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A Functional Analysis of the Temporomandibular Joint in *Homosapiens sapiens* and *Homo sapiens neanderthalensis*

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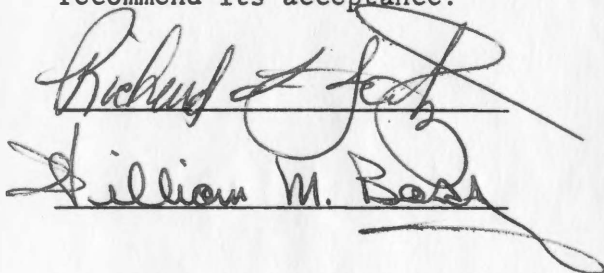
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Richard L. Smith
William M. Bass

Accepted for the Council:



Vice Chancellor

Graduate Studies and Research

A FUNCTIONAL ANALYSIS OF THE TEMPOROMANDIBULAR
JOINT IN HOMO SAPIENS SAPIENS AND
HOMO SAPIENS NEANDERTHALENSIS

A Thesis
Presented for the
Master of Arts
Degree
The University of Tennessee, Knoxville

Janice Lynn Foxworthy

June 1978

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Above all, I would like to thank my parents, Mr. and Mrs. Milton K. Foxworthy, for all their love, support, and encouragement they continue to give me in everything that I undertake. Without their support I would not be completing this thesis.

ABSTRACT

Analysis of the temporomandibular region in Homo sapiens neanderthalensis reveals diagnostic morphological differences in comparison to the morphological pattern typically expressed in the temporomandibular joint region of Homo sapiens sapiens. The temporomandibular joint region in Neandertals is characterized by a (1) thickened tympanic ring, petrosal area, mandibular fossa roof, and temporal squama; (2) pronounced postglenoid process; (3) more oval external auditory meatus, directed anteriorly and superiorly, positioned relatively higher on the temporal bone; (4) wide shallow glenoid fossa; (5) formation of the medial glenoid fossa wall; and (6) prominently developed articular eminence. This thesis concentrates on the morphological variations expressed in the glenoid fossa and its immediate surroundings of Homo sapiens neanderthalensis in comparison to the total morphological pattern present in Homo sapiens sapiens in an attempt to understand the possible significance of the differences expressed.

The primary focus of this thesis is directed toward the basic question: Do the mandibular fossa and postglenoid process exhibit the morphological pattern they do in Neandertals as (1) an adaptive response to stress generated during the habitual use of the anterior dentition for nonmasticatory purposes, or (2) a secondary response to the general neurocranial growth pattern characteristic of Neandertals? In order to propose a possible explanation for the variations expressed in the

temporomandibular joint region in Neandertals in comparison with modern man, the joint region in modern man is carefully reviewed within the framework of the functional matrix theory. Analysis of the gross aspects of hard tissue morphology alone suggests the Neandertal glenoid fossa and postglenoid process may be adapted to withstanding stress generated during the functioning of the mandible for masticatory and nonmasticatory purposes. However, a review of the temporomandibular joint as a diarthrodial joint, functional requirements of a diarthrosis, principles of biomechanical functioning, and morphology of the soft tissues contributing to joint formation indicate the functional components of the temporomandibular joint include only the articular eminence and mandibular condyle. The mandibular fossa and postglenoid process are not functional components of the temporomandibular joint. Stress generated during mandibular functioning is transmitted through the mandibular condyle and articular eminence and not the mandibular fossa as evidenced by the morphology of the fossa roof, composition, vascular/avascular pattern of the articular disk, and functional movements of the articular disk.

Analysis of the temporomandibular joint embryogenesis and general cranial and neurocranial development also strengthens the hypothesis that the form of the mandibular fossa seen in Homo sapiens sapiens does not have a functional adaptive significance. Interpreted within the framework of the functional matrix theory the morphology and configuration of the central and posterior portions of the temporomandibular joint in Homo sapiens sapiens and Homo sapiens neanderthalensis appear

to be a secondary response to the extrinsic and intrinsic factors responsible for general cranial growth and configuration. From this analysis it appears the morphology and configuration of the mandibular fossa and postglenoid process of the temporomandibular joint are not functional prerequisites to efficient biomechanical functioning of the temporomandibular joint and thereby do not have a direct adaptive basis.

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CHAPTER I

INTRODUCTION

I. INTRODUCTION TO THE PROBLEM

Sharing an interest in the phenomena of man's evolutionary history and adaptation, hominid paleontologists have sought an understanding of the diverse morphological developments of man as preserved in the fossil record. Descriptive analyses of morphological variations enable the hominid paleontologist to glimpse the evolutionary sequence of man's development yet do not contribute to a complete understanding of the processes responsible for these variations. In order to more fully understand man's evolutionary development one must also approach the problem from a functional viewpoint, indicating not only the unique characteristics of man's ancestry but also investigating how these characteristics may have been adaptive.

II. STATEMENT OF THE PROBLEM

The temporal bone morphology characteristic of Homo sapiens neanderthalensis exhibits distinctive differences compared to that normally seen in Homo sapiens sapiens. Neandertal temporal bone morphology differs from that exhibited by modern man in that, for Neandertals, the (1) squamous portion is thicker and smaller in vertical and horizontal dimensions; (2) external auditory meatus is more oval, directed anteriorly and superiorly, and positioned relatively higher

on the temporal; (3) zygomatic process is more curved and massive; (4) mastoid process, small and weakly developed, is positioned relatively higher and usually does not project below the cranial base; (5) squamous surface behind the supramastoid crest is not convex; (6) digastric groove and fossa are wide and deep; (7) postglenoid process is pronounced; (8) tympanic plate and petrosal area are thickened; (9) supramastoid ridge is prominent extending above the entire width of the mastoid process; (10) stylomastoid foramen is unusually large; (11) temporal projection not sphenoid plate forms the medial wall of the glenoid fossa; (12) glenoid fossa is wide and shallow; and (13) articular eminence appears more prominent (Alexeyev 1976; Angel 1972; Debénath 1977; Guth 1963; Heim 1974; Howell 1957; Howells 1973, 1974; Keith 1920; Mann and Trinkaus 1973; McCown and Keith 1939; Riquet 1974; Smith 1976; Stewart 1962, 1974; Stringer 1974; Vallois 1969; Vlček 1958) (Figure 1 and Figure 2). It is the purpose of this thesis to investigate a possible functional explanation for certain of these differences, specifically those relating to the form of the temporomandibular joint, which is composed of the anterior articular eminence, glenoid or mandibular fossa, posterior postglenoid process, and mandibular condyle (Figure 3). The basic question under consideration is whether the posterior portion of the Neandertal mandibular fossa exhibits the form it does in order to resist direct shearing and compressive stress due to the use of the masticatory apparatus or whether this form develops as a secondary result of the total morphological pattern of the Neandertal cranium. In the latter case, the Neandertal fossa morphology would not have a direct functional or adaptive basis.

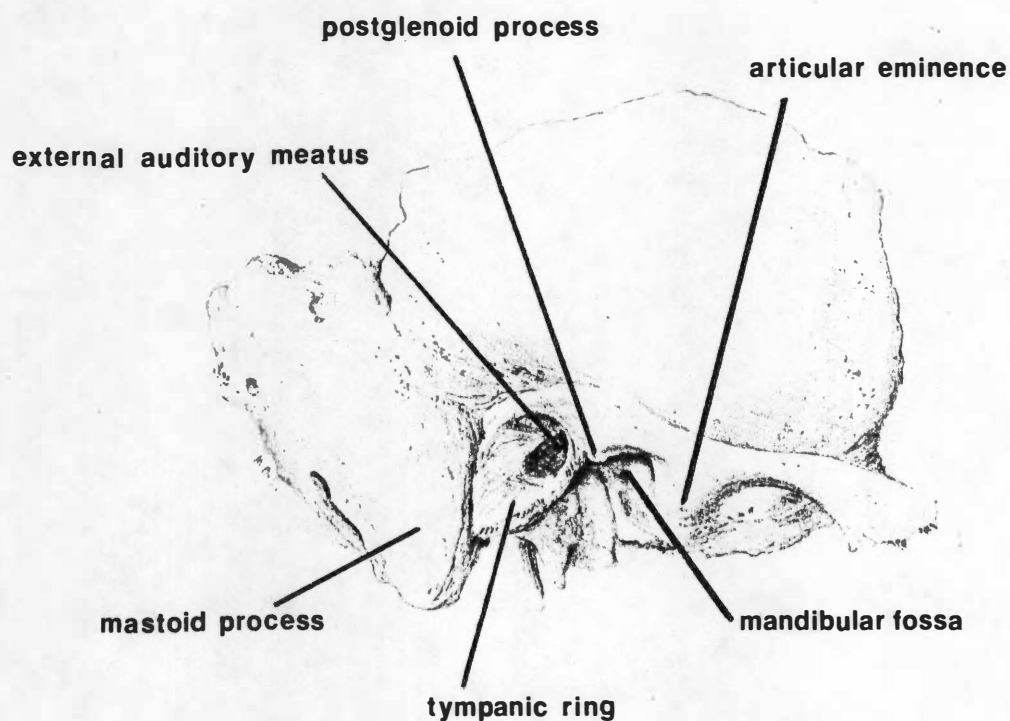
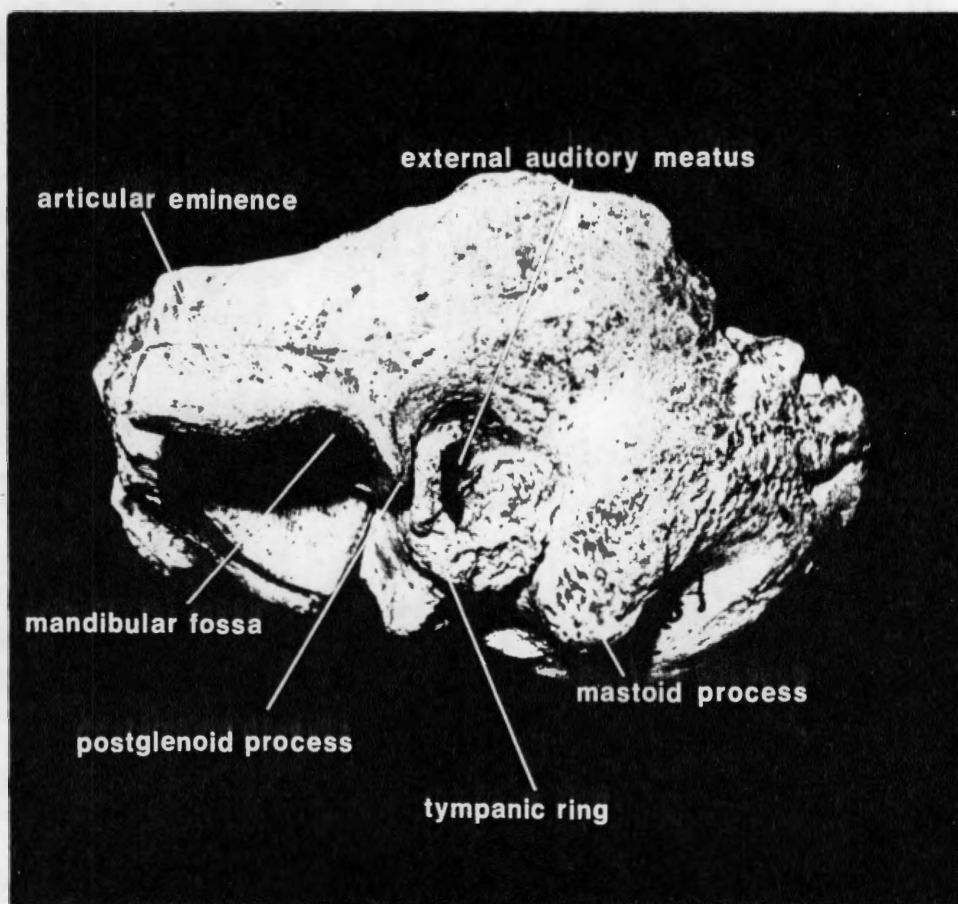


Figure 1: Temporal bone showing diagnostic morphology typically seen in Homo sapiens sapiens.

Drawing courtesy of Maria O. Smith.

TEMPORAL BONE FROM KRAPINA



(original photograph courtesy of Fred H. Smith.)

Figure 2: Temporal bone showing diagnostic morphology characteristic of Homo sapiens neanderthalensis.

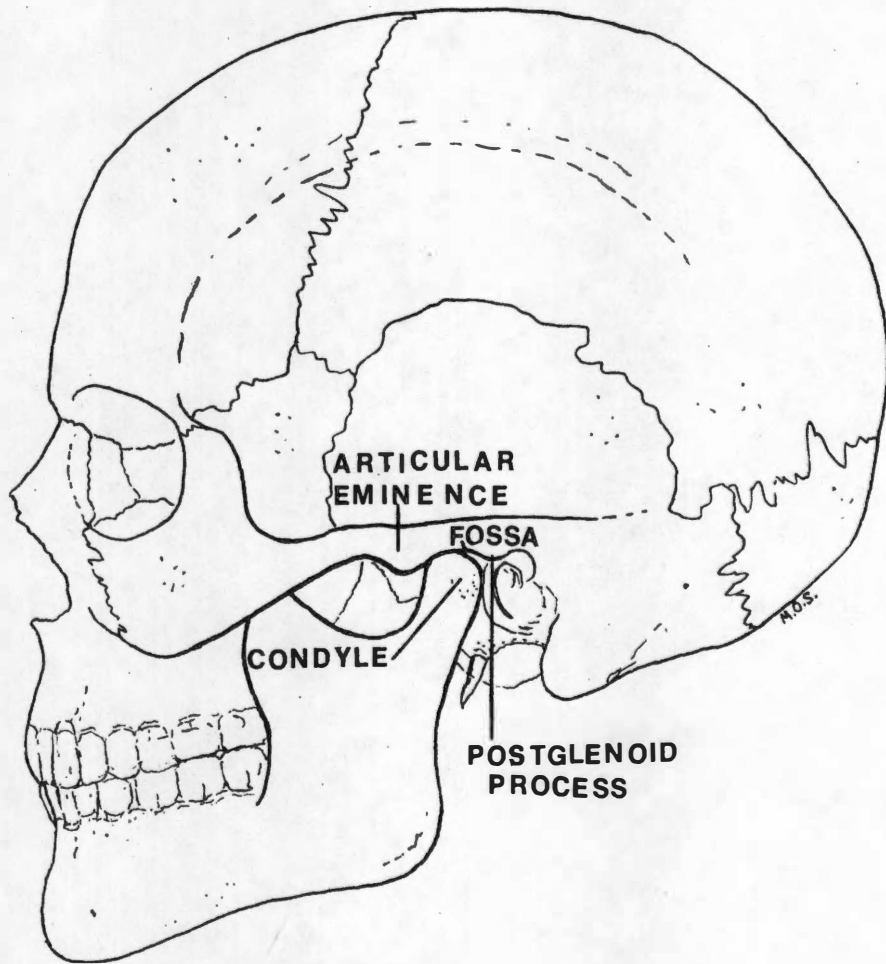


Figure 3: The temporomandibular joint is composed of the bony components including the articular eminence, mandibular fossa, postglenoid process, and mandibular condyle.

