of orang-utans (Pongo pygmaeus) and chimpanzees (Pan troglodytes) assume a series of manipulatory and storage functions which partially compensate for the locomotor demands placed upon the hands of feeding animals.

Behavorial observations

A series of experiments were performed at Yerkes Regional Primate Research Center in order to identify differences in the way chimpanzees, organ-utans, and gorillas use their lips, teeth and hands to process foods having different nutritional mechanical characteristics (Walker, '73). Feeding observations were made on a group of 29 wild born great apes that contained approximately equal number of males and females (Table 1) during approximately 1, 500 individual feeding sessions (425 hours of observation). Animals were observed during morning and afternoon feeding sessions in their home cages at distances ranging between a few inches and four feet. Individuals from each pongid genus were tested by presenting them with standardized tasks such as the processing and mastication of pieces of carrot of a specific size and weight. By analyzing the relative frequencies of manipulatory behaviors elicited by these standardized tasks, it was possible to identify consistencies in the behavior of each species that were not the product of either sexual dimorphism or individual variation. Presumably differences in behavior, identified in this way, have a high probability of reflecting interspecific contrasts in feeding adaptation.

Two distinct patterns of behavior involving manipulation with the lips were elicited by the experimental foods tested. During the initial stage of food processing, the lips often assumed a prehensile role. Chimpanzees and gorillas, for example, frequently held pieces of food on the lower lip or between the upper and lower lips while additional pieces of food were processed in the molar region. The lips of Pan and Pongo (fig. 1a) are also used for food storage. Members of these genera often held partially masticated boluses of food in the area between the lower lip and the mandibular incisors (fig. 1b). Several other behaviors involving the lips occurred much less frequently and, therefore, could not be used to make meaningful intergeneric comparisons. Orang-utans, for example, occasionally peeled oranges employing only their lips and both orang-utans and chimpanzees sometimes used their lips to pick up objects.

Data on the relative frequency of lip use indicate that gorillas differ from the other pongids by using their lips infrequently to hold or store food (Table 2). For three of the five foods tested (carrots, cabbage leaves, and oranges), orang-utans employed their lips more often during the processing of one kilogram of food than did chimpanzees. While eating "chimpcrackers" (Bourne, '71), a hard friable dogbiscuit-like food, and sugarcane stem, chimpanzees used their lips more frequently than did either orang-utans or gorillas. Chimpanzees often employed their lower lip in its storage capacity while eating sugarcane (Table 2). After initially splitting and crushing sugarcane stems with the canines and molars, chimpanzees usually sucked on the resultant bolus pressing it forcefully against the mandibular incisors by contracting the musculature of the lower lip. The dry bolus of fiber that resulted from this processing was almost always discraded onto the floor. Gorillas contrasted with chimpanzees and orang-utans by consistently swallowing sugarcane fiber rather than discarding it. Analogous intergeneric differences were observed in the processing of unshelled peanuts. Gorillas usually eat peanuts in their entirety without removing the shell. Orang-utans and chimpanzees, on the other hand, show a special preference for the peanut seed and frequently use their lips and incisors to remove the shell.

The apes studied often held small fragments of food on the lower lip while the hands were occupied in locomotor and postural acitivites. Use of the lips in this way was especially frequent while eating foods such as carrots and chimpcrackers which tend to fragment during processing (Table 2).

Discussion

If the terms adaptation and function are to be useful for analysis of evolutionary processes, they must be employed in a way which implies the action of natural selection (Williams, '66; Hinde, '75). While numerous beneficial consequences could result from the manipulatory capacities of pongid lips, none of these beneficial effects are necessarily pathways through which natural selection has acted. It is possible, for example, that the intergeneric differences noted during feeding are incidental consequences of contrasts between the species studied in the communicative rather than the feeding functions of the lips. This interpretation of the intergeneric differences observed seems unlikely, however, since the high frequencies of lip use were found in Pongo, a genus characterized by markedly less sociality than Pan or Gorilla (Rodman, '73; Rijksen, '78; Lawick-Goodall, '68; Schaller, '63).

