CHAPTER 1) EVOLUTION OF THE HUMAN MASTICATORY SYSTEM

THE ROLE OF MASTICATION IN EVOLUTION

Masticatory systems generally led the way in evolution. Ineffective masticatory systems were invariably fatal. Improved ones provided new sources of nutrition that made possible whole new lines of species. In this manner the masticatory system exerted a profound and compelling influence on the whole evolutionary process.

"Feeding is a function of such paramount importance that natural selection seldom acts with such decisive vigour as when a process of such fundamental nature is involved. Thus it is postulated that even the speed which the primitive vertebrate predator gained by the development of a flexible backbone and large paired fins was largely complementary to the improvement in the functional efficiency of the jaws in procuring food."[1]

“Without the predatory powers of jaws and teeth and the possibility of swift and accurate pursuit of prey there would have been no evolution of the sense organs of smell, sight and hearing, of elaborate muscular coordination, of prevision of how to get from here to there and the possible consequences of the transit - in short, there would have been no centralization of the nervous system such as ultimately produced the brain, and the earth would never have known the phenomenon of consciousness, at least of an order superior to that of the lobster, scorpion, or butterfly."[2]

EARLY MOUTHS

Mouths became important in evolution shortly after organisms developed an internal tube through which portions of the external environment could pass. The mouths of early unicellular protozoans were just gashes in their sides. The mouths of jellyfish became surrounded by tentacle-like folds to help engulf food. The mouths of early fish were used to suck food off the ocean floor.

One of the first big steps in the evolution of the masticatory system took place roughly 300,000,000 years ago when the space between the lips and the throat widened to accomodate moveable jaws. This modification of the food intake mechanism created the basis for many subsequent developments.

“Plankton gathering is neither the quickest nor easiest way of obtaining food and, therefore, it is not surprising that in the succeeding vertebrates a number of evolutionary experiments occurred, aimed at changing from a microphagous to a macrophagous habit. Such experiments included, for example, the development of a horny-toothed oral sucker and tongue for rasping away the flesh of other animals which still survives today in the lampreys. However, the one really successful experiment was the modification of the skeleton supporting the two anterior gill arches to form opposable jaws."[3]

The mandible was the primary moveable part in this system. It was the first bone to be attached to the body by a flexible joint, and the mechanism created for that joint paved the way for attaching arms, legs, and all other appendages.

"It seems that other joints in the fishes' body are never as highly developed as the jaw joint... When jaws were devised, they were the first speedy, wide swinging, vigorous appendages to be attached to the body. The true diarthrodial joint was first formed here in fishes, and its basic structure remained essentially unchanged when it was appropriated by the limbs of land animals... Thus, the jaws led the way in all joint evolution."[4]

The property which made moveable jaws especially valuable was their ability to bear teeth which could be used as tools to crush or incise food. Teeth arose almost simultaneously with moveable jaws by the simple modification of the dermal denticles surrounding the mouth. The first teeth were epithelial outgrowths in the skin or mouth lining. Soon afterwards teeth became attached to the underlying bones - appearing on all the jaw bones, several palatal bones, and the rod-like tongue in many primitive fish. At this time jaw action simply consisted of approximation of upper and lower teeth which were specialized for different food sources. Thus sharp teeth for cutting were found in sharks, and flat teeth for crushing were found in rays and skates.[5]

Life on land provided impetus for major new evolutionary developments, because vast nutritional sources were stored there in nuts, seeds, and vegetable matter. With the increase in metabolic activity needed to hold the body out of water and transport it around on land, these nutritional sources had to be efficiently utilized. Breaking them down in the beginning of the gut was a way to greatly increase the surfaces accessible to the digestive juices. The many possible ways a moveable jaw could prepare food for digestion gave rise to many new types of masticatory systems.

However, reptiles and amphibians could still not really chew. The mandible was moved straight up and down and used in combination with the neck muscles to tear off food before swallowing it. The simple, slightly recurved, identical, conical teeth which were easily broken off or blunted during function acted as grasping or restraining devices rather than tools for chewing. Food could be torn and punctured, but the postcanines were not capable of processing it to a significant extent. Thus, these early masticatory systems did not yet provide full access to the vast nutritive sources locked up inside cell walls and still unavailable to the digestive process.

THE MAMMALIAN JAW JOINT

The breakthrough that made real chewing possible was the development of a temporomandibular joint at the squamo-dentary about 70 million years ago. Where the dentary bone moved back far enough to make direct contact with the skull, a synovial bursa appeared between two layers of rubbed periosteum and an intercepted muscle tendon to form a whole new type of joint.[6]

The mammalian temporomandibular joint was an entirely new creation and not an adaptation of a previously existing structure.[8] The reptilian jaw joint had served both the hearing and chewing mechanisms. The large stapes, which was also involved in chewing, formed the single middle ear bone; and making it large enough to support vigorous chewing limited the sensitivity of frequency response of the middle ear. In the mammal-like reptiles, the dentary bone increased in size, developing a coronoid process for muscle insertions and a temporal fossa for muscle origins; but the quadrato-articulate joint continued to operate the sound conducting mechanism. In the true mammals, support for the dentary bone became entirely the responsibility of a new joint between the back of the dentary and the squamosal part of the temporal bone, and the articular-quadrate joint was completely removed from any role in jaw support. The quadrate and articular bones became incorporated into the middle ear where they joined the stapes to produce a chain of three tiny ear ossicles. Thus a new mammalian jaw joint developed right beside the old reptilian jaw joint, completely seperating the masticatory and auditory systems and thereby giving mammals the advantage of being able to chew and hear simultaneously.