Drawing courtesy of Maria O. Smith.

III. DISCUSSION OF THE PROBLEM

The functional hypothesis for explaining Neandertal posterior temporomandibular joint morphology draws support from several areas. First, the thickening of the tympanic ring and marked development of the postglenoid process make it attractive to suggest that these areas were direct stress-bearing areas. Second, the suggestion by certain paleontologists that Neandertals may have habitually utilized their anterior dentition for nonmasticatory purposes (Brace 1962, 1964, 1967; Brose and Wolpoff 1971; Smith 1976; Wolpoff 1971) would mean that more stress would be generated at the point of contact between the mandibular condyle and the cranium during mandibular activity (Hylander 1975). The rather high incidence of osteoarthritis affecting Neandertal mandibular condyles (Alexandersen 1967; Kallay 1963; Smith 1976) is also indicative of stress bearing. If Neandertals are utilizing their anterior dentition habitually in nonmasticatory functions, the force necessary to grip efficiently would be greater than the force necessary to grind food on the molars, due to the proximity of the latter to the fulcrum represented by the temporomandibular joint. Third, the edge-to-edge bite pattern characteristic of Neandertals may also be a factor contributing to the need for strengthening the joint area. In Neandertals functional occlusion between the anterior dentition might not necessitate the action of gliding the mandibular condyle onto the articular eminence because the overbite characteristic for modern Caucasoids and Negroids is absent. The edge-to-edge bite pattern is not unique to Neandertals but is expressed in many modern populations,

particularly those of Mongoloid descent. However, the overbite pattern is characteristic of modern Caucasoids and Negroids. The presence of an overbite could suggest that the mandibular condyle remained within the mandibular fossa during use of the anterior dentition instead of sliding down onto the articular eminence as in normal modern man. In such a case, modification of the mandibular fossa into a stress resistant complex would appear logical. In Homo sapiens sapiens bruxing the dentition results in pressure generated in the area of the ear causing pain in that region (Gregg 1976). If strong gripping is done with an edge-to-edge bite, the thickening of bone noted around the external auditory meatus of Neandertals might logically be related to stress passing through the posterior aspect of the joint area.

On the other hand, it is possible that the general temporal bone morphology including the posterior temporomandibular joint structure of Neandertals, is not directly functional in itself but is simply a secondary result of the development and total morphological pattern of the cranium. It has been suggested, for example, that certain of the distinctive Neandertal temporal bone characteristics may simply relate to the long, low, broad general cranial configuration of Neandertals (Bilsborough 1972; Heim 1974; Howell 1957; Howells 1973, 1974; LeGros Clark 1964; Mann and Trinkaus 1973; Riquet 1974; Smith 1976; Stringer 1974; Suzuki 1970; Suzuki and Takai 1970; Thoma 1975; Vlček 1958; Weidenreich 1945).

In order to decide which of these two possible explanations is most suitable, it is necessary to closely examine the temporomandibular joint

area in modern man, and to consider its morphology and role in utilization of the mandible. It is realized that variation in the form of the temporomandibular joint exists in Homo sapiens sapiens but the extent and causes of these variations have not been researched to date. Data included in this thesis are based on the form of the temporomandibular joint typically seen in modern Caucasoid and Negroid individuals. Additionally, it is necessary to examine the functional requirements of a synovial joint during biomechanical activity and the general embryological development of the temporomandibular joint area in an effort to determine if the morphology of the posterior aspect of the fossa is a functional prerequisite to efficient biomechanical functioning of the joint. All of this will be accomplished within the framework of the functional matrix theory as it applies to the temporomandibular joint. The synergistic morphology of the joint area must be analyzed in terms of the functional significance of each component and its relationship to each of the other components. Based on such an understanding, one is better equipped to postulate possible explanations for the differences in morphology expressed in Homo sapiens neanderthalensis. By comparing the functional morphology of the temporomandibular joint of Homo sapiens sapiens with that seen in Neandertals one can propose possible reasons for the differences in morphology exhibited.

CHAPTER II

TEMPORAL BONE MORPHOLOGY IN HOMO SAPIENS SAPIENS AND HOMO SAPIENS NEANDERTHALENSIS

I. INTRODUCTION

The temporal bone composes a portion of the lateral wall and base of the skull, and middle and posterior cranial fossae. Components of the middle ear and inner ear are housed within the temporal bone. Five components, including the squamous, tympanic, mastoid, petrous, and styloid portions, form the temporal bone. A detailed comparative analysis of temporal bone morphology in modern man and Neandertals is necessary to proceed with investigation of the meaning of the differences expressed. The following discussion of temporal bone morphology/osteology relates to that seen normally in Homo sapiens sapiens unless otherwise noted.

II. SQUAMOUS PORTION OF THE TEMPORAL BONE

The thin fan-shaped squamous portion forms the anterior and cranial portion of the temporal bone and dorsal wall of the temporal fossa. Anteroinferiorly the thickened border articulates with the greater wing of the sphenoid along the sphenosquamous suture. Superiorly the thin cranial border, bevelled medially, articulates with the parietal along the squamosal suture (Bass 1971). The lateral surface exhibits a smooth texture and convex configuration. Along the posterior portion extends

the temporal ridge providing attachment for the origin of the temporalis muscle.

Morphology of the squamous portion exhibited in Neandertals indicates distinct characteristics in comparison with that present in modern man. In Neandertals the squamous portion is thicker (as is characteristic of the Neandertal cranial bones in general) (Smith 1976; Suzuki and Takai 1970) yet smaller in vertical and horizontal dimensions than found in Homo sapiens sapiens. Conforming to the general Neandertal pattern, the temporal fragments from La Quina (Guth 1963; Vallois 1969) exhibit small yet very robust squama. The vertical plate extends more superiorly in the Gibraltar and La Quina (H-5, H-16, H-27) temporal bones than in Shanidar I, La Chapelle Aux Saints, and Le Moustier. The temporal bones from La Chaise Abri Bourgeois Delaunay (Mann and Trinkaus 1973) and Krapina C skull (Smith 1976) exhibit a squamous portion reduced in size. In Amud I the temporal squama is reduced yet fits within the lower range of variation present in Homo sapiens sapiens (Suzuki 1970). The temporal bone from La Chaise Abri Suard presents a thick squama and lower, less rounded squamosal suture. Curvature along the squamosal suture is more pronounced in Neandertals. The Gibraltar and La Quina material exhibit greater curvature along the superior border of the squamosal plate than seen in La Chapelle Aux Saints and La Ferrassie, indicating a range of variation exists within Neandertals regarding this characteristic (Guth 1963; Mann and Trinkaus 1973; Vallois 1969). The degree of curvature displayed in the temporal from Amud I fits within the lower range of that present in modern man.

Temporal squama representing the Mt. Carmel populations indicate an intermediate height and curvature between Neandertals and Homo sapiens sapiens (McCown and Keith 1939). One possible explanation for the lower squamous diameter and degree of curvature may be related to the doliocranic configuration of Neandertal crania (Angel 1972; Guth 1963; Smith 1976).

Projecting from the lower portion of the squama, the zygomatic process extends laterally and anteriorly to join the temporal process of the zygomatic bone forming the zygomatic arch. The cranial border is long, thin, and sharp providing attachment for the temporal fascia. The short, thick, arched caudal border and concave medial surface provide attachment for the masseter muscle. Three roots, including the anterior, middle, and posterior roots, join the zygomatic process to the temporal bone. Directed medially, the short broad anterior root terminates in the rounded articular eminence forming the anterior portion of the temporomandibular joint and anterior wall of the glenoid fossa. At the union of the anterior root and zygoma a tubercle is present affording attachment of the external lateral ligament. Separating the mandibular portion of the glenoid fossa from the external auditory meatus, the middle root terminates at the Glaserian fissure. Between the anterior and medial roots lies an oval depression comprising a portion of the deep glenoid fossa. The posterior root extends from the cranial border of the zygomatic process posteriorly over the external auditory meatus in the form of the supramastoid crest, forming the lower temporal ridge.

In Neandertals the zygomatic process is more massive and strongly developed than in Homo sapiens sapiens. Amud I, the adult Krapina

temporals, and La Quina H-16, for example, all present a prominent, massive zygomatic process. The transverse zygomatic root is thickened in Neandertals. The inferior border, marked by a small bulge, corresponds to the shallow glenoid cavity (Guth 1963). Extension of the cranial border in La Quina H-16 and Amud I forms a wide, deep zygomatic sulcus limited medially by a pronounced projection from the squama and laterally by the longitudinal root of the zygomatic process (Guth 1963; Suzuki 1970). Fibers of the temporalis muscle attach along this sulcus. The rugged external surface of the squama and large sulci evidence the powerful development of the temporalis muscle. Krapina 39-1 illustrates a robust zygomatic root which is continuous with the supramastoid crest (Smith 1976). La Ferrassie I shows a long, high, and prominently angled zygomatic arch (Heim 1974). According to Howells (1974) the anterior extension of the zygomaxillary suture assumes an extreme anterior position in Neandertals resulting in a more anterior origin of the masseter muscle.

Typical Neandertal external auditory meatus morphology indicates a more oval configuration directed anteriorly and superiorly than that normally seen in Homo sapiens sapiens. For example, the external auditory meatus preserved on the left temporal from La Quina is relatively small and presents an elliptical configuration with the long axis parallel to the supramastoid crest and lower border. Typical Homo sapiens sapiens morphology reveals a more rounded external auditory meatus. The right temporal bone from Darra-I-Kur (Angel 1972) presents a thickened rim encircling the external auditory meatus. Regularly

thickened throughout, the external auditory meatus of La Quina H-16 exhibits no exostoses. La Quina H-27, a right temporal bone, illustrates the typical Neandertal pattern in that the external auditory meatus shows an oblique orientation. Neandertal temporal bones from La Quina, Krapina C skull, La Chapelle Aux Saints, Darra-I-Kur, La Chaise Abri Bourgeois Delaunay, and La Chaise Abri Suard exhibit an elliptical external auditory meatus configuration. A range of configurational variation is expressed by the roundness of the external auditory meatus seen in Amud I, La Quina H-5, Krapina 39-3 (Smith 1976), Gibraltar, and La Ferrassie I (Heim 1974).

Anteriorly the glenoid fossa in Homo sapiens sapiens is formed by the articular eminence, and is bordered posteriorly by the tympanic plate separating the fossa from the external auditory meatus. The Glaserian fissure divides the glenoid fossa into two portions. The smooth mandibular portion, formed by the squamous portion of the temporal bone, is covered with cartilage and provides articulation with the mandibular condyle. Comprising the anterior aspect of the tympanus and external auditory meatus, the postglenoid process forms the posterior portion of the glenoid fossa. Formed primarily by the tympanic plate which terminates superiorly at the Glaserian fissure, the posterior portion of the fossa houses a portion of the parotid gland. Caudally, the tympanic plate comprises the vaginal process from which originates the tensor palati muscle. The Glaserian fissure leads into the tympanus and ". . . transmits the tympanic branch of the internal maxillary artery" (Pick and Howden 1974:66). Temporal arteries are transmitted through the posterior groove on the lateral surface.

Neandertal temporal bone morphology is characterized by a wide shallow glenoid fossa, well developed Glaserian fissure, and pronounced postglenoid process. The fossa is formed anteriorly by the articular eminence and posteriorly by the postglenoid process and a portion of the temporal squama (Guth 1963; Smith 1976). The internal border of the fossa is thickened. Hominid 16 from La Quina conforms to the basic Neandertal pattern (Vallois 1969). The large shallow oval glenoid cavity is characterized by its transverse orientation. Temporal bones from La Quina H-10 and H-27 (Guth 1963; Vallois 1969), La Ferrassie I (Heim 1974), and La Chaise Abri Bourgeois Delaunay (Mann and Trinkaus 1973) display wide shallow glenoid fossae.

Juvenile Neandertal morphology may be glimpsed in the juvenile temporal bones from Krapina. Krapina temporals 39-2, 39-3, and 39-4 depict very shallow glenoid fossae with ill-defined borders (Smith 1976). The fossae grade ". . . into the articular tubercle(s) almost without any slope" (Smith 1976:91). The diminished gradient may be due to the fact the articular eminence is not yet fully developed. The postglenoid processes are not prominently developed in the Krapina juveniles.

Amud I exhibits a deeper glenoid fossa than is seen in La Chapelle Aux Saints and Shanidar thereby displaying an intermediate depth between most Neandertals and Homo sapiens sapiens (Suzuki 1970). The gradient between the fossa and articular eminence is also more pronounced in Amud I than is typical for Neandertals.

The postglenoid process is very prominent in the right temporal, H-27 from La Quina, Krapina 38-1 and 39-14, and Amud I. Illustrating

characteristic Neandertal morphology the Krapina C temporal bone displays a short, wide, and shallow glenoid fossa (Smith 1976). Separating the roof of the glenoid cavity from the endocranial surface is a thickened bony plate in Neandertals whereas Homo sapiens sapiens exhibit a very thin bony plate. Anteriorly the fossa in the Krapina C temporal presents a gentle curvature sloping into the articular eminence. Forming the posterior fossa wall is the moderately pronounced postglenoid process (Smith 1976). The steep medial fossa wall is formed by a projection of the temporal bone which is also seen in La Chapelle Aux Saints, Tabun I, and Gibraltar fossae (Smith 1976). In Homo sapiens sapiens the medial fossa wall is formed by the spina angularis of the sphenoid bone (Smith 1976). Temporal 39-1 from Krapina also indicates this morphological pattern (Smith 1976). Forming the posterior fossa wall are the pronounced postglenoid process and thick anterior portion of the tympanic ring. The Glaserian fissure separates the thick tympanic ring from the posterior fossa wall (Smith 1976).

General Neandertal temporal bone morphology is characterized by the prominently developed postglenoid process contributing to the formation of the posterior portion of the mandibular fossa. For example, the left temporal bone from La Quina reveals a prominently developed postglenoid process, more so than that seen in La Chapelle Aux Saints (Guth 1963). Whereas all Neandertals exhibit prominent postglenoid processes, there is a range of developmental variation present as exhibited by these two specimens.

III. TYMPANIC PORTION OF THE TEMPORAL BONE

The tympanic portion of the temporal bone, formed by a thin bony plate concave anteriorly and inferiorly, lies anterior to the styloid and mastoid processes and inferior to the squama. The posterosuperior surface fuses with the petrous portion forming the floor, anterior and inferior walls, and a portion of the posterior wall of the external auditory meatus (Hollinshead 1974; Bast and Anson 1949; Anson and Donaldson 1967). Forming the remaining portion of the canal is the squama. The external auditory meatus leading to the tympanus, is present in the basal portion of the lateral aspect of the petrous portion. The opening to the external auditory meatus is bounded by the tympanic margin. Attaching to the lateral free border is the cartilaginous portion of the external auditory meatus (Bast and Anson 1949). Medially the tympanic portion presents a depression along which tympanic membrane attaches. Along the posterior aspect the tympanic portion unites with the squama and mastoid portion forming the anterior extension of the tympanomastoid fissure. The tympanosquamous fissure may be noted posterior to the mandibular fossa and anterior to the lateral aspect of the tympanic portion. The superior border fuses laterally behind the postglenoid process.