Correlations between a behavior or structure and specific environmental factors are one source of evidence that a behavorial trait has biologically advantageous consequences through which natural selection acts (Hinde, '75). The intergeneric differences in lip use exhibited by captive apes appears tobe associated with contrasts in the distribution and nutritional quality of the foods each species characteristically exploits in the wild. The feeding adaptation of Gorilla differs in a number of respects from that of Pan and Pongo. Gorillas spend most of their feeding time of the ground where they consume a diet composed primarily of stems, leaves,

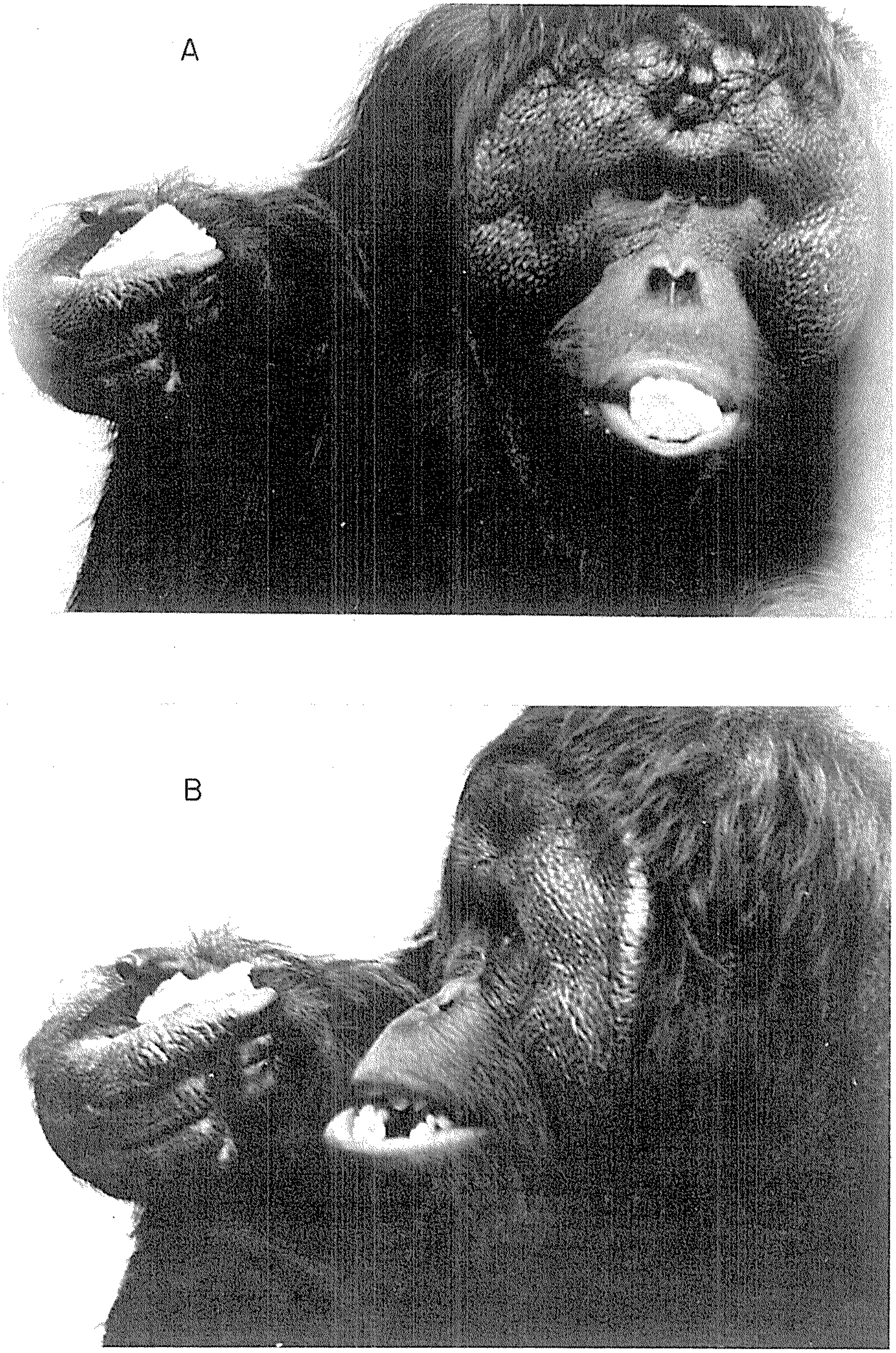


Fig. 1. Orang-utan (1a), holding pieces of food in the lower lip; (1b), holding pieces of masticated food between the mandibular incisors and lower lip.