One advantage of the new jaw joint was that it could withstand significant compressive forces. Using it as a fulcrum allowed the rigid mandible to function like a class 3 lever and transfer strong compressive forces from muscle masses near the middle of the skull to the front of the mandible where they were needed to bite things off.

A second advantage of the new jaw joint was the wide range of movement it permitted. Because a small convexity on the posterior end of the lower (dentary) bone made contact with a generally much larger concavity on the underside of the squamous portion of the temporal bone, the dentary bone could translate as well as rotate.

A third advantage of the new jaw joint was its ability to adapt its growth to be sure the teeth fit together. Petrovic said, “The responsiveness of condylar cartilage growth to local factors may account for the evolutionary success of the phylogenetically new, mammalian joint between the skull and the lower jaw… The regulatory possibility for the mammalian lower jaw to adjust in length to the upper jaw, during growth, certainly favored the selection of genetic variations resulting in facial posteroanterior shortening, in molarization of post-canine teeth, and subsequently, in mastication.”(14)

The combination of increased compressive forces and a new wide range of mandibular movement permitted precise powerful movements of the tooth bearing jaws so that food could be prepared before digestion to a much greater extent than was previously possible. Smaller quantities more thoroughly masticated provided more nutrients with less energy spent procuring the food. In this manner, chewing provided the efficiency needed to maintain a constant high body temperature, and the new temporomandibular joint ushered in the age of mammals.

"In the later part of the Triassic epoch, some 200 million years ago, mammals came into existence. This was a gradual process of evolution from a group of reptiles called the Therapsida or mammal-like reptiles. The earliest representatives were probably unlike any modern mammal. They were very small creatures - smaller even than the tiny pigmy shrew. We do not know if they were viviparous or if they suckled their young. We do not even know if they were warm-blooded (they could probably keep their body temperature above that of their surroundings, but not maintain it constant). We do, however, know that they had developed the mammalian jaw joint between the dentary and squamosal bones - our temporo-mandibular joint, and, in zoological terms, this classifies them as mammals... At this stage we see, also for the first time, attrition of upper and lower teeth."[7]

Soon improvements in the design of the mammalian temporomandibular joint made chewing more efficient. The joint developed a tough disc to separate it into upper and lower compartments; permitting better variability of movement, shock-absorbing capacity, and a mechanism for helping to circulate synovial fluid. The development of a rigid symphysis enabled the body of the mandible to pivot around the working side condyle and thereby transfer significant elevator forces from the balancing side to the bolus, nearly doubling the force available for power-crushing.

THE MAMMALIAN SKULL

The mammalian skull was almost entirely designed to support the movements of the jaws in chewing. Thin membrane bones were perfectly aligned to withstand the compressive pressures generated by chewing, and bony protuberances supported by flying buttresses protruded like handles wherever the jaw muscles needed attachment for applying tensile forces during chewing. The sense organs, areas for airway passage, and any other structures not concerned with chewing were fit in the remaining spaces.[9]

The new mammalian cranium was designed around a simple recurrent architectural theme, with viscerocranium, neurocranium, and vertebral column all aligned sequentially. In front was the viscerocranium, an elongated pyramid which housed the upper air and food passages and supported the sense organs. Its upper surface was formed by the nasal bones, its sides by the premaxillae and maxillae, and its underside by the premaxillae, maxillae, palatine, and pterygoid bones. Behind the viscerocranium, the neurocranium housed the brain and provided passage for the spinal cord. Reinforcing the connection between the viscerocranium and the neurocranium, the zygomatic arches formed wide laterally placed braces. At the back of the neurocranium, a flat occipital plane faced squarely backward to connect with the neck, and the spinal column continued straight backward.[11]

"Disregarding the distraction of detail, the basic plan of the mammalian skull is laid out along quite simple lines. The cranial base, as a forward extension of the vertebral axis, seems to govern its gross form. Growing vital organs are supported above and below the base. The brain, sitting on its upper surface, is covered by a carapace of dermal bone which normally enlarges according to the dictates of brain growth. The several organs of the face and neck, hanging from the lower basal surface, are also encased in dermal bone. The snout is filled by a cartilaginous nasal capsule (an extension of the cartilage of the base) and its derivatives which crowd the casing forward in macrosomatic animals. The mandible acts as an added curved shield molded to fit around the tongue, hyoid, pharynx, larynx and the temporary remnant of the primary jaws, Meckel's cartilage."[12]

“In the viscerocranium were the structures essential for mastication. The upper teeth formed a platform which had to be well buttressed to absorb antero-medially directed power-crush strokes from chewing. The alveolar processes, in which the teeth were embedded, were braced against the maxillary bones by ramps of bone palatal to the upper molars, just as they were braced by thick bone buccal to the lower molars in the mandible. The two maxillae were in turn braced by pillars of bone extending in many directions to areas dispersed around the skull. In the front of the face, compressive forces were transferred directly up to the roof of the neurocranium via the triangular nasal septum as well as around the nasal cavity and the orbit, necessitating the presence of horizontal connectors.”[13]

THE MAMMALIAN MASTICATORY MUSCLES

Nearly all the muscles of the craniocervical area were involved in eating. Flexible cheek and lip muscles, innervated by the facial nerve, helped pick up food and manipulate it in the mouth. The tongue muscle worked together with these cheek and lip muscles to keep pushing the food back onto the occlusal table. The neck muscles pulled the head straight backward to help tear food off, rotated the head back to help open the mouth, and braced the head during chewing and swallowing