Developing from membrane, the tympanic portion possesses one ossification center. At birth, the tympanic portion ". . . consists of a ring of bone (anulus tympanicus or tympanic ring) incomplete above . . .; after birth the lower part of the ring expands medially,

laterally, and downward to form the tympanic plate visible on the base of the skull" (Hollinshead 1974:812).

Neandertals exhibit a much thicker tympanic plate than do Homo sapiens sapiens (Smith 1976). The anterior portion of the tympanic plate is oriented more vertically and the posterior portion less robust in the early Neandertals. Classic Neandertals exhibit a more horizontally oriented tympanic plate. Both the anterior and posterior portions are large and robust. Amud I and Krapina 38-11 present thick tympanic plates in the posterior half as is common in Neandertals. The vaginal ridge (near the middle of the inferior surface), commonly found in Neandertals like La Chapelle Aux Saints and Shanidar, is absent in the Amud I temporal. Caudally the broad, rough tympanic plate exhibits two parallel crests. The anterior crest divides the tympanic plate into anterior and posterior portions. Extending outward the posterior crest joins another crest extending lateral to the stylomastoid foramen (Suzuki 1970) which is equivalent to the crest found on the tympanic plate in Homo sapiens sapiens. In this respect, the Amud I temporal morphology does not differ from modern man. Krapina temporal 39-3 (a juvenile) possesses a thin tympanic plate (Smith 1976). In the Darra-I-Kur temporal the tympanic bone terminates medially in a scroll-like process inferior to the Eustachion and tensor tympani semicanal openings (Angel 1972). Homo sapiens sapiens do not show this morphological pattern. Originating from the tympanic bone is the tendon of the levator veli palatine muscle. Angel (1972:55) hypothesizes the scroll-like process ". . . is for a tendon of origin for the levator veli

palatini, one of the muscles which helps to open the Eustachian tube to equalize middle-ear and outside atmospheric pressures in altitude change such as occurs in this eastern part of Afghanistan." The petrotympanic fissure is large in comparison with modern man but the range of Neandertal variation regarding the size of the fissure is not known to date.

IV. MASTOID PORTION OF THE TEMPORAL BONE

The mastoid portion forms the posterior aspect of the temporal bone. The roughened external surface provides attachment for the occipitalis and auricularis posterior muscles. Ventrally and cranially the mastoid portion fuses with the squama while caudally the portion contributes to the formation of the external auditory meatus and tympanic cavity. Superiorly, the broad serrated border of the mastoid portion articulates with the parietal along the parietomastoid suture. Posteriorly, the serrated border articulates with the inferior border of the occipital via the occipitomastoid suture. Along the posterior border is located the large mastoid foramen through which pass veins and arteries to the dura mater. Numerous small foramina transmitting blood vessels throughout the area are located on the lateral surface. Posterosuperior to the external auditory meatus is a sharp bony crest, the suprameatal spine. Posterior to the suprameatal spine is a depressed area, the mastoid fossa. The mastoid portion continues caudally in a thickened conical projection, the mastoid process, which provides attachment for the sternocleidomastoideus, splenius capitis,

and longissimus capitis muscles. Internally, the mastoid process is composed of cellular spaces, the mastoid cells, varying in size and number which develop fully following puberty. In the anterosuperior portion the large irregular cavity, the tympanic antrum, contains air cells whereas posteriorly and caudally the cells, decreased in size, contain marrow. Mucous membrane lines the tympanic antrum and mastoid cells. A deep groove, the mastoid incisure, extends along the inferomedial surface of the mastoid process providing attachment for the origin of the digastric muscle. Medial to the mastoid incisure is a shallow furrow, the occipital groove, for transmission of the occipital artery (Bast and Anson 1949). A deep curved groove, the sigmoid sulcus, extends along the medial surface for transmission of the sigmoid venous sinus of the dura mater. The mastoid process, the bony projection dorsal to the external auditory meatus, forms ". . . the posterior end of the petrous portion of the temporal bone . . ." (Hollinshead 1974: 792).

The mastoid portion in Neandertals exhibits differences when compared to that in Homo sapiens sapiens. Morphological differences expressed in the mastoid portion of Neandertals include the smaller weakly developed mastoid process positioned relatively higher on the mastoid portion, and prominent supramastoid ridge extending cranially over the entire process (Alexeyev 1976; Guth 1963; Heim 1974; Howell 1957; LeGros Clark 1964; Mann and Trinkaus 1973; Smith 1976; Stringer 1974; Vallois 1969). The total mastoid portion is large and robustly developed in Neandertals in general (Guth 1963; Mann and Trinkaus 1973;

Smith 1976; Vallois 1969). Pronounced development is also noted in the mastoid portion of the adult right temporal from La Quina (Vallois 1969); the mastoid process is small but strongly marked by muscle attachments, a typical feature of Neandertals in general (Smith 1976). The mastoid processes of the left temporal from La Quina, Krapina 39-1, and Krapina C (Smith 1976) do not project beyond the cranial base, a pattern characteristic of Neandertals but not Homo sapiens sapiens. Temporal fragments from Krapina, 38-13, 39-3, and 39-14, exhibit mastoid processes extending below the cranial base (Smith 1976) indicating there is a range of variation present in Neandertals. Moderate pneumatization, noted on the La Quina temporal, is also seen in the temporal bone from Spy but not in La Chapelle Aux Saints or La Ferrassie (Guth 1963). In comparison with a Homo sapiens sapiens temporal of the same age the juvenile Staroselye temporal bone is small and the mastoid process weakly developed (Alexeyev 1976).

The supramastoid crest is normally much more strongly pronounced in Neandertals than in more modern crania (Smith 1976). In La Quina H-16, for example, the large, blunt supramastoid crest is raised forming the anterior supramastoid tubercle prior to meeting the posterior border of the vertical plate (Guth 1963). Bordering the mastoid process are two crests: a superior crest extending parallel to the supramastoid crest where the sternocleidomastoid muscle inserts and the inferior large, deep digastric sulcus (Guth 1963). Krapina 38-11 and Krapina C both display a wide, deep digastric sulcus (Smith 1976). Shanidar I (Solecki 1960; Stewart 1964), the juvenile temporal from Krapina, 39-3, and Amud III show a very deep digastric sulcus.

A narrow moderately deep digastric sulcus is seen in Krapina temporal 39-14, while temporal 38-1 shows a wide and shallow digastric sulcus (Smith 1976). Juvenile Krapina temporal 39-4 has a deep and narrow digastric sulcus (Smith 1976). Indicating the variability expressed in Neandertals the digastric groove on the Krapina 39-1 temporal is wide but not deep (Smith 1976). In Neandertals the digastric sulcus is usually wider and deeper than in Homo sapiens sapiens. In between these two crests the roughened surface provides attachment for the strongly developed splenius capitis muscle. In modern man the inferior aspect of the mastoid portion remains free from the mastoid area. This zone (for the attachment of the splenius capitis and sternocleidomastoideus) is reduced in Neandertal (Vallois 1969). Considering the robust morphology of Neandertal crania one would expect to see large mastoid processes for supportive muscle attachments. However, generally Neandertal mastoid processes are small and non-projecting although a range of variation is noted. Smith (1976:97) hypothesizes that

. . . mastoids act to shift attachments of the sternocleidomastoids forward to aid in turning and balancing the head. It is possible that the expansion of the occipital area made the additional attachment area on the mastoids unnecessary, and/or the relationship of the sternocleidomastoid insertion to the axis of the skull was different in Neanderthals.

V. PETROUS AND STYLOID PORTIONS OF THE TEMPORAL BONE

The petrous portion of the temporal bone is the dense pyramidal shaped process wedged between the sphenoid and occipital bones forming a portion of the posterior cranial floor adjacent to the occipital bone.

Directed medially, anteriorly, and slightly upward (Bast and Anson 1949), the petrous portion houses the components forming the inner ear. The petrous portion including the mastoid process develops from cartilage and

. . . is ossified about the internal ear from four centers that fuse together (but at birth, although most of the petrous part of the temporal bone is well formed, the mastoid process is a mere nubbin; it develops as an inferior projection at the time of puberty, when the mastoid air cells develop) [Hollinshead 1974:812].

The anterior surface, continuous with the endocranial surface of the squamous portion, contributes to the formation of the posterior portion of the middle cranial fossa which is marked by depressions corresponding to the convolutions of the brain. Laterally the anterior surface articulates with the squama along the petrosquamous suture.

The posterior surface, representing an almost vertical plate, is continuous with the inner surface of the mastoid portion and forms the anterior wall of the posterior fossa. Along the cranial border at the superior angle, lies the sulcus for the superior petrosal sinus located in the margin of the cranial dura mater. Caudally, along the posterior angle, the petrous portion articulates with the occipital. Between the base and anterior angle is the circular opening of the internal acoustic meatus which transmits facial and acoustic nerves and the internal auditory branch of the basilar artery (Anson and Donaldson 1967; Bast and Anson 1949).

Presenting a roughened irregular inferior surface the petrous portion forms a portion of the exterior skull base and provides partial attachment for the levator veli palatini muscle. In conjunction with

the occipital bone the inferior surface forms the jugular fossa and foramen.

Anterior to the jugular fossa along the basal aspect of the petrous apex is the opening of the carotid canal through which pass the internal carotid artery, veins, and sympathetic nerves (Hollinshead 1974).

On the lateral aspect of the jugular surface, directed caudally is a slender bony projection, the styloid process. Located between the styloid and mastoid processes, the stylomastoid foramen is the external opening of the facial canal through which pass the facial nerve and stylomastoid artery. Originating from the styloid process are the stylopharyngeus, stylohyoideum, and styloglossus muscles and the stylohyoid and stylomandibular ligaments.

Morphology of the petrous portion in Neandertals is not well known. It appears to be larger and thicker than the petrous process seen in Homo sapiens sapiens. The Krapina C temporal preserves a thicker, more robust petrous portion than is characteristic of modern man (Smith 1976). A large arcuate eminence and pronounced sigmoid sulcus are noted on the thickened, robust petrosal area. The petrous portion of Krapina 39-1 is fragmented yet all indications suggest the portion was probably thick (Smith 1976). Internally the Amud I petrous pyramid is characterized by a low, roughened internal surface typical of Neandertal morphology. The internal surface is broader than that found in modern man. Anterior and medial to the circular arcuate eminence the surface is depressed. Near the anterior border the sulcus for the superior petrosal nerve is very wide and similar to the deep sulci present in the Krapina temporals. In

Amud I and Amud III the sulcus for the superior petrosal sinus is very broad relative to the size of the petrous pyramid (Suzuki 1970). In Amud I the posterior surface of the pyramid is lower than in Homo sapiens sapiens and exhibits an almost vertical orientation. The pyramid of the petrous portion preserved in the left temporal from La Quina is massive. The crest of the petrous portion, formed by the inferoposterior portion of the squamous, terminates in the vaginal process (Guth 1963). The left temporal from La Quina indicates the vaginal process constitutes the posterior extremity of the petrous crest (Guth 1963). In Homo sapiens sapiens this portion extends laterally over the stylomastoid foramen due to the posterior bony expansion. This portion is absent on the La Quina temporal so that comparison is not possible. The superior surface of the petrous portion of the Darra-I-Kur temporal shows

. . . a barely discernible edge anteriorly for the tegmen tympani (roof of the middle ear) where it joins the squamous plate, a very large double hiatus of the facial canal (for greater superficial petrosal branch of VII and superior tympanic or petrosal branch of the middle meningeal artery) and a puffed up expansion of bone over the arcuate eminence for the superior semicircular canal [Angel 1972:55].

The area between the mastoid antrum and petrous tip contains air cells (Angel 1972). Along the medial wall of the petrous pyramid is noted the very large opening of the internal acoustic meatus. In the Darra-I-Kur temporal the internal acoustic meatus is nearly three times the size of the canal in Homo sapiens sapiens (Angel 1972). However, the internal acoustic meatus on the Krapina C temporal is the same size as seen in modern man (Smith 1976). Conforming to characteristic Neandertal

morphology, the sigmoid sinus groove in Darra-I-Kur is wide and deep. Inferiorly the stylomastoid, jugular, and carotid foramina are comparable in size and form to those present in Homo sapiens sapiens (Angel 1972). Krapina C conforms to the pattern exhibited by modern man with reference to the form and location of the jugular fossa, carotid foramen, and vaginal process (Smith 1976). A sharp delineation of the triangular fossa (for the ninth cranial nerve) and cochlear aqueduct is noted on the Darra-I-Kur petrous portion. In comparison with modern man the left temporal from La Quina preserves a very gracile styloid process and relatively large stylomastoid foramen. The Darra-I-Kur temporal does not preserve the styloid process. However, according to Angel (1972: 54) "... the sharp-edged and quite high (13 mm.) tympanic plate makes a 3 mm. deep by 6 mm. wide excursion for the styloid process so that this must have been robust."

Internally the temporal bone presents a concave surface marked by a series of irregular depressions corresponding to the convolutions of the temporal lobe of the brain (Bast and Anson 1949). Arboriform grooves transmit branches of the middle meningeal arteries to the dura mater (Bast and Anson 1949).

While sharing certain morphological characteristics of the temporal bone with Homo sapiens sapiens, the endocranial surface of the Neandertal temporal bone expresses morphological differences (Debénath 1977; Vlček 1958). An endocranial stone cast of the brain from Gánovce (Vlček 1958) indicates the cranium was very low and the brain basically symmetrical with some noted irregularities in the temporal lobes and

prolonged occipital lobes. Both sigmoid sinuses are present, the left sinus being larger than the right. The course of the venous sinuses can be followed along the endocast. The superior sagittal sinus exhibits an "S"-shaped curvature. Impressions of the *juga cerebri* are noted only on the temporal lobes. Impressions from the cerebral arteries are also present on the inferior aspect of the right temporal lobe (Vlček 1958).

Internally the skull base or cranial floor is divided into three levels. The anterior cranial fossa is the highest level and forms the orbital roofs. At a somewhat lower level, posterior to the anterior cranial fossa, lies the middle cranial fossa. The deep, lateral aspects of the middle cranial fossa ". . . are separated from the anterior fossa by sharp ridges of bone, often known as the 'sphenoid ridges,' but are united across the midline by a narrower and higher portion (the *sella turcica*) . . ." (Hollinshead 1974:803). The posterior cranial fossa, the lowest and most posterior of the three levels, is located around the circumference of the foramen magnum. The petrous ridges separate the middle and posterior cranial fossae.

A comparative osteological analysis of the temporal bone in *Homo sapiens sapiens* and *Homo sapiens neanderthalensis* indicates distinct differences in morphology. Specifically the differences include the size, curvature and thickness of the vertical squamous, configuration and position of the external auditory meatus, robustness of the zygomatic process, position and development of the mastoid process, degree of postglenoid process development, thickness of the tympanic plate and petrosal area, development of the supramastoid crest,

morphology of the digastric sulcus and fossa, formation of the medial glenoid fossa wall, prominence of the articular eminence, and depth of the glenoid fossa.