and other vegetative plant parts (Schaller, '63; Kawai and Muzuhara, '59; Fossey, '74; Jones and Sabater PI, '71). Chimpanzees, in contrast, frequently feed in trees on fruit, blossoms, seeds, buds, and other reproductive parts of plants (Jones and Sabater PI, '71; Goodall, '63; Suzuki, '69; Nishida, '76; Reynolds and Reynolds, '65). Orang-utans descend to the gróund relatively infrequently and throughout most of the year are predominately frugivorous (Mackinnon, '74; Rodman, '76; Rijksen, '78). While each of the pongids have been reported to occasionally hold and manipulate food with their lips in the wild (Schaller, '63; Goodall, '63; Reynolds and Reynolds, '65; Mackinnon, '74), temporary storage of food inside the lower lip has been reported only for Pan and Pongo (Goodall, '63; Mackinnon, '74). The predominance of fruit in the diets of free-ranging chimpanzees and orang-utans is consistent with the tendency for capitve individuals from these species to hold and store food with the lips. The ability to securely grasp objects eith the lips probably confers an important advantage to orang-utans and chimpanzees feeding on fruit located in the terminal branches of trees by reducing the rate at which these nutritious food items are dropped. As manipulatory organs the lips can partially assume the role of the hands in feeding and thus free an additional limb to serve in postural activites. The prehensile capability of the lips of Pan and Pongo, therefore, appears to have the adaptively significant consequence of facilitating feeding in arboreal environments where the even distribution of weight is of critical importance. The contrast between gorillas and the other pongids in the frequency of manipulatory behaviors involving the lips is consistent with this interpretation since gorillas normally feed in a sitting position on the ground (Schaller, '63; Jones and Sabater PI, '71) and thus have free access to both hands for food procurement and processing.

The tendency for captive chimpanzees and orang-utans to suck on boluses of sugarcane stem, cabbage leaves, and other fibrous foods has at least one beneficial consequence since it relieves these species from the energetic expense of passing material with a large indigestible component through the alimentary canal. Natural historical observations indicate that fibrous foods of relatively low nutritional value are important food sources for chimpanzees and orang-utans during periods of food scarcity. Use of the lower lip for preliminary extraction of nutrients from such foods may, therefore, confer an important adaptive advantage to these primates. Chimpanzees living in an area of Tanzania where there are marked seasonal fluctuations in fruit availability, for example, apparently rely heavily on bark as an "emergency food" (Nishida, '76). Free-ranging populations of orang-utans are subject to marked variations in food availability. MacKinnon reports than when fruit was scarce the Bornean orang-utans he studied "fed on less nutritious foods such as leaves, lianas, bark and epiphytes which are rarely eaten when fruit is abundant although they are always plentiful" (MacKinnon, '74:27). Rijksen observed similar feeding behavior in the Sumatran orang-utans he studied: "when the availability of figs and other fruits was rather poor ... the apes showed some increase in feeding from the growth layers under the bark of certain trees. Such a change in diet towards more widely available food sources was especially apparent in the disabled, adult female Josh.. ..She showed an obviously higher incidence of 'bark-feeding' than other orang utans. We observed her stripping the bark of a variety of trees and lianas on several occasions and she not only used to scrape off the growth layers but also chewed the bark. As she could not range over a larger area because of her lameness, she probably faced a shortage of fruits in her restricted range and had to utilize alternative sources" (Rijksen, '78:72).

In its storage capacity the lower lip could assume some of the roles suggested for the cheek pouches of cercopithecine monkeys (Murray, '76). It is possible that the ability to hold food inside the lower lip allows chimpanzees to effectively compete with conspecifics during periods of food shortage. Although I have no quantitative data relating to this possible lip function, I observed a few interactions between captive chimpanzees in which competition over oranges was clearly a motivating factor for use of the lower lip in its storage capacity.

The remarkably mobile lips of chimpanzees and orang-utans are undoubtedly the result of selective factors relating to communication as well as feeding. My analysis of behavorial and natural historical data indicates, however, that the lip mobility exhibited by Pan and Pongo was selected for primarily because it facilitates aboreal feeding. Captive gorillas differ from the other pongids by swallowing fibrous food such as sugarcane stem and by manipulating food items relatively infrequently with the lips. These features of gorilla feeding behavior apparently reflect an adaptation that involves eating large quantities of foliage and plant stems in a terrestrial environment. The behavorial data presented have important implications for reconstructing the manipulatory capabilities of extinct apes since use of the lips in their prehensile and manipulatory capacities could modify in important ways selective pressures acting on the hands.

Acknowledgements

I thank Geoffry Broune and the staff of Yerkes Regional Primate Research Center for their assistance during the course of this research. I am also grateful for Albert Dahlberg,Russell Tuttle and Donald Symons for the the help they gave me. This research was supported by USPHS grant DE173-01-03, the Hines Fund of the University of Chicago, and the Committee on Research of the University of California.

References

Bourne, G.H. 1971 Nutrition and the diet of the chimpanzee. In G.H. Bourne (ed.): The Chimpanzee, Vol. IV, 373-400. Basel, Karger.

Fossey, D. 1974 Observations on the home range of one group of mountain gorillas (Gorilla gorilla beringei). Anim. Beh. 22, 568-581.

Goodall, J. 1963 Feeding behavior of wild chimpanzees. Symp. Zool. Soc. Lond. 10, 39-48.

Hinde, R.A. 1975 The concept of function. In G. Baerends, C. Beer and A. Manning (eds.) Function and Evolution in Behavior, 3-15. Oxford, Clarendon Press.

Jones, C. and J. Sabater Pi 1971 Comparative ecology of Gorilla gorilla (Savage and Wyman) and Pan troglodytes (Blumenbach) in Rio Muni, West Africa. Bibl. primatol. No. 13, pp. 1-96. Basel, Karger.

Kawai, M. and H. Mizuhara 1959 An ecological study of the wild mountain gorilla (G. g. beringei). Primates 2, 1-42.

Lawick-Goodall, J. van 1968 The behavior of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. Vol. 1, part 3, pp. 161-311.

Mackinnon, J. 1974 The behavior and ecology of wild orang-utans (Pongo pygmaeus). Anim. Beh. 22, 3-74.

Murray, P.F. 1976 The role of cheek pouches in cercopithecine adaptive strategy. In R.H. Tuttle (ed.): Primate Functional Morphology and Evolution, 151-194. The Hague, Mouton.

Nishida, T. 1976 The bark-eating habits in primates, with special reference to their status in the diet of wild chimpanzees. Folia primatol. 25, 277-287.

Reynolds, V. and F. Reynolds 1965 Chimpanzees of the Budongo forest. In I.Devore (ed.) Primate Behavior, 368-424. New York, Holt, Rinehart and Winston.

Rijksen, H.D. 1978 A field study on Sumatran orang-utans (Pongo pygmaeus abelii Lesson 1827) Ecology Behavior and Conservation (Medelingen Landbouwhogeschool Wageningen, Netherlands).

Rodman, P.S. 1973 Population composition and adaptative organization among orang-utans of the Kutai reserve. In R.P. Michael and J.H. Crook (eds.) Comparative Ecology and Behavior of Primates, 171-209. New York, Academic Press.

Schaller, G.B. 1963 The Mountain Gorilla. Chicago, University of Chicago Press.

Suzuki, A. 1969 An ecological study of chimpanzees in a savanna woodland. Primates 10, 103-148.

Williams, G.C. 1966 Adaptation and Natural Selection: a critique of some current evolutionary thought. Princeton, Princeton University Press.

TABLE 1.

Great Apes Observed

Species	Males	Females	Total
Pan troglodytes	5	5	10
Gorilla gorilla	3	7	10
Pongo pygmaeus	5	4	9

TABLE 2

Frequencies of behaviors involving the lips elicited from _Pan_, _Pongo_ and _Gorilla_ during feeding experiments

Food/Species	Number of Subjects Tested	Total Number of Lip Behaviors Elicited	Total Number of Mouth-Food Contacts Observed	Frequency of lip behaviors/ kilograms of food consumed	
				Food Held on or Between the Lips	Food Stored Inside the Lower Lip
Carrot					
Gorilla	9	4	932	.35	.00
Pongo	9	146	1063	15.85	1.04
Pan	11	87	1020	4.80	.36
Cabbage					
Gorilla	9	1	480	.23	.00
Pongo	9	27	180	4.78	5.98
Pan	11	18	198	1.57	3.13
Cracker					
Gorilla	9	8	221	6.60	.94
Pongo	9	53	300	17.68	1.84
Pan	11	82	363	33.09	8.02
Orange					
Gorilla	9	4	470	.00	.57
Pongo	9	27	352	.14	3.59
Pan	11	31	528	.27	1.83
Sugarcane					
Gorilla	6	2	265	.00	1.40
Pongo	6	9	151	4.84	1.38
Pan	5	26	203	6.16	8.40

Vol. 6, pp. 285-288, Lund. ISSN 0345-8865.

Dr. Albert A. Dahlberg's publications:

Abbreviations:

AJHG	American Journal of Human Genetics
AJPA	American Journal of Physical Anthropology
IADR	International Association for Dental Research
IDJ	International Dental Journal
JADA	Journal of the American Dental Association
JAMA	Journal of the American Medical Association
JDR	Journal of Dental Research
Abst	Abstract

-- "Prosthetic Treatment of Cleft Palate," The Dental Students' Magazine, 10(4): 6-12, 38. Jan 1932

-- "Heterotopic Formation of Dentine and Enamel by Transplantation of Epithelium and Pulp Tissue," Proc. of the Society for Experimental Biology and Medicine 31:525-526. 1934. Co-authors: CB Huggins, HR McCarroll

-- "Transplantation of Tooth Germ Elements and Experimental Heterotopic Formation of Dentin and Enamel," J of Experimental Medicine 60(2):199-210. Aug 1934. Co-authors: CB Huggins, HR McCarroll

-- "Dentigerous Cysts Treated Conservatively: Case Reports," The Bur 36(2):82-86. July 1936. Co-author: CP Danreiter