The significance of the morphology of these characteristics exhibited by Neandertals is not fully understood to date and certainly to attempt to deal with all of these is beyond the scope of this thesis. Thus, while it is necessary to have reviewed all of the difference in temporal bone morphology between Homo sapiens neanderthalensis and Homo sapiens sapiens and to be aware that the development and functioning of all are somewhat interrelated, it is now desirable to focus attention on the area of specific concern here. The remainder of the thesis will concentrate on the glenoid fossa and its immediate surroundings in an attempt to understand the differences in this area between Neandertals and modern man. From the standpoint of the gross aspects of hard tissue morphology alone, it would appear that the entire fossa may be adapted to resisting shearing and compressive stresses in Neandertals and not just the anterior portion of the fossa (specifically the articular tubercle) as is the case in modern man. It is tempting to explain such features as the generally thick fossa roof, large postglenoid process, and thick tympanic ring in Neandertals in this light. However, before this explanation can be accepted it will be necessary to investigate certain other factors relating to this possibility.

CHAPTER III

TEMPOROMANDIBULAR JOINT STRUCTURE IN HOMO SAPIENS SAPIENS

I. INTRODUCTION

Functional explanations for certain of the differences, specifically those relating to the form of the Neandertal temporomandibular joint in comparison with Homo sapiens sapiens, may be suggested upon analysis of the joint structure and biomechanical functions characterizing the temporomandibular joint in modern man and then extrapolating back to Homo sapiens neanderthalensis. However, it is clearly recognized the inherent problems involved with this approach. The human paleontologist does not have the advantage of studying soft tissue morphology but only hard tissue morphology. In light of this problem we can only assume a similar configuration of soft tissue anatomy persisted in the Neandertal temporomandibular joint region realizing that variation may have been present, but this the human paleontologist will never know for certain.

The temporomandibular joint is a highly integrated, functionally complex system involving the (1) osteological components of the joint region, (2) dentition, (3) articular capsule and meniscus, and (4) corresponding ligaments and muscles of mastication necessary for efficient biomechanical functioning. Moss (1959a:73) notes, "At the outset it must be stressed that a full understanding of the functional anatomy of this joint is not possible from the examination of a skeletal

preparation alone." Moss emphasizes that soft tissues contributing to joint function need also to be considered. In order to understand any facet of this integrated system, it is necessary to first view the system as a synergistic whole. One needs to have a basic understanding of the (1) structure of the temporomandibular joint region, (2) location and function of the masticatory muscles, (3) biomechanics of joint motion, and (4) interrelatedness of these components, prior to hypothesizing the functional basis for the variation seen in any one facet of the functional complex. A discussion of these factors is necessary to judge whether or not the central (mandibular fossa) and posterior (postglenoid process) portions of the temporomandibular joint are functional, stress-bearing areas in Neandertals.

II. THE TEMPOROMANDIBULAR JOINT AS A DIARTHRODIAL JOINT

Architecture of the temporomandibular joint is structured to permit a wide range of mandibular movements. As such, the human temporomandibular joint is classified as a diarthrodial or freely moveable synovial joint. Joints classified as diarthroses share certain characteristics (Moss 1959a; Dempster 1955) which include the following: (1) articular surfaces with diagnostic configurations such as convex (male) and concave (female) articular surfaces, (2) contiguous but not necessarily congruous articular surfaces, (3) tissue resistant to compressive forces overlying articular surfaces, and (4) ligamentous attachments such as to enhance free motion.

Each temporomandibular joint articular surface has a diagnostic shape. Cranially, the articular surfaces are composed of the convex

(male) articular eminence and the ellipitical mandibular fossa concave (female) anteroposteriorly and laterally. Forming the inferior articular surface, the oblong condyloid process of the mandible presents a convex posterior articular surface and a concave anteroinferior surface. According to Naylor (1960) and Wheeler (1965) the restricted articular surface of the condyle is convex on all bearing surfaces. In order to facilitate movement and reduce friction, the articular surfaces of the joint area are incongruous (Kraus et al. 1969; Wheeler 1965). The intervening articular disk or meniscus ". . . compensates functionally for this incongruity" (Moss 1959a:75).

The temporomandibular joint differs from other diarthroses in that thick fibrous connective tissue rather than hyaline cartilage overlies the articulating surfaces (Boucher 1962; Kraus et al. 1969). The most superior portion of the condyloid process of the mandible, the posterior margin, is covered with avascular fibrous tissue (Figure 4). The presence of fibrous connective tissue suggests the articular surfaces are not static weight-bearing structures (Kraus et al. 1969). In most synovial joints the articulating surfaces are covered with smooth cartilage which permits motion with reduced friction and elasticity. During motion the intervening cartilage functions to absorb shock. Whereas cartilage is resistant to compressive forces and adapted to withstand both pressure and pull (Hollinshead 1974), fibrous connective tissue is adapted to withstand shearing forces (Hollinshead 1974; Leeson and Leeson 1970; Moss 1959a). Lateral mandibular movements generate shearing forces on the joint surfaces. However, according to Moss (1959a:76) the

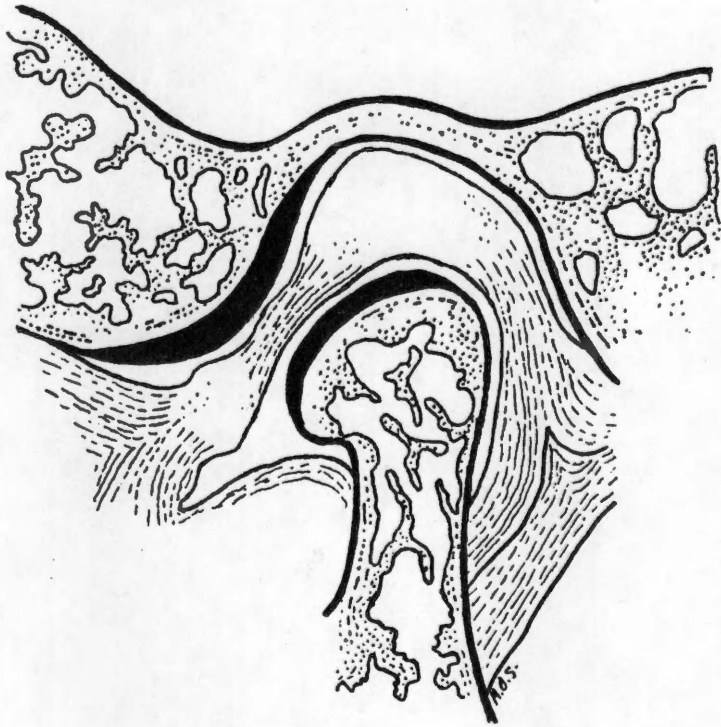


Figure 4: Diagram of the bony components of the temporomandibular joint. Blackened area indicates aspects of joint overlain by avascular fibrous tissue.

Diagram courtesy of Maria O. Smith.

. . . lack of dense fibrous tissue in the depths of the articular fossa and its presence along the posterior portion of the articular eminence emphasizes the fact that during function the fossa is not really a part of the temporomandibular articulation [Figure 4, page 31].

The anterior portion of the temporomandibular joint, specifically the thickened bony articular eminence, is structured to withstand shear force vectors generated during chewing motions.

Morphological analysis of the mandibular fossa reveals that the cranial portion of the fossa is composed of a thin bony plate thus suggesting pressure/stress is not being exerted on the fossa roof (Kraus et al. 1969; Yuodelis 1966a). Therefore both the presence of vascular tissue and the thin bony mandibular fossa roof suggest the mandibular fossa itself is not structured to withstand stress (Kraus et al. 1969; Robinson 1946; Yuodelis 1966a). The mandibular fossa appears to be simply the "resting place" for the articular disk and mandibular condyle whereas the functional articular surface of the temporal components of the joint is the articular eminence.

The arrangement of the capsular, temporomandibular, sphenomandibular, and stylomandibular ligaments in the temporomandibular joint region facilitates motion (Jamieson 1962). The fibrous ligaments reinforce the joint capsule medially and laterally. Naylor (1960:1038) notes that:

Each condyle, with its interarticular fibrocartilage, is suspended loosely in the glenoid fossa by the four parts of the capsular ligament (which includes the anterior, posterior, external lateral, and internal lateral bands of fibrous connective tissue). The capsular ligament is the only ligament within the fossa and the only ligament directly concerned with movement in the fossa. (The sphenomandibular and stylomandibular ligaments suspend the mandible as a unit from the base of the cranium and function to limit extreme movement of the mandible.)

The loose fibrous arrangements within the anterior and posterior portions form the inner portion of the capsule permitting the condyle to move within the fossa and limiting extreme protrusive and retrusive mandibular movements. Completely surrounding the condyloid process of the mandible, the capsular ligament of the joint capsule is the superior ligament encasing the joint. Fibers from the meniscus and capsular ligament merge along the periphery forming the superior and inferior portion of the joint. When the mandible is depressed, the upper portion or compartment slides anteriorly and caudally to the articular eminence in order to permit the articular disk to shift into position and stabilize the mandibular condyle, which has shifted inferior to the articular eminence (Figure 5). The caudal portion or compartment extends downward along the posterior aspect of the condyle.

Forming the external aspect of the capsular ligament, the temporomandibular ligament functions to (1) strengthen the lateral aspect of the capsule to which it attaches (Boucher 1962), and (2) suspend the mandible within the fossa during initial hinge movements when condylar movement is slight. As the mandible is further depressed the condyles are required to move forward more rapidly thus relaxing the temporomandibular ligament as the internal lateral capsular ligament, the sphenomandibular ligament, tautens. The sphenomandibular and stylomandibular ligaments do not limit retrusive motion but aid in the limitation of lateral and protrusive movements (Jamieson 1962). Together, the temporomandibular and sphenomandibular ligaments act as suspensatory ligaments. According to Hollinshead (1974:35) ligaments

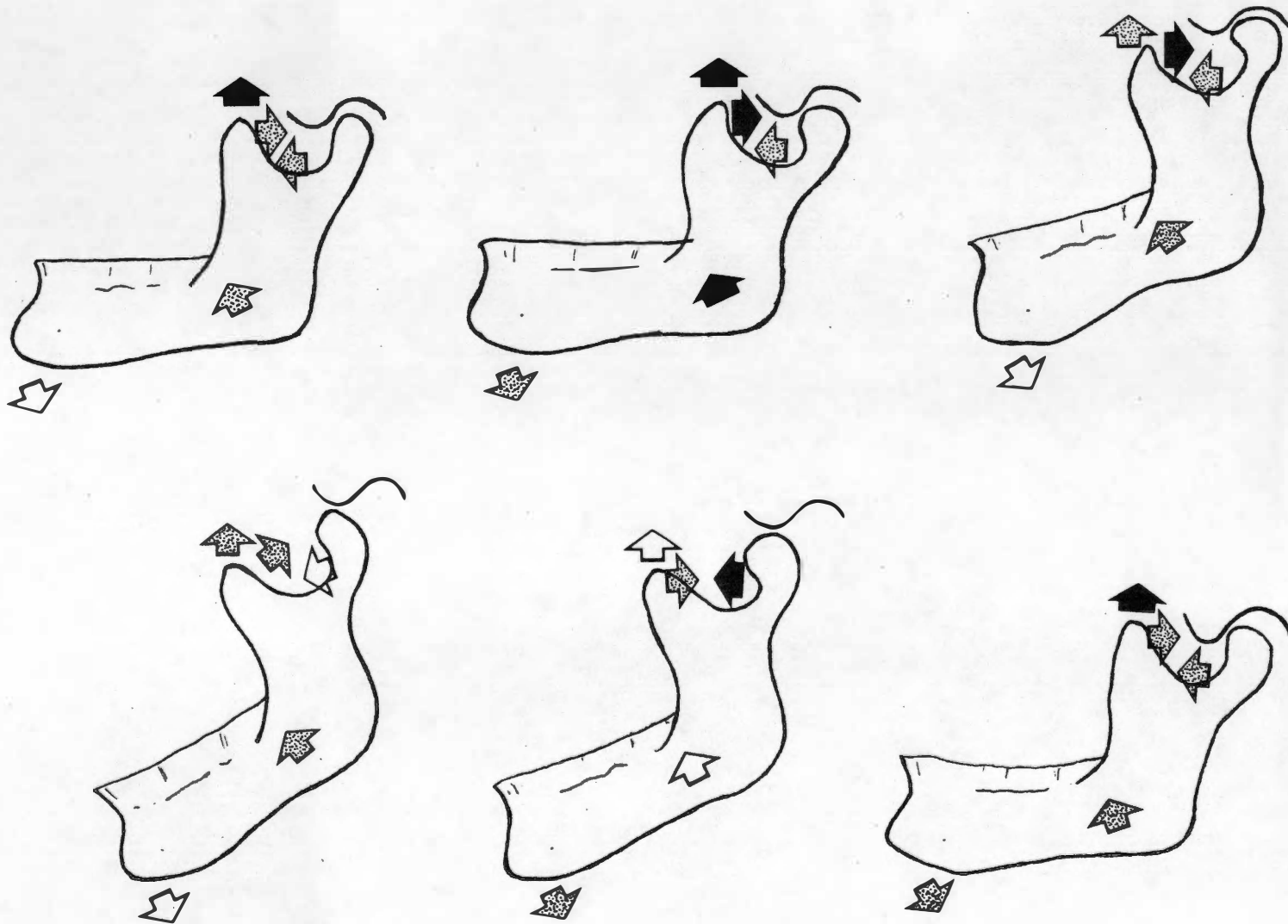


Figure 5: Drawing illustrates the basic biomechanical movements of the mandible during motion. (After Kraus et al. 1969). Drawing courtesy of Maria O. Smith.

. . . that check movements often do so as the joint reaches the most stable position, and as a consequence of being most taut in this most stable position they frequently play a very important role in stabilizing the joint.

Ligaments guide mandibular movements. For example, as the mandible is depressed, the condyle rotates and moves forward on the caudal surface of the articular disk, the disk moving forward with the condyle. At the point where the ligaments become taut the condyle begins to swing forward and downward in order to continue movement. The disk is drawn forward between the articular eminence and mandibular condyle. The disk then rests at the location affording maximum contact between the articular surfaces and stabilization for the mandible.

III. FUNCTIONAL REQUIREMENTS OF A DIARTHROSIS

The temporomandibular joint conforms to the functional requirements of a diarthrosis (Moss 1959a) which include the following characteristics: (1) during motion the joint requires stabilization of its freely moving components, and (2) the joint morphology must be such that each component is capable of free motion during related muscle activity. The joint is stable when the teeth are occluded and the mandible is in a state of physiologic rest. During motion the mandible is momentarily stabilized by muscle activity. For example, during chewing motions stabilization of the mandibular condyle in articulation with the articular eminence is necessary. Moss (1959a:76) states:

When a solid or semisolid object is placed between the opposing jaws and a shearing or compressive force is exerted on this object it is necessary that the joint remain, for the moment, quite stable; otherwise the object would slip out from between the jaws.

Stabilization is maintained by neuromuscular coordinating mechanisms, joint morphology, and anatomy of the articular disk (orientation of the disk fibers and disk configuration) (Moss 1959a; Rees 1954). As the mandible protrudes to achieve edge-to-edge bite, the articular disk slides over the condyle as it is carried onto the articular eminence to aid in joint stabilization. The external pterygoid muscle, the only muscle which attaches to the disk, contracts only when the meniscus is required to stabilize the mandibular condyle. However, an edge-to-edge bite is characteristic of Neandertals. Therefore, the mandibular condyle may not have to glide forward onto the articular eminence to achieve functional dental occlusion. At the same time, the shallowness of the anterior margin of the Neandertal mandibular fossa (Smith 1976) may reduce the degree to which the mandibular condyle must move in order to create functional articulation with the articular eminence.

The temporomandibular joint morphology permits freedom of motion including movements of opening, closing, protrusion, retrusion, and lateral displacement. The limitations of these movements are determined by the joint morphology, ligaments, and muscles. It should be noted that

. . . only at the extreme limits of normal motion . . . [do] the connective tissues of the ligaments and muscles begin to exceed their normal physiologic tensile limits. As the tensile limits of the ligaments are reached, the stretch receptors in the tendons of the muscles begin to transmit painful sensations to the central nervous system [Moss 1959a: 79].

Composed of dense, tough fibrocartilage, the articular disk maintains separation of the condyle and fossa at all times. When viewed

from the cranial aspect the articular disk is ovoid in outline. The caudal surface is concave in order to accommodate the shape of the underlying condyle. In order to compensate for the configuration of the mandibular fossa the cranial surface of the articular disk is convex. However, it should be noted the articular disk alters shape as it shifts position during mandibular movements in order to fill the spaces generated between the moving articular surfaces and to promote smooth articulation and movement.

Three distinctive zones contribute to the formation of the articular disk: a thick posterior band, a thinner intermediate zone, and a somewhat thicker anterior band (Figure 4, page 31). Both the anterior and central zones of the articular disk are avascular, thereby indicating that considerable pressure is exerted on these aspects of the articular disk (Kraus et al. 1969; Robinson 1946) during mandibular movement. The posterior zone of the articular disk exhibits vascularization. Should stress be transmitted through the posterior zone the small blood vessels would be damaged (Kraus et al. 1969; Robinson 1946).

The articular disk attaches caudally, medially and laterally to the medial and lateral poles of the condyle which affords greater mandibular flexibility during movements of protrusion and retrusion. During movements involving lateral displacement, the condyloid attachment permits the articular disk to twist slightly on the condyle (Kraus et al. 1969). The articular disk loosely attaches to the posterior aspect of the articular capsule while presenting a strong attachment to the anterior portion of the capsule ". . . where part of the tendon of

the lateral pterygoid muscle blends with it" (Hollinshead 1974:836). Along its posterior border the articular disk attaches to a layer of vascular connective tissue covered with synovial membrane. The presence of vascular tissue in the posterior portion of the temporomandibular joint indicates this area of the joint does not receive stress. Boucher (1962:467) states:

The differentiation of islands of cartilage in the fibrous layer (present on the posterior slope of the articular eminence), and, more rarely, in the disk occurs, as a rule, in higher age periods and can be regarded as a response of the tissue to pressure and friction.

The avascular pattern exhibited by the meniscus in modern man suggests stress is being transmitted through the anterior and central zones of the articular disk as it is pulled forward over the mandibular condyle and onto the articular eminence during functional activity. However, the vascular pattern present in the posterior zone of the meniscus suggests the fossa roof and posterior portion of the mandibular fossa do not receive stress vectors during motion.

During the initial phases of protrusion of the mandible, the meniscus and condyle move forward (Higley 1940) ". . . either because of the pull of the lateral pterygoid muscle or because of the strength of the capsule attaching it to the mandible . . ." (Hollinshead 1974:836). During mandibular movements the condyle slides forward on the anterior band of the disk as it begins to glide out of the fossa onto the articular eminence. As the mandible moves the articular disk shifts position in order to conform to the altered spaces generated by the movement. The configuration of the articular disk

. . . creates reciprocal and essentially congruous surfaces on both the upper and lower joint cavities. In function then, both the head of the condyle and the articular eminence of the temporal bone are in contact not with each other but with the opposing surface of the meniscus [Moss 1959a:76].

The articular disk cushions the surface between the condyle and articular eminence when the condyle rests against the tubercle. When in this position the intermediate portion of the articular disk, which is avascular and devoid of nerves is located between the eminence and condyle and is compressed (Moffett 1957). The thinness of the intermediate zone permits the articular disk to flatten and become more curved to conform to the corresponding surfaces.

In the temporomandibular joint the fibrocartilaginous disk thus functions to (1) divide the synovial joint into two cavities, a superior cavity composed of the temporal elements (the mandibular fossa, articular eminence, and cranial surface of the meniscus), and an inferior cavity composed of the caudal aspect of the meniscus and the mandibular condyle (Moffett 1957; Naylor 1960); (2) absorb shock; (3) stabilize the joint components; (4) facilitate gliding movements; and (5) lubricate the joint.

A discussion of the soft tissue contributing to the joint region must also include a brief review of the muscles of mastication, including the temporalis, masseter, internal and external pterygoid muscles. These muscles contract whenever the mandible is in motion.

The fan-shaped, radiate temporalis muscle functions primarily to (1) exert an upward pull on the mandible, and (2) act in the capacity of a retruder muscle to pull the mandible backward (Crouch 1965: Kraus

et al. 1969; Pansky and House 1969). The primary function of the thick, quadrangular masseter muscle is to exert pull upward and forward on the mandible during closing movements. Functioning primarily to close the mandible, the internal or medial pterygoid muscle acts synergistically with the masseter muscles forming a mandibular sling which suspends the gonial angle of the mandible. When the internal pterygoid and masseter muscles contract the mandible moves using the temporomandibular joint as a guide (Crouch 1965). During grinding movements the medial pterygoid muscle functions to pull the mandible to the opposite side (Crouch 1965).

Categorized as a depressor muscle, the lateral or external pterygoid muscle functions mainly to depress, protrude, and rotate the mandible by moving the condyles forward, thus permitting hinge activity in the inferior joint cavity (Wheeler 1965). During mandibular protrusion, a translatory movement in which all portions of the mandible are moving in the same direction at the same rate (Naylor 1960), the external pterygoid muscle pulls the condyle and articular disk forward ". . . so that they slide downward along the sloping posterior surface of the articular eminence" (Moffett 1957:22). The working limit of mandibular protrusion is achieved when the mandibular incisal edges contact the maxillary incisal edges (Naylor 1960). Closing the mandible relaxes the external pterygoid muscle as the mandibular condyle and articular disk resume the rest position located more superiorly on the dorsal aspect of the articular eminence (Moffett 1957). Acting alternately with the external pterygoid muscle on the opposite side of the mandible, the external pterygoid muscles produce side to side

movements necessary during grinding motions. Contraction by one external pterygoid muscle produces lateral movements of displacement (Naylor 1960). The external pterygoid muscles, the only muscles capable of both protrusive and lateral movements,

. . . are responsible for placing the mandible in positions from which the crushing of food is performed by the masseter, temporal, and internal pterygoid muscles when they return the mandible to centric relation (mandibular position during deglutition) [Naylor 1960:1040].

When the mandible is in a protruded or lateral position the external pterygoid muscle acts to stabilize the articular disk.

The primary actions of each of the masticatory muscles is important in understanding the functioning of the masticatory system as a whole because the ". . . muscles of mastication exert great force" (Pansky and House 1969) and propose limitations of mandibular movements. The arrangement and function of each of the muscles of mastication are directly related to the bony structures involved in mastication. For example, the muscles exert force during mastication which is transmitted through the mandibular condyle and articular eminence of the temporomandibular joint.

IV. THE BIOMECHANICS OF JOINT FUNCTIONING

Movements of the temporomandibular joint may be of two basic types, rotation and/or translation. Movements involving rotation take place in the lower story of the temporomandibular joint with the axis of rotation passing through the condylar head (Moss 1959A) (Figure 6). Translatory movements involve a sliding motion in the upper joint cavity and

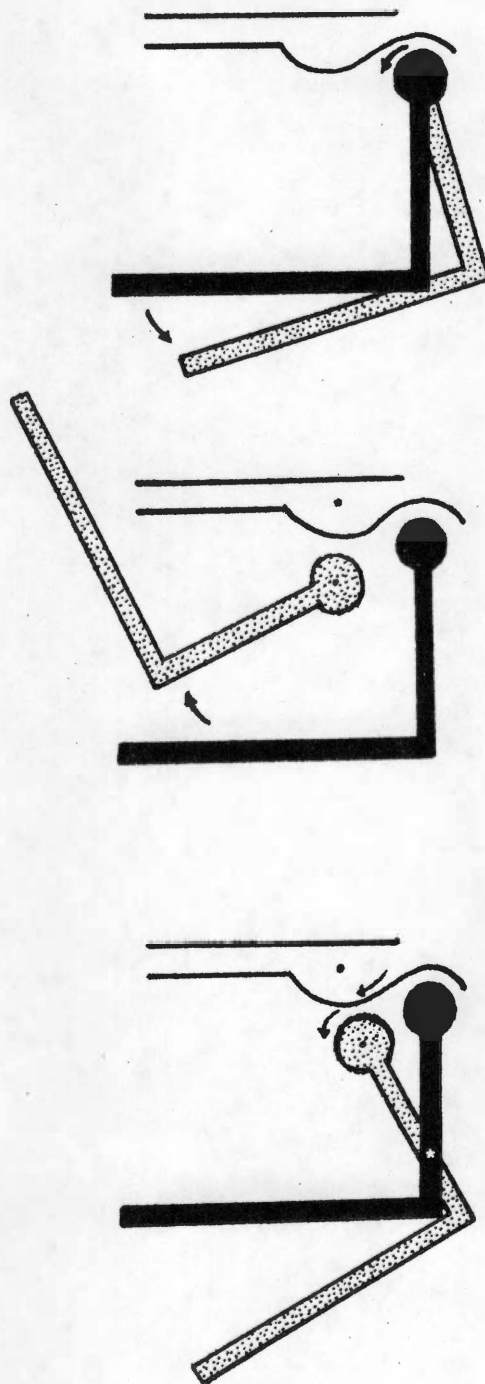


Figure 6: During movements involving caputular rotation the mandibular condyle rotates forward, slides onto the articular eminence, and continues forward rotation. (After Kraus et al. 1969).

Drawing courtesy of Maria O. Smith.

"... the motion of the condyle and the meniscus relative to the articular eminence" (Moss 1959a:80). During movements of opening, closing, protrusion, and retrusion the axes of rotation occur around the condylar head and articular eminence simultaneously. During movements involving lateral displacements the axis/axes of rotation remain controversial; however, it is known the axis "... does not pass vertically through the respective condylar heads" (Moss 1959a:83).

The mandibular component of the temporomandibular joint functions as

... a free body which may rotate in any angular direction in space, i.e., it rotates in any of the three dimensions of space. It has, therefore, three degrees of freedom. ... Each of these degrees of freedom has associated with it a separate axis of rotation [Moss 1959a:83].

As the freely moveable component of the temporomandibular joint, the mandible acts as the lever arm. Muscular force and gravitational pull both act on the lever arm. Muscular contraction results in force being exerted at the muscles' origins and insertions.

Mandibular position "... reflects the resultant tonus of all of the muscles which attach to the mandible" (Moss 1959a:83). The contribution of each muscle is a function of the cross-sectional area of the muscle and the subsequent distance of the muscle "... from these 'lines of action' to the resultant axis of the joint" (Moss 1959a:84).

V. CONCLUSIONS

The temporomandibular joint is a typical diarthrosis with respect to morphology and function; however, the temporomandibular joint

articular surfaces including the posterior margin of the mandibular condyle and posterior portion of the articular eminence are covered with dense fibrous connective tissue adapted to withstand shearing forces rather than hyaline cartilage adapted to withstanding compressive forces present in most diarthroses (Boucher 1962; Hollinshead 1974; Kraus et al. 1969; Leeson and Leeson 1970; Moss 1959a). The central and posterior portions of the mandibular fossa are not functional components of the temporomandibular joint. Stress generated during mandibular function is transmitted through the articular eminence, not the mandibular fossa as evidenced by the morphology of the fossa roof, composition and vascular pattern of the articular disk, and functional motions of the articular disk.

Composition of the Neandertal articular disk is assumed to be similar to that present in modern man. The possibility exists that the Neandertal articular disk may have exhibited differences in composition and function compared with Homo sapiens sapiens. However, this does not seem logical, and it does not appear likely that the central and posterior portions of the Neandertal mandibular fossa were anymore modified as stress bearing regions than these regions in modern man.

Analysis of the temporomandibular joint embryogenesis and general cranial and neurocranial development strengthens the hypothesis that the form of the mandibular fossa seen in Homo sapiens sapiens does not have a functional adaptive basis.

CHAPTER IV

EMBRYOGENESIS AND DEVELOPMENT OF THE TEMPOROMANDIBULAR JOINT IN HOMO SAPIENS SAPIENS

I. INTRODUCTION

In an attempt to discern the functional significance of the posterior portion of the temporomandibular joint structure, a brief review of temporomandibular joint embryogenesis is included. Factors contributing to the postnatal development of the mandibular fossa are also outlined in order to determine if the posterior portion of the temporomandibular joint develops its characteristic structure as a response to stress vectors transmitted through the fossa during mandibular functioning or whether this form develops as a secondary response to general cranial growth patterns. From this analysis the general mandibular fossa configuration characteristic of Neandertals will be evaluated.

II. EMBRYOGENESIS OF THE TEMPOROMANDIBULAR JOINT

The components of the human temporomandibular joint develop from "Highly condensed regions of undifferentiated mesenchymal cells . . . seen throughout the early stages at the dorsal end of the developing mandible and at the primordial mandibular fossa" (Yuodelis 1966A:188). These regions, the condylar and glenoid blastemata, are functional in the histodifferentiation of the temporomandibular joint elements (Bäume

1962; Baume and Holz 1970; Yuodelis 1966a). Temporomandibular joint components develop from the two blastemata at different rates and then merge together to complete the joint morphology (Yuodelis 1966a).

Differentiation of the condylar blastema begins during the 9th week of embryonic development. Structures developing from the condylar blastema include the bony condyle of the mandible, condylar cartilage, aponeurosis of the external pterygoid muscle, anterior portion of the articular disk, and the capsular components of the lower joint cavity (Baume 1962; Baume and Holz 1970; Yuodelis 1966a). Dissections made from human embryos (Baume and Holz 1970:864) reveal that ". . . the glenoid blastema . . . [develops] in close relationship with the primordial quadrate-meckelian joint to form the bony temporal joint components, including the capsular elements of the upper joint story." Coronal sections of eleven week old fetuses reveal the first appearance of the upper joint cavity developing from the glenoidal blastema. Growth of the glenoidal, as well as the condyloid blastema, is appositional and directed medially (Moss 1954).

Early during embryological development the condylar and glenoidal blastemata are separated by a layer of dense tissue which later contributes to the formation of the articular disk. The larger, anterior portion of the articular disk originates in the condylar blastema whereas the smaller, posterior portion takes its origin in the glenoidal blastema. In defining the articular disk Moffett (1957:27) states:

. . . the term articular disk is frequently limited to the fibrous, hard, glistening portion of the intra-articular

tissue. This definition excludes a considerable quantity of less-dense connective tissue, vascularized and innervated, which connects the fibrous portion of the disk on all sides of the joint capsule. Developmentally, there is no basis for this distinction. Only after the central portion of the disk is compressed between the condyle and temporal bone does this portion become avascular. In the fully developed joint the peripheral portions of the disk still retain their blood and nerve supply. . . . The complete vascularization of the disk seen in the fetus indicated that both the vascular and avascular portions in the fully developed joint should be included in the definition of the articular disk.