-- "Electrochemical Ulcer of the Buccal Mucosa: Report of Case," JADA 23(9): 1652-1654. Sept 1936. Co-author: NW Roome

-- "Inherited Congenital Absence of Six Incisors, Deciduous and Permanent," JDR 16(1):59-62. Feb 1937

-- "Treatment of the Lip and Cheek in Cases of Facial Paralysis," JAMA 124: 503-504. Feb 19. 1944

-- "The Paramolar Tubercle (Bolk)," AJPA 3(1):97-103. Mar 1945

-- "The Changing Dentition of Man," JADA 32(11):676-690. June 1945 (Reprinted in Lasker, GW, ed., Yearbook of Physical Anthropology 1945, pp. 48-62. New York, The Viking Fund Inc., 1946)

-- "The Shovel-shaped Character in the Teeth of the Pima Indians," AJPA 5(2): 234. June 1947. Co-author: O Mikkelsen. Abst

-- "The Milk and Permanent Dentitions of the Tarsius philipensis," AJPA 6(2): 239-240. June 1948. Abst

-- "The Evolutionary Significance of the Protostylid," AJPA 8(1): 15-25. Mar 1950

-- "The Dentition of the American Indian," in Laughlin, WS ed., The Physical Anthropology of the American Indian, pp. 138-176. New York, The Viking Fund, Inc., 1951

-- "Concepts of Occlusion in Physical Anthropology and Comparative Anatomy," JADA 46(50):53-535. May 1953

-- "A Preliminary Study of the Population History of the Pima Indians," AJHG 5(4):377-388. Dec 1953. Co-authors: BL Hanna, HH Strandskov

-- "Punch Cards and Dentition Data," American Anthropologist 56(1):104. Feb 1954

-- "Major Variant Dimensional Proportions of Tooth Components as Viewed as Attributes in Genetic and Morphological Studies of the Dentition," JDR 33(5): 704-705. Oct 1954. Abst

-- "Genetics of Primary Tooth Characters," JDR 34(5):681. Oct 1955. Abst

-- "Materials for the Establishment of Standards for Terminology, Descriptions and Classifications of Tooth Characters, Attributes and Techniques in Morphological Studies of the Dentition," Chicago, Zoller Laboratory of Dental Anthropology, Department of Anthropology, University of Chicago, 1955. (Descriptive material issued with 17 stone model plaques.) Read at IADR meeting (Chicago Section) Nov 20, 1955.

-- "Standardization of Terminology, Descriptions and Classification of Tooth Characters, Attributes and Techniques Used in Morphological and Genetic Studies of the Dentition," IADR 34:59. 1956. Abst

-- "Sequence and Timing of Permanent Tooth Emergence in Pima Indians," IADR 35:82. 1956. Co-authors: P Epling and R Bock. Abst

-- "Criteria of Individuality in the Teeth," J of Forensic Sciences 2(4):389-401. Oct 1957 (Abst: J Am College of Dentists 24(3):193-194, Sept 1956)

-- "The Distribution of Blood Group Alleles Among Indians of the Southwest, North America," AJHG 10(2):175-195. June 1958. Co-authors: KS Brown, BL Hanna, HH Strandskov

-- "Anthropological Aspects of Human Dentition," IDJ 8(2):158-159, 168. June 1958

-- "Emergence of the Permanent Teeth in Pima Indian Children," JDR 37(6):1123-1140. Nov-Dec 1958. Co-author: R-M Menegaz-Bock

-- "Rotated Maxillary Central Incisors," J of Japanese Ortho. Soc.17(2):157-161. Dec 1958

-- "Teeth", in Benton, W., pub., Encyclopedia Britannica. Vol 21:875-878. 1959. Revised: 1963, 1967.

-- "Wing-like Appearance of Upper Incisors Among American Indians," JDR 38(1): 203-204. Jan-Feb 1959. Abst

-- "Clinical Aging Patterns in Teeth of Different Population Groups," in Shock, NW, ed., *Aging--Some Social and Biological Aspects*, pp. 357-366. Washington, D.C., AAAS (Publication No. 65), 1960

-- "Microscopic Studies of Abrasion and Attrition on Tooth Surfaces," JDR 39(4): 713-714. Jul-Aug 1960. Abst

-- "The Dentition of the First Agriculturalists (Jarmo, Iraq)," AJPA 18(4):243-256. Dec 1960

-- "The Olduvai Giant Hominid Tooth," Nature 188(4754):962. Dec 10, 1960

-- "Relationship of Tooth Size to Cusp Number and Groove Conformation of Occlusal Surface Patterns of Lower Molar Teeth," JDR 40(1):34-48. Jan-Feb 1961

-- "The Dentition of the Magdaleanian Female from Cap Blanc, France," Man 61: 49-50. Mar 1961 Co-author: V Carbonell

-- "Genetic Aspects of Evolution of the Human Dentition," in Witkop, CJ, ed., *Genetics and Dental Health*, pp. 113-120. New York, McGraw Hill, 1962

-- "On the Teeth of Early Sapiens," in Kurth, G, ed., *Evolution und Hominisation*, pp. 205-211. Stuttgart, Germany, Gustav Fischer Verlag, 1962. Second (revised) edition 1968, pp. 273-280.