The mesenchyme differentiating into the articular disk is separated from that developing into the zygomatic process via an area of a few cells which later will become the superior joint cavity. The origin and appearance of the articular disk is recognized as mesenchymal cell condensation by 44-46 days gestation age and is associated with the appearance of the external pterygoid and masseter muscles. The articular disk develops in association with the mandible and masticatory muscles.

The secondary cartilage contributing to the growth of the mandibular condyle begins development at the end of the 10th week with its center of histodifferentiation in the condylar blastema. In the interval between the 10th and 12th weeks the condyloid process of the mandible increases in size and begins to develop its characteristic shape due to the 10th week appearance of the secondary cartilage core. The rapid growth of the condyle results in a narrowing of the intra-articular space. Yuodelis (1966b:198) suggests ". . . the rapid manner in which this core . . . [is] invested by an osteoid shell, and its subsequent endochondral ossification, . . . [gives] specific direction to the growth of the condyloid process." By week 11 the condylar

cartilage, continuing to expand superiorly and anteriorly, shapes the condylar articular surface into a hemisphere (Moffett 1957). With development of the intervening articular disk the condylar articular surface attains additional congruity with the articular surface of the developing temporal bone, although contact between the inferior and superior articular components remains absent.

During the 12th week the mandibular condyle continues growth in a posterior direction resulting in the lower joint components attaining contact with the cranial glenoid elements (Baume and Holz 1970). By the end of the 12th week the condyloid process attains its terminal position relative to the position of the mandibular fossa and unites with the developing mandible. Midsagittal serial sections through the condyle illustrate the primary formation of the temporomandibular joint due to the positioning of the condylar and glenoidal elements (Baume and Holz 1970).

Growth of the condylar process is characterized by a

. . . simultaneous apposition of the cartilage and its replacement by bone in the deep layers and all the surrounding periphery except its dorsolateral and superior surface. This zone of cartilage . . . [remains] covered by a fibrous layer, thus enabling the cartilage to increase in thickness almost entirely by appositional growth. The fact that the dorsolateral and superior surface . . . [remain] free of trabeculation . . . [allows] for its rapid increase in length in a specific direction. This, as well as the probable guidance given by Meckel's cartilage, may help to explain why the condylar process meets the temporal element with such precision in the early stages of development [Yuodelis 1966a:189].

Intramembranous ossification of the temporal squamous, zygomatic process, and fossa begins at approximately the same time the condylar cartilage makes its first appearance (Moss 1959b). The roof of the

mandibular fossa continues development enclosed by a thin translucent lamina of bone (Yuodelis 1966b). The anterior portion of the fossa roof is flat and limited by the anterior zygomatic root. The mandibular fossa develops in close approximation to the dorsal end of the condylar cartilaginous core (Yuodelis 1966b). The medial wall of the mandibular fossa elongates caudally and medially during the 12th week of development (Yuodelis 1966a). The roof of the fossa is now thickened and the postglenoid process visible. In discussing the developmental sequence of the mandibular fossa at the 12th week stage Yuodelis (1966b:196) states "Trabeculation was more extensive and dense throughout (in comparison to that seen in the 10th week). A still denser axis of bone extended dorsosuperiorly from the posterior zygomatic root" At this time the temporal squama widens as the mandibular and temporal joint components attain their closest approximation. A growth spurt is expressed by the formation of the ". . . secondary cartilage nodule within the anterior temporal bone portion" (Baume and Holz 1970: 869).

Yuodelis (1966a:188) notes that although

. . . the temporal components began their differentiation later than the mandibular components, they reached the mandibular rate of development rapidly, as seen in the tenth-week specimens. In the following 2-week interval, however, the differentiation of all articular elements coincided with the final approximation of the skeletal elements and formation of both superior and inferior joint cavities.

The mandibular fossa exhibits an increased width and length by the 14th week. The fossa roof which exhibits thickening and increased density is now ". . . continuous with the inferiorly and medially

developing medial wall. The posterior aspect of the fossa . . . [is] at a lower level relative to its anterior aspect, thus causing its more concave appearance" (Yuodelis 1966b:196).

Analysis of embryonic development patterns indicates the mandibular fossa develops independently of the mandibular condyle and thereby is not dependent upon condylar morphology to achieve its prenatal configuration. At birth formation of the mandibular fossa remains incomplete yet a functional joint exists (Moss 1959a). According to Moss (1959a:74) the mandibular fossa is therefore ". . . not a functional component of the temporomandibular joint. It serves merely as a receptacle for the condyle when the jaws are approximated." Factors other than embryological developmental patterns must be considered in order to determine possible explanations for the development of adult mandibular fossa morphology. One such factor contributing to the development of the fossa is craniofacial growth.

III. A FUNCTIONAL ANALYSIS OF CRANIAL GROWTH AND MORPHOLOGY

In discussing patterns of craniofacial growth Moss (1971:5) stresses the need for a complete understanding of biological processes involved saying ". . . students of craniofacial growth generally have studied the growth of skeletal tissue, per se (cartilage as well as bone), and have mistakenly assumed that these same processes of skeletal tissue growth were their own primary cause." A functional analysis of cranial growth and morphology should include a basic discussion of neurocranial growth, calvarial sutures, and components contributing to

each (Moss and Young 1960). The morphology of the cranium is related to its function. The calvarial bones function primarily to support and protect the brain, and provide muscle attachments. Cranial development is but one aspect of the functional complex which includes the brain, tissues, eyes, muscles, dentition, oral cavity, nasal cavity, and their subsequent blood supplies (Moss and Young 1960). Soft tissues encased in the calvarial bones impose functional demands on cranial form.

Composition of the cranium reflects the demands imposed by a series of functional components including a neural and facial component. Cranial development responds to neural and visceral functions independently.

The neural component contributing to the development of the skull includes the following functional components: cerebral capsule, ear capsule, and nasal capsule (Moss and Young 1960). Calvarial bones develop in response to three functionally independent components: the outer table, diploe, and inner table (Moss and Young 1960).

A functional analysis of neurocranial growth indicates the cerebral capsule develops from the tissues surrounding the developing brain. As the brain grows functional demands are imposed on the cerebral capsule. During fetal life the cerebral capsule is composed entirely of soft tissues encasing the neural mass which are responsive to spatial demands on the growing brain. Layers of the scalp, bones, and dura differentiate within the cerebral capsule. The differentiation of the dural fiber systems ". . . divides the calvarial surface of the capsule into a number of 'fields.' Approximately at the center of these fields ossification begins . . ." (Moss and Young 1960:282). Skeletal

differentiation occurs immediately superior to the dural layer. Osseous expansion proceeds via transformation. Growth in height and length occur at differing yet relatively constant absolute rates. The rate of cerebral capsule expansion is determined by that of the enclosed contents. For example, the parietal bone continues growth as it is passively carried outward, thus translation and transformation occur simultaneously due to capsular expansion (Moss and Young 1960) (Figure 7). Parietal bone transformation occurs independently of translation. The parietal bone results from ossification of a portion of the cerebral capsule itself. The outer cranial dural layer forms the inferior surface of the calvarial bones. Therefore the configuration of the internal aspect of the skull is a direct reflection of the dural form, which in turn, is determined by the outline of the neural mass (Moss and Young 1960). Capsular size and configuration is dependent on the size, volume, and form of the neural mass. The rate of brain growth decreases with age resulting in a subsequent decrease in the absolute rate of capsular expansion. Ossification also proceeds less rapidly as the adjacent bony edges approximate. The means of skeletal growth then changes to that of surface apposition in which the osteoblastic layers become more predominant as the bone thickens. In essence, ". . . the area attained by the individual bones within the capsule depends upon the location of their ossification center, and the duration and rate of peripheral osseous deposition" (Moss and Young 1960:283). The developing enclosed neural mass ". . . provides the magnitude of the neural growth vectors" (Moss and Young 1960:283). Direction of the

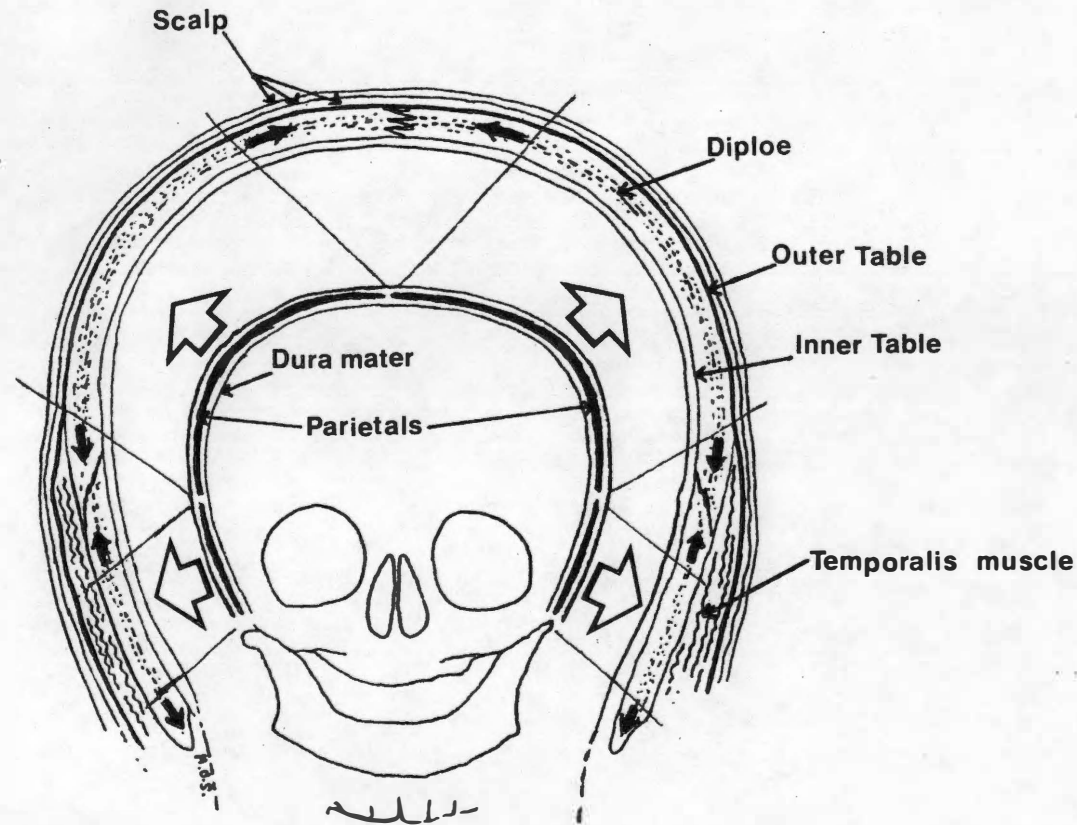


Figure 7: Growth of the neurocranial capsule results in the translation and transformation, simultaneously, of the cranial bones. Growth of the calvarial bones is a secondary, compensatory response to the primary growth of the neurocranial capsule. (After Moss 1971; Moss and Young 1960).

Drawing courtesy of Maria O. Smith.

growth vectors is dependent upon the orientation of the dural fibers. Therefore the skull base, neural mass, calvaria and dura form a functional unit. The dura remains the unossified portion of the cerebral capsule whereas the calvarial bones represent the ossified portions. In summary, the size and shape of the normal neural skull is ". . . the resultant of the preferential direction of the growth vectors of the expanding neural mass by these dural fiber systems" (Moss and Young 1960:284).

Calvarial sutures also develop within the functional matrix and are not developmentally self-regulating. Soft tissues separating the calvarial bones are remnants of the membranous cerebral capsule (Moss and Young 1960). Sutural areas refer to the soft tissues and bony edges of the approximating skeletal units. Sutures function to resist bone separation while simultaneously permitting some movement. It should be noted that the location of sutures does not predetermine the configuration of calvarial bones. Instead, the ". . . location of a suture is determined by the relative growth of adjacent bones . . ." (Moss and Young 1960:284). Sutures are not the primary locations for cranial bone growth. Bone may be deposited along the sutural areas to compensate for corresponding openings ensuing from capsular expansion and ensuing bony translation. According to Moss and Young (1960:284) the ". . . intrinsic morphology of all calvarial sutural areas freed from normal functional demands is flat, butt-end articulation. Both beveling and interdigitation are responses to extrinsic forces which normally are operative when the bones are in their functional matrix" Extrinsic forces aid in sutural fusion.

Muscle activity remodels the outer bony table by the forces of stress and strain generated during functioning of the appropriate muscles. Thus, ectocranial morphology responds to extrinsic forces whereas the endocranial morphology responds to intrinsic functional demands. In essence, it may be concluded that ". . . the form of the ectocranial surface of the neurocranium is functionally unrelated to that of the endocranial surface . . ." (Moss and Young 1960:289). The fundamental hypothesis forming the foundation of the functional matrix theory proposed by Moss (1959b) and Moss and Young (1960:290) is that ". . . ontogenetically the form of the osseous skull at any moment accurately reflects the resultant of the functional demands of the protected and supported soft tissues." It is hypothesized that morphological changes seen in calvarial configurations documented throughout the human fossil record are secondary adaptive responses to the primary changes occurring in the soft tissues (Moss and Young 1960:290). Specifically, cranial morphology is a function of both intrinsic (cerebral capsular growth) and extrinsic (muscle functioning) factors (Moss 1971).

Olfaction, hearing, neural integration, balance, and vision comprise only a brief portion of the functions performed within the head and neck areas. Each function is executed within a functional cranial component, each of which is independent relative to form of the other components (Moss 1971). Composing each cranial component is a functional matrix and corresponding skeletal units. The functional matrix is responsible for performing the particular functions whereas the skeletal

elements protect and support the matrix (Moss 1971). Composing the functional matrix are ". . . all of the tissues, organs, glands, and functioning spaces necessary to carry out a given single function completely" (Moss 1971:6). Functional matrices are one of two types: periosteal or capsular (Moss 1971). Skeletal units are composed of osseous, cartilaginous and tendinous tissues.

Individual bones encompass a series of microskeletal units. For example, microskeletal units forming the mandible include the alveolar, coronoid, angular, condylar, and basal portions (Moss 1971). The size and morphology of the microskeletal units ". . . is always and without exception a secondary response to morphogenetically prior and primary demands of specifically related functional matrices" (Moss 1971:7). For example, development of the coronoid process responds to the dynamic requirements of the temporalis muscle. Removal or denervation of the temporalis muscle results in atrophy and decreased vascularization of the coronoid process (Moss 1971:7). The angular process is responsive to the dynamic requirements of the medial pterygoid and masseter muscles in the same manner. Moss (1971) hypothesized skeletal growth is not under direct genetic control but proceeds as compensatory growth to ensure efficient biomechanical functioning. Genetic control primarily affects the surrounding tissues or functional matrices thereby indirectly affecting the skeletal tissues (Moss 1971:10). Various theories have been proposed to explain cranial growth processes. Weinmann and Sicher (1947) proposed growth of calvarial bones is generated within the sutural tissues. Experimental research with laboratory animals

conducted by Moss (1954), Sarnat (1963), and Selman and Sarnet (1957) among others does not support this hypothesis. Sutures are locations of secondary, compensatory growth rather than centers of primary growth.

Cartilaginous centers within the cranium are also not centers of primary growth nor are they centers exerting expansive forces (Moss 1971). For example, removal of the condylar articular cartilages does not interrupt orofacial growth (Gianelly and Moorrees 1965). The condylar cartilages are secondary compensatory growth centers (Moss 1960;1971).

Resorption of the endocranial calvarial surface and subsequent osseous deposition along the ectocranial surface in addition to growth in the sutural areas and cartilaginous tissues does result in dimensional increase of the neurocranium. Transformative growth processes do not account for the magnitude, however, of cranial growth (Cleall, Wilson, and Garnett 1968; Moss 1971; Moss and Young 1960).

Translative growth is due primarily to the volumetric increase with the capsular matrices resulting in secondary growth of the surrounding capsule (Moss 1971; Moss and Young 1960). Consequently all ". . . enclosed and embedded skeletal units and periosteal matrices are thus passively translated in space" (Moss 1971:14). Transformative growth occurs simultaneously with translative growth (Figure 7, page 53). Compensatory growth of the neurocranial capsule results in response to the proceeding growth of the enclosed neural mass. Passive translation occurs in order to prevent bone separation creating gaps in the protective osseous framework. Secondary transformative growth proceeds along the sutures (thickening and curvature) as a compensatory mechanism.

Growth of the orofacial capsule results in passive translation of the mandible downward and forward. The condyles move away from the temporomandibular joint. Condylar growth proceeds in order to maintain the temporomandibular joint functionally but is not the cause of mandibular translation. Development of the condyles occurs as secondary, compensatory growth. Transformative growth results in changes in the ascending ramus which are secondary and compensatory responses ". . . to their periosteal matrices which are themselves being passively translated" (Moss 1971:16).

Cephalic growth results from periosteal and capsular matrices' activity. Analysis of cranial growth should include consideration of changes occurring in spatial location in addition to changes in size and form, each of which is produced by different types of matrices and growth processes. In summary, the periosteal matrix (acting directly on skeletal tissues in the form of deposition, resorption, and endochondral growth thereby altering the size and shape of the skeletal tissues through transformative processes) and the capsular matrix (acting indirectly on the skeletal tissues by altering their spatial position) are the ". . . primary morphogenetic agencies in cephalic growth" (Moss 1971:16-17).

The masticatory muscles begin developing prior to the beginning of intramembranous osteogenesis (Baume 1962). It has been noted (Baume 1962:1335-1336) that areas ". . . of future muscle attachment are sites of rapid bone formation throughout the early formative stages. Expansive bone formation first occurs at the lower border in the

vacinity of the ends of the masseter and internal pterygoid muscles."

Baume (1962:1336) hypothesized that

. . . it is conceivable that primitive fibrillar muscle contractions may be conducive to these increased osteal growths. Since the lateral pterygoid muscle remains undifferentiated, however, until the condylar head has developed, a different mechanism must be operative in the formation of the condylar process.

Moss (1959b) illustrates the necessity to consider the role neural growth plays in relation to the development of the temporal bone. The orientation of the temporal bone is dependent upon the integrated growth processes of the temporal lobe of the cerebrum, tympanic ring, and external auditory meatus (Moss 1959b). Noback and Moss' (1956:544) study of brain growth indicates a ". . . constant relationship exists between the specific growth rates of many dimensions of the developing human brain." The growth ratio of any two elements is constant. Such a relationship exists beginning at the end of the second month of fetal life through adulthood with the exception of the corpus callosum and width of the cerebellum (Noback and Moss 1956:544-545). Noback and Moss (1956: 547-548) propose

. . . alterations in the shape of the brain during ontogeny result from changes in the relative proportionality of its components and the expression of the integration of these changes is the constant ratio between the specific growth rates of these components of the brain.

The postnatal development of the temporal lobe of the brain has significant implications for the development of the mandibular fossa, the internal aspect of which serves as the floor of the middle cranial fossa. One such factor is the ". . . relative outward and downward displacement of the entire floor of the middle cerebral fossa, with

age . . ." (Moss 1959b:90). As development of the temporal lobe continues the floor of the middle cranial fossa lowers. The lowering of the floor is ". . . associated with a flattening of that floor, both ectocranially and endocranially. This ectocranial flattening is directly responsible for the assumption of a horizontal position by the articular fossa and articular eminence . . ." (Moss 1959b:90) (Figure 8). Davenport (1940) and Moss (1959b) state the external auditory meatus shifts position considerably during postnatal development. According to Moss (1959b:91) the

. . . direction of this movement may be in any direction, but generally includes a downward component. Needless to say any shift in position of the external auditory meatus implies a shift in the entire ectocranial surface of the temporal bone. Both of these processes are coordinated with the growth of neural viscera and may be considered to result in a lowering of the joint relative to the chondrocranial skull base. In so far as they do lower the position of the joint they will cause a lowering of the entire mandible without the necessity of any mandibular growth contributing toward this end.

The mandibular fossa assumes its adult configuration during postnatal life with the development of the articular eminence, the functional element of the temporomandibular joint (Moffett 1957). The articular eminence completes development by age 12 years (Boucher 1962), thus the temporomandibular joint attains its adult contours (Moffett 1957). Prior to development of the articular tubercle the fossa appears more shallow as it gradually grades into the tubercle.

Growth of the human cranium is highly complex. Patterns of cranial development change with age, from a prenatal to a postnatal osteological growth pattern. Somatic growth rates, however, are not constant. Growth of the cranium is rapid during the first year following birth and

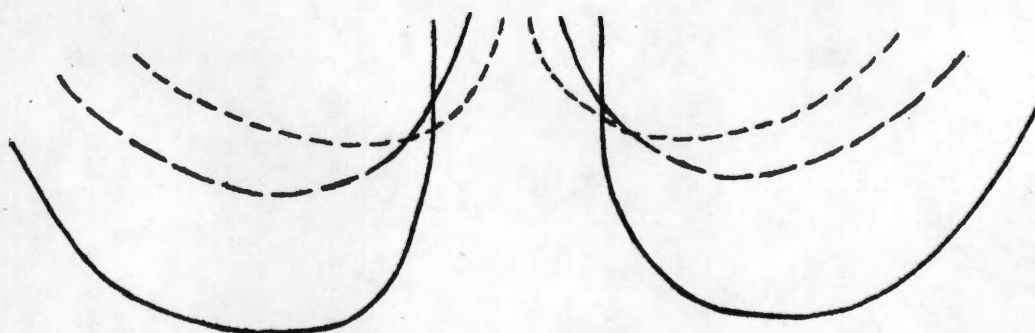


Diagram A

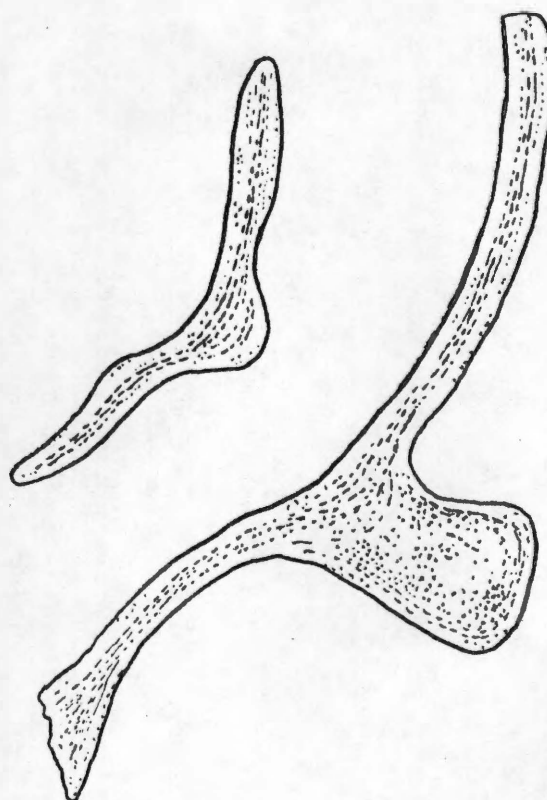


Diagram B

Figure 8: Development of the temporal lobe of the cerebrum results in the flattening of the cranial floor of the middle cerebral fossa. Diagram A illustrates the contours of the middle cranial floor both endocranially and ectocranially prior to expansion by the temporal lobe of the brain. Diagram B illustrates the contours of the mandibular fossa following lateral expansion of the temporal lobe of the brain. (After Moss 1959b).

Drawing courtesy of Maria O. Smith.

continues until approximately the age of seven years. By age six years the brain has achieved 90 percent of its adult size (Moore and Lavelle 1974). Growth progresses more slowly thereafter ". . . until the age of puberty, at which time growth again is accelerated" (Hollinshead 1974: 810).

From a functional viewpoint the concave fossa "... is not a functional component of the temporomandibular joint. It serves merely as a receptacle for the condyle when the jaws are approximated" (Moss 1959a:74). According to Moss (1959a:74)

. . . the form of the articular fossa is a response to the growth of adjacent structures. The roof of the fossa serves as a portion of the floor of the middle cranial fossa. Also, much of the fossa's morphology is related to the development of the external auditory meatus.

At birth no fossa per se is evident; however,

Only with the downward and outward growth of the middle cerebral fossa, the fusion of the tympanic ring, and the development of the external auditory meatus does the mandibular fossa as a whole develop. The shift from a vertical to a horizontal position in space occurs postnatally [Moss 1959a:75].

In essence, the newborn possesses a functional temporomandibular joint while lacking a fossa (Moss 1959a).

In summary Yuodelis (1966a:188) comments, saying

It was evident throughout the subsequent stages that these fibrous mesenchymal layers, in their germinal capacity, are an important factor in the shaping of the skeletal units. . . . Factors such as the musculature, widening neurocranium and, probably, Meckel's cartilage cannot be disregarded in later stages. Moss's "functional matrix" theory, attributing important functions to muscles, brain, neurovascular triads, tongue, and other soft tissue in the development of bones, most probably accounts for influences on the final shaping of these joint elements.

CHAPTER V

CONCLUSIONS AND SUMMARY

I. CONCLUSIONS

Analysis of the temporomandibular joint region morphology characteristic of modern man, conducted within the framework of the functional matrix theory, suggests the morphology of the central and posterior portions of the temporomandibular joint is most reasonably a secondary response to the pattern of neurocranial growth. When viewed in light of the functional matrix theory and functional requirements of a synovial joint necessary to ensure efficient biomechanical functioning, it appears the morphology of the central and posterior portions of the temporomandibular joint is not a functional prerequisite to efficient functioning of the temporomandibular joint and thereby does not have a direct adaptive basis. Application of the functional matrix theory to general Neandertal cranial morphology in addition to a consideration of the morphological variation expressed in the temporomandibular joint area, biomechanical prerequisites of a synovial joint, and the general embryological development of the temporomandibular joint area contribute to a better understanding of the specific morphological variations present in the temporomandibular joint region seen in Homo sapiens neanderthalensis when compared to that normally seen in Homo sapiens sapiens. In comparison to modern man, Neandertals characterically exhibit a (1) longer, lower, broader cranial configuration; (2) robust

squama smaller in vertical and horizontal dimensions; (3) wide, shallow mandibular fossa; (4) more oval external auditory meatus positioned relatively higher on the temporal bone; (5) thickened squama, tympanic plate, petrosal portion, external auditory meatus, mandibular fossa roof, zygomatic process, and articular eminence; (6) pronounced development of the postglenoid process and articular eminence; (7) small, weakly developed mastoid process positioned relatively higher on the temporal bone usually not projecting below the cranial base; (8) squamous surface behind the supramastoid crest not convex; (9) wide, deep digastric fossa; (10) prominent supramastoid ridge extending above the entire width of the mastoid process; (11) unusually large stylo-mastoid foramen; and (12) temporal projection not sphenoid plate forming the medial wall of the mandibular fossa (Alexeyev 1976; Angel 1972; Debénath 1977; Guth 1963; Heim 1974; Howell 1957; Howells 1973, 1974; Keith 1920; Mann and Trinkaus 1973; McCown and Keith 1939; Riquet 1974; Smith 1976; Stewart 1962, 1974; Stringer 1974; Vallois 1969; Vlček 1958). Certain of these characteristics, specifically those relating to the configuration of the central and posterior components of the temporo-mandibular joint, are tentatively explained within the confines of the functional matrix theory, whereas the configuration of the anterior portion of the temporomandibular joint may be explained in terms of its adaptive or functional significance.

The thickening noted in the tympanic ring and postglenoid process in Neandertals makes it attractive to suggest that these components of the temporomandibular joint area may have an adaptive or functional

basis in that they show modification to bearing stress directly. Such a functional hypothesis regarding thickening of the bony posterior joint components would serve to strengthen the hypothesis proposed by several hominid paleontologists (Brace 1962, 1964, 1967; Brose and Wolpoff 1971; Smith 1976; Wolpoff 1971) that Neandertals habitually utilized their anterior dentition for nonmasticatory functions. Habitual use of the anterior dentition for nonmasticatory functions would generate excessive stress vectors at the point of contact between the mandibular condyle and the temporal components of the temporomandibular joint (Hylander 1975). Extensive use of the anterior dentition for nonmasticatory functions, for example, to affect efficient gripping, would necessitate additional force than normally generated during mastication due to the distance of the anterior dentition from the fulcrum as represented by the temporomandibular joint. The hypothesis that Neandertals may have habitually used their anterior dentition for nonmasticatory functions is further strengthened by the relatively high incidence of osteoarthritis exhibited by Neandertal mandibular condyles (Alexandersen 1967; Kallay 1963; Smith 1976). The edge-to-edge bite pattern characteristic of Neandertals may also be a contributing factor necessitating such bony strengthening of the joint area. During functional occlusion the edge-to-edge bite typical of Neandertals may preclude the necessary forward gliding movement of the mandibular condyle onto the articular eminence to achieve functional articulation as seen during mandibular functioning in modern man, characterized by the typical overbite pattern. The presence of an edge-to-edge bite may suggest the mandibular

condyles remain within the confines of the central portion of the temporomandibular joint during mandibular movement and functional use of the anterior dentition. Provided the mandibular condyle remained within the mandibular fossa during mandibular functioning modification of the mandibular fossa into a stress resistant structure would seem logical. Such a modification of the mandibular fossa would appear consistent with the regular thickening noted throughout the external auditory meatus in Neandertals. If stress vectors generated during nonmasticatory functioning of the anterior dentition were being transmitted through the central and posterior aspects of the temporomandibular joint in Neandertals, the thickening noted around the external auditory meatus may have been an adaptive compensation to divert or dissipate the stress forces away from the internal ear structures.

On the other hand, the general thickening present in the external auditory meatal region, postglenoid process, tympanic ring, zygomatic process, and temporal squama may simply be related to the general thickening characteristic of Neandertal cranial bones in general. In order to determine which of these hypotheses appears more viable it is necessary to examine the temporomandibular joint as a synergistic whole. Any functional analysis of the temporomandibular joint region would be inconclusive if the soft tissue morphology contributing to the total morphological pattern, formation, and functioning of the temporomandibular joint were not discussed.