-- "Preliminary Report of the Dentition Study of Two Isolates of Kodiak Island," Arctic Anthropology 1(1):115-116. 1962

-- "Anthropology in Dentistry," in Paffenbarger, GC and S Pearlman, eds., *Frontiers of Dental Science*, pp. 113-121. Vistas of Science 3, National Science Teachers Assn. New York, Scholastics Book Services Division of Scholastics Magazines, Inc. 1962

-- "Etude Microscopique de l' Abrasion et de l' Attrition sur la Surface des Dents," Bulletin du Groupement Internationale pour la Recherche Scientifique en Stomatologie 5(2):245-251. Apr 1962. Co-author: WG Kinzey

-- "IADR: Abstracts of Papers Presented at the Eighth Annual Meeting of the Japanese Division," JDR 41(3):503-509. May-June 1962. Co-editor: K Tomita

-- "Analysis of the American Indian Dentition," in Brothwell, DR, ed., *Dental Anthropology*, pp. 149-177. London, Pergamon Press, 1963

-- "Dental Traits as Identification Tools," Dental Progress 3(3):155-160. Apr 1963

-- "Comparison of Dental Traits in Different Age Groups Within the Same Population," AJPA 21(3):421. Sept 1963 Co-authors: S Kobayashi, K Tomita

-- "Dental Evolution and Culture," Human Biology 35(3):237-249. Sept 1963 (Reprinted in Garn, SM, ed., *Culture and the Direction of Human Evolution*, pp. 19-31. Detroit, Wayne State University Press, 1964)

-- "Introduction" and "Summation," JDR 42(6:1):1260, 1369. Nov-Dec 1963 (Conference on Genetic Aspects of Oral Structures)

-- "Edward James Ryan," (Obituary), Proceedings of the Institute of Medicine of Chicago 24(12):339. Nov 1963

-- "Hereditary Patterns of the Protostylid Cusp of Mandibular Molars," JDR 43 (5:2):811. Sept-Oct 1964. Co-author: T Fukuhara. Abst

-- "Aging Patterns in Teeth," IDJ 14(3):376-380. Sept 1964. (Reprinted in New Mexico Dental Journal 16(2):16-20. Aug 1965)

-- "Evolutionary Background of Dental and Facial Growth," JDR 44(1:2):151-160. Jan-Feb 1965

-- "Geographic Distribution and Origin of Dentitions," IDJ 15(3):348-355. Sept 1965

-- "Virginia Carbonell, 1920-1965," (Obituary), AJPA 24(2):276. Mar 1966

-- "Cusp Number, Occlusal Groove Pattern and Human Taxonomy," Nature 210 (5032):224-225. Apr 1966. Co-authors: SM Garn, AB Lewis, RS Kerewsky

-- "Groove Pattern, Cusp Number and Tooth Size," JDR 45(3:2):970. May-June 1966. Co-authors SM Garn, AB Lewis, RS Kerewsky

-- "Genetic Independence of Carabelli's Trait from Tooth Size and Crown Morphology," Archives of Oral Biology 11(7):745-747. July 1966. Co-authors: SM Garn, AB Lewis, RS Kerewsky

-- "Interaction Between Relative Molar Size and Relative Number of Cusps," JDR 45(5):1240. Jul-Aug 1966. Co-authors: SM Garn, AB Lewis, RS Kerewsky

-- "Fluoride and Occlusal Surface Tooth Morphology," AJPA 25(2): 208. Sept 1966. Co-author: T Sakamoto. Abst

-- "Analysis of Incisor Morphology," AJPA 25(2):208. Sept 1966. Co-authors: RN Staley, M Feer. Abst

-- "Relative Eruption Precedence of Mandibular and Maxillary Teeth in Two Populations," JDR 46(2):456. Mar-Apr 1967. Co-authors: H Israel, SM Garn, RS Kerewsky

-- "Proceedings of the International Symposium on Dental Morphology," JDR 46 (5:1):769-992. Sept-Oct 1967. Editor

-- "A Comparison of the Dentin and Enamel Surfaces of Upper Incisor Teeth," AJPA 27(2):240. Sept 1967. Abst