Morphology of the soft tissue contributing to the total morphological pattern of the temporomandibular joint region suggests

that the central and posterior aspects of the temporomandibular joint are not adapted to withstanding the transmission of force vectors generated during mandibular functioning. For example, thick fibrous connective tissue rather than hyaline cartilage as is typically present in all diarthroses overlies the articular surfaces contributing to formation of the temporomandibular joint (Boucher 1962; Kraus et al. 1969). Whereas cartilage is resistant primarily to compressive forces, fibrous connective tissue is more resistant to both compressive and shearing forces (as would be generated during lateral movements of the mandible (Hollinshead 1974; Leeson and Leeson 1970; Moss 1959a). Specifically, the posterior margin of the mandibular condyloid process is overlain with avascular fibrous tissue suggesting the mandibular condyle is a stress bearing component of the temporomandibular joint (Kraus et al. 1969). According to Moss (1959a:76) the cerebral and posterior portions of the temporomandibular joint are not overlain with a lining of dense fibrous tissue which is also present on the posterior surface of the articular eminence. This factor suggests that the central and posterior aspects of the temporomandibular joint are not actively involved during mandibular functioning whereas the mandibular condyle and articular eminence comprise the functional components of the temporomandibular joint.

The morphology and composition of the intervening articular disk does not lend support to the hypothesis that stress is being transmitted through the central and posterior aspects of the temporomandibular joint despite the thickening of specific bony elements. Composed of dense

tough fibrocartilage the intervening articular disk is divided into three distinct zones. The anterior and central zones of the articular disk are avascular and devoid of nerves suggesting these aspects of the articular disk are adapted to withstanding stress (Moffett 1957; Yuodelis 1966b), whereas the posterior zone is vascularized. When the mandible is in the state of physiologic rest the mandibular condyle remains separated from the temporal components of the temporomandibular joint by the articular disk. As the mandible is depressed the mandibular condyle rotates downward and forward on the articular disk as the condyle glides onto the articular eminence pulling the fibrocartilaginous disk forward simultaneously. The central avascular zone of the articular disk is now compressed between the mandibular condyle and articular eminence indicating considerable stress is being exerted on the anterior and central avascular zones of the articular disk, whereas the vascular posterior zone of the meniscus is drawn forward into the central portion of the temporomandibular joint. If stress were to be generated through the posterior zone of the meniscus, the minute blood vessels would be damaged (Kraus et al. 1969; Robinson 1946; Yuodelis 1966b). The vascular posterior zone of the articular disk does not appear to be adapted for withstanding stress and thereby strengthens the hypothesis that the central and posterior aspects of the temporomandibular joint are not functional components of the joint complex, at least in modern man.

The hypothesis that stress is not generated through the central and posterior portions of the temporomandibular joint is further strengthened

by the fact that the roof of the mandibular fossa in modern man is composed of a very thin bony plate. However, the mandibular fossa roof in Neandertals is separated from the endocranial surface by a thickened plate of bone. Assuming the composition of the intervening articular disk was the same in Neandertals as that normally seen in Homo sapiens sapiens, and considering the functioning and the role of the mandibular condyle and articular disk during mandibular functioning, it is hypothesized that this thickened mandibular fossa roof may simply be related to the general thickening noted for Neandertal cranial bones.

A functional analysis of the morphology of the temporomandibular joint components in modern man indicates that force vectors generated during mandibular functioning are transmitted only through the mandibular condyle and articular eminence, and that these areas form the functional components of the temporomandibular joint, as evidenced by the trabecular patterning of the articular eminence and composition of the fibrocartilaginous disk. The central and posterior aspects of the temporomandibular joint are not functional components of the joint per se. According to Moss (1959a:74) the mandibular fossa ". . . serves merely as a receptacle for the condyle when the jaws are approximated." Mandibular fossa morphology does not attain its adult contours until the articular eminence completes formation around twelve years of age. Until this time, the mandibular fossa appears more shallow as it gradually grades into the articular eminence. By age twelve the mandibular fossa has attained its adult contours. The final adult mandibular fossa configuration may be explained in terms of the functional matrix theory which attributes

. . . important functions to muscles, brain, neurovascular triads, tongue, and other soft tissue in the development of bones, and most probably accounts for influences on the final shaping of these joint elements [Yuodelis 1966a:188].

Craniofacial growth patterns in Homo sapiens sapiens indicate the morphological form of the cranium is a direct function of both intrinsic and extrinsic factors. Therefore, the total morphological pattern of the cranium may be related to its function, that being to (1) support and protect the enclosed neural viscera, and (2) provide the necessary bony attachments for the muscles of facial expression, mastication, deglutition, and the nuchal muscles. Growth and development of the soft tissues encased within the calvaria impose intrinsic functional demands of the endocranial form resulting in translatory and transformative growth of the cranial bones, and the diagnostic configuration of the inner bony table whereas the ectocranial morphology is a function of extrinsic forces such as muscle activity operative in the cranial area. Morphology and size of the temporal squama may logically be explained in this light. For example, as the temporal lobe of the cerebrum develops, the temporal bone, affording support and protection to this portion of the brain, initiates growth in a superior direction to ensure functional articulation with the parietal bone is maintained. The variation present in the vertical and horizontal diameters of the temporal squama exhibited between modern man and Neandertals may be explained in terms of the general cranial configuration characteristic of Homo sapiens sapiens and Homo sapiens neanderthalensis. Neandertal general cranial morphology is characterized by a long, low, broad cranial configuration whereas the cranial form of modern man is generally higher, narrower,

and shorter. The respective size of the temporal squama may, therefore, have a direct relationship with the pattern of growth of the cerebral capsule in the area of the temporal lobe of the cerebrum. It is suggested that in modern man growth of the temporal lobe of the brain is oriented in a more superior direction resulting in the necessity of the temporal squama to continue compensatory growth in a more superior direction than is characteristic in Neandertals in order to ensure maintenance of functional articulation with the parietal bone. Conversely, the lower squamous diameter characteristic of Neandertal temporal bones may be a function related to the growth pattern of the temporal lobe of the cerebrum in Neandertals. Due to the doliocranic cranial configuration characteristic of Neandertals it is hypothesized that growth of the temporal lobe of the cerebrum in Neandertals is directed in a more lateral direction as opposed to development in a more superior direction seen in Homo sapiens sapiens. Therefore, the degree and direction of cerebral capsular growth in Neandertals would not necessitate the same degree of compensatory growth in squama height as is present in modern man to maintain functional articulation with the developing parietal bone, thereby resulting in a lower squamosal diameter. The robustness of the Neandertal squama may be explained in terms of the extrinsic forces generated by the massiveness of the temporalis muscle in Neandertals in comparison with that normally seen in modern man.

Morphology of the central and posterior portions of the temporomandibular joint may also be related to the general growth

patterns of the neural mass and cerebral capsular matrix. According to Moss (1959a:75) the configuration of the mandibular fossa is a function of the combined growth pattern of the temporal lobe of the cerebrum, tympanic ring fusion, and development and positioning of the external auditory meatus. As the temporal lobe of the cerebrum develops it grows in an inferior and lateral direction causing a lowering and flattening of the middle cranial fossa floor. This general lowering and flattening of the middle cranial fossa floor is associated with a flattening of the floor expressed both endocranially and ectocranially. The roof of the mandibular fossa thereby flattens as a secondary response to the growth pattern of the temporal lobe of the brain. Morphology of the mandibular fossa in Neandertals exhibits a wide, shallow (measured from the articular eminence) configuration in comparison to that normally seen in Homo sapiens sapiens. The increased width and shallow configuration of the mandibular fossa as expressed in Neandertals may be a function of the broadness of the general cranial form. Growth of the temporal lobe of the cerebrum in a more lateral direction would have the effect of widening the mandibular fossa as the middle cranial fossa expands to accommodate the expanding temporal lobe of the brain. The shallowness of the Neandertal mandibular fossa would thus be associated with the degree of lowering and flattening of the middle cranial fossa floor.

The role of the external auditory meatus cannot be discounted in contributing to the total morphological configuration of the mandibular fossa. Completion of the external auditory meatus component occurs postnatally. During the postnatal developmental stage the external

auditory meatus shifts position in association with the development of the petrous portion of the temporal bone. The shift in position of the external auditory meatus and petrous portion usually includes a downward component (Davenport 1940; Moss 1959b). As mentioned previously Moss (1959b:91) points out

. . . any shift in position of the external auditory meatus implies a shift in the entire ectocranial surface of the temporal bone. Both of these processes (the downward movement of the external auditory meatus and growth of the cerebral capsule) are coordinated with the growth of neural viscera and may be considered to result in a lowering of the joint relative to the chondrocranial skull base.

In Neandertals the more oval, anterosuperiorly directed external auditory meatus is positioned relatively higher on the temporal bone thereby suggesting a relationship between the neurocranial growth pattern and morphology of the joint area may be expressed as a variation in positioning of the external auditory meatus in Neandertals.

The third factor contributing to the configuration of the mandibular fossa is the development of the tympanic portion of the temporal bone. Neandertals characteristically exhibit a thickened tympanic portion in comparison to that normally seen in Homo sapiens sapiens which also contributes to the variation expressed in the mandibular fossa between modern man and Neandertals. In summary, the width, depth, and general morphological configuration of the mandibular fossa appears to be a secondary response to the dynamic requirements of the growth vectors of the cerebral temporal lobe, positioning of the external auditory meatus, and fusion of the tympanic ring.

A functional analysis of the temporomandibular joint area in Homo sapiens sapiens and Homo sapiens neanderthalensis indicates that the

morphology of the central and posterior aspects of the temporomandibular joint are probably secondary responses to neurocranial growth patterning of the crania, and therefore do not have a functional or adaptive basis. The variations noted in the Neandertal middle and posterior temporomandibular joint area in comparison with that normally seen in modern man can best be explained in terms of the functional matrix theory as secondary responses to the primary growth vectors characteristic of the Neandertal neural capsule and associated extrinsic (muscle) factors. It is, of course, possible that the vascularization pattern of the articular disk and cartilaginous coverings of the joint area were not the same in Neandertals as in modern man. If this were true and these soft tissues were adapted for stress bearing and for functioning as a workable joint, the functional hypothesis would be defensible. It is obviously impossible to know what the exact nature of these soft tissues was in Neandertals, and the possibility of such differences cannot be excluded from consideration. However, the modern hominid temporomandibular joint morphology is the closest living approximation of the Neandertal temporomandibular joint available and, as long as it is recognized that differences might exist, it seems logical to accept it as a model. In light of this analysis it appears that the morphology of the middle and posterior portions of the temporomandibular joint characteristic for Neandertals does not have a primary adaptive function and is most likely a result of the general Neandertal cranial configuration.

II. SUMMARY

Hominid paleontologists are primarily interested in understanding the evolutionary development of Homo sapiens sapiens. Clues to understanding the origins and evolutionary history of modern man are expressed in the total morphological patterns and variations preserved in the fossil record. Descriptive analyses of such morphological patterns and variations are useful in determining the lineages of ancestral development of Homo sapiens sapiens but do not contribute to an understanding of the adaptive significance of these variations. Functional analyses of the morphological patterns expressed in the fossil record contribute to a more comprehensive understanding of the processes responsible for these variations.

It is the purpose of this thesis to investigate the morphological variations seen in the temporomandibular joint region in Homo sapiens neanderthalensis in comparison to the patterning present in Homo sapiens sapiens in order to determine whether the variations expressed in the Neandertal temporomandibular joint area have an adaptive basis or are simply secondary responses to the growth pattern of the neurocranium and total morphological configuration of the Neandertal cranium in general. This investigation will be conducted within the framework of the functional matrix theory.

Neandertal temporal bone morphology in the vicinity of the temporomandibular joint exhibits distinctive differences in comparison to the total morphological pattern of the temporomandibular joint area in Homo sapiens sapiens. For example, Neandertal morphology is

characterized by the following features: (1) robust, thickened squamous portion reduced in vertical and horizontal diameters; (2) oval external auditory meatus positioned relatively higher on the temporal bone; (3) thickened tympanic plate, petrosal portion, mandibular fossa roof, and postglenoid process; (4) wide, shallow mandibular fossa; and (5) pronounced articular eminence. A functional analysis of these variations exhibited by Neandertals would endeavor to explain the variations in terms of an adaptive response to the degree of stress generated in the temporomandibular joint region during masticatory and nonmasticatory functioning of the dentition. However, morphology of the soft tissues contributing to a functional temporomandibular joint in Homo sapiens sapiens does not coincide with the functional hypothesis.

A review of basic soft tissue morphology and principles of biomechanical functioning of the temporomandibular joint indicates the functional components of the temporomandibular joint structure include only the articular eminence and mandibular condyle. The configuration of the mandibular fossa itself appears to be a secondary response to intrinsic factors precipitating cranial growth, general cranial configuration, fusion of the tympanic plate, and positioning of the external auditory meatus. The noted thickening of the Neandertal squama, tympanic plate, petrosal portion, mandibular fossa roof, and postglenoid process may simply be related to the increased thickening characteristic of Neandertal cranial bones in general.

Analysis of the temporomandibular joint morphology, role of the mandible during functional occlusion, functional requirements of a

diarthrodial synovial joint to ensure efficient biomechanical activity, and general embryological development of the components contributing to the formation of the temporomandibular joint indicates the morphology of the posterior portion of the mandibular fossa in Homo sapiens sapiens does not have a direct functional or adaptive basis and that the variation expressed in this joint area in Neandertal crania may be explained in this light. The morphological variations presented in the Neandertal temporomandibular joint area may be logically explained as a secondary result of the total morphological pattern of the Neandertal cranium in general and growth patterns of the neurocranial capsule.

III. RECOMMENDATIONS FOR FURTHER RESEARCH

Analysis of the temporomandibular joint region in populations characterized by an edge-to-edge bite would be beneficial in determining differences in biomechanical functioning of the mandibular condyle in articulation with the temporal components of the temporomandibular joint. It remains necessary to determine the degree of forward and downward movement required by the mandibular condyle during functional occlusion. Currently, in populations characterized by an edge-to-edge bite it is not clearly understood whether the mandibular condyle glides slightly forward to achieve functional articulation with the articular eminence or whether mandibular movements are executed within the confines of the mandibular fossa itself. An additional factor consisting of the affects a worn dentition may contribute to the degree of stress generated during masticatory functioning should also be

investigated. If the configuration of the mandibular fossa is a secondary response to neurocranial growth vectors, alterations of these patterns due to artificial cranial deformation should be expressed as variations in the form of the corresponding temporomandibular joint. Therefore, an osteological analysis of the temporomandibular joint regions in artificially deformed crania should be undertaken in order to verify or discount this hypothesis. In conclusion, additional research needs to be conducted regarding the principles and functional requirements necessary to ensure efficient biomechanical functioning in the temporomandibular joint region in living individuals. The morphology of the soft tissues contributing to the formation of the temporomandibular joint needs to be examined in animals in which the mandibular condyle does not slide forward onto the articular eminence in order to determine the vascularization patterns characteristic of the structures in this type of articular pattern.

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