-- "Comparison of Dental Traits in Populations by Expressivity Scores," AJPA 27(2):240. Sept 1967. Co-author: T Sakamoto. Abst

-- "Occlusal Relationship of American Indian (Pima)Dentitions," AJPA 27(2): 240-241. Sept 1967. Co-author: M Irie. Abst

-- "Genetic Studies of Tooth Size Factors in Pima Indian Families," AJHG 20(2): 89-110. Mar 1968. Co-authors RHY Potter, P-L Yu, AD Merritt, PM Conneally

-- "Identifying Factors Accounting for Tooth Size Association Patterns in Males and Females," IADR Program and Abstracts of Papers, p. 147, Mar 1968. Co-authors: RHY Potter, P-L Yu, JA Norton, AD Merritt. Abst

-- "Intrinsic Nature of Dental Traits Used in Comparative Studies of Populations," Proceedings of the Eighth International Congress of Anthropological and Ethnological Sciences, Tokyo and Kyoto, 1968. Vol I, pp. 296-298. Tokyo, Science Council of Japan, 1969

-- "Trait Analysis of the Dentition of the Tarahumara Indians and Mestizos of the Sierra Madre Occidental, Mexico," AJPA 31(1):65-76. Jul 1969. Co-authors: RG Snyder, C Snow, T Dahlberg

-- "Tours Mandibularis in an Alaskan Eskimo Population," AJPA 33(1):57-60. Jul 1970. Co-authors: J Mayhall, DG Owen

-- "Dental Caries in the Eskimos of Wainwright, Alaska," JDR 49(4):886. Jul-Aug 1970. Co-authors: J Mayhall, DG Owen

-- Dental Morphology and Evolution. Papers and Proceedings of the Second International Symposium on Dental Morphology. Editor. Chicago, University of Chicago Press, 1971

-- "Penetrance and Expressivity of Dental Traits," in Dahlberg, AA, ed., Dental Morphology and Evolution, pp. 257-262. Chicago, Univ of Chicago Press
-- "Bulging of the Lingual Aspects of Buccal Cusps in Posterior Teeth of Skolt Lapps from Northern Finland," JDR 51(5:2):1513. Sept-Oct 1972. Co-authors: P Kirveskari, B Hedegård
-- "Problems in Developing Standards for Dental and Other Craniofacial Metric and Morphological Analyses," AJPA 37(3):433-434. Nov 1972. Abst
-- "Biology of Occlusion," J of the Japanese Stomat Soc 22: 157-161 Apr-Jun 1973
-- "Biology of Occlusion," Dental Abstracts 19(1):8-9. Jan 1974. Abst
-- "Definition and Standardization of the Traits Used in Metrical and Morphological Studies in the Dentition," AJPA 40(1):134. Jan 1974. Abst
-- "An Historical Brief on Studies of Dental Morphology," AJPA 42(2):296-297. Mar 1975. Abst
-- "Forensic Dentistry," JADA 93(5):991-995. Nov 1976
-- Orofacial Growth and Development. Co-editor: TM Graber. The Hague and Paris, Mouton Publishers. World Anthropology Series. 1977
-- "Craniofacial Description of Wainwright Alaskan Eskimos." Co-author: R. Cederquist. In Dahlberg, AA and TM Graber, eds., Orofacial Growth and Development, pp. 263-267. The Hague and Paris, Mouton Publishers. 1977
-- "Uto-Aztecan Premolar: the Anthropology of a Dental Trait." Co-authors: DH Morris, S Glasstone Hughes. In PM Butler, and KA Joysey, eds., Development, Function and Evolution of Teeth. London: Academic Press, 1978.

Orofacial Growth and Development (The Hague: Mouton Publishers), which Thomas M. Graber co-edited with me, appeared in 1977. This is part of the World Anthropology Series.

"Eskimo Craniofacial Studies," written in collaboration with R.Cederquist, J.May-Hall and D.Owen, appeared in Eskimos of Northwestern Alaska, P.Jamison, S. L. Zegura and F.A. Milan eds. (Stroudsberg, Penn.: Dowden, Hutchinson and Ross, Inc.), in 1978.

"Changes in Arch Dimensions With Age in Pima Indian Dental Materials," written in collaboration with Dr. Yasuhide Takahama of Kyushu University, Japan, is presently in press.

I have written the chapter, "Craniofacial Studies" for The Human Biology of Circumpolar Populations, F.A. Milan, ed., which is about to be published by the Smithsonian Institution through Cambridge University Press. This is part of the Smithsonian's International Biological Program series.

"Inheritance of Dental Morphological Traits" was presented to the University of Turku, Finland, in May, 1978. This was the report on an analysis of the Pima Indian materials conducted in the Dental Anthropology Laboratory in February and March of 1978 with Dr. Pentti Kirveskari of the University of Turku.

I am currently completing the chapter, The Dentition of the American Indian," in collaboration with Richard Scott of the University of Fairbanks, Alaska, to appear in The Handbook of North American Indians, Volume III, Frederick Hulse, ed.

Addendum

ARTICLES:

Chapter on "Eskimo Dentition" in Frederic A. Milan, ed., The Human Biology of Circumpolar Populations: Alaska, Cambridge University Press. In press.

Chapter on "Indians and Eskimos" in Paul L. Jamison, ed., International Biological Program on Arctic Research, International Biological Program. In press.

Review of Berkovitz, Holland and Moxham, Color Atlas of Oral Anatomy, for The Quarterly Review of Biology, June,1979.

Review of The Radiological Atlas of the Mummies of the Pharaohs of Egypt, for the University of Chicago Press, June 1978.

Instructions to Authors

Manuscripts are to be sent to the general editor. The author's permanent and temporary addresses are to be given. The manuscript will not be returned to the author until the article has been printed, and the author is requested to retain a complete copy. Proofs will be sent to the author once; the author is expected to read them carefully and to return them promptly to OSSA, Nils-Gustaf Gejvall, Gnejsvägen 1, S-310 40 HARPLINGE — Sweden. The author will be charged for changes against the manuscript made by him in the proof. Reprints in addition to the 50 free copies are to be ordered with the proofs.

MANUSCRIPT

The manuscript must be typewritten (carbon copy not acceptable) on one side of standard-sized paper, double spaced, and with an ample left margin. The text must be clear and concise, and written preferably in English; German manuscripts may be submitted. Manuscripts should be arranged in the following order: (1) Informative but brief title. Avoid titles with interrogative form, abbreviations, formulae, and parentheses. (2) Author's name; one or more of his forenames unabbreviated. (3) A *short* abstract, always in English, not exceeding 1330 letters and spaces, and starting with a repetition of 2 and 1, with a translation in parentheses of non-English titles. (4) The author's professional address and a dating of the manuscript. (5) The main text. Use three or fewer grades of headings. Indicate in the left hand margin the approximate position of figures and tables. The words 'Fig.' ('Figs.') and 'Table' (unabbreviated) are to be written with capital initials in the text. In the main text, OSSA does not use small capitals or bold-face. Instead of footnotes, insert paragraphs which can be composed in smaller type or use parentheses. (6) References shall conform to the examples given below. Abbreviations used should be consistent; necessary editorial changes will adhere to the usage in *International List of Periodical Title Word Abbreviations* (UNISIST/ICSU AB 1970). It is essential that the punctuation conforms exactly with the examples given below. Use ampersand for joint authorship in the text references and the entries in the reference list (but not elsewhere). (7) Captions of illustrations, if any. Add an English caption below captions in other languages. *Figure captions and tables must be submitted on separate sheets.* (8) Tables, if any, with captions, numbered with arabic numerals. When possible, try to simplify table material so that it can be run in with the text.

ILLUSTRATIONS

Illustrations should be reducible to a maximum size of 14.0 × 20.3 cm or less. It is recommended that figures be constructed *either* for the entire width of the type area (14,0 cm) *or* for the column width of 6.7 cm. If possible, avoid figures *between* 10.4 and 14.0 cm. On all figures should be the author's name and the figure number. Do not attach captions to the figure. Photographs are to be clear, sharply contrasted, and printed on white paper with glossy finish. Figures may be composed of several quadrangular units separated by 1 mm broad spaces. The items in composite figures should be similar to each other in tone. If the natural background is to be deleted, blackening is preferred.

All illustrations should be termed figures, even if occasionally covering an entire page, and the items of composite figures should be designated A, B, C, etc. (*not* a,b,c, etc.).

REFERENCES

Ballance, P. F. 1964: Streaked-out mud ripples below Miocene turbidites, Puriri Formation. New Zealand. *Jour. Sed. Petrology 34,* 91—101. Menash, Wisconsin.

Pettijohn, F. J. & Potter, P. E. 1964: *Atlas and Glossary of Primary Sedimentary Structures.* 370 pp. Springer-Verlag, Berlin, Göttingen, Heidelberg, New York.

Seilacher, A. 1963: Lebensspuren und Salinitätsfazies. *In* Unterscheidungsmöglichkeiten mariner und nichtmariner Sedimente. *Fortschr. Geol. Rheinl. Westf. 10,* 81—94. Krefeld.

OSSA VOLUME 6 1979

PAGES 1–288 · SOLNA 1980

ISSN 0345-8865. CODEN OSSA 6 1979

CONTENTS:

Printed in Sweden by Berlings, Arlöv 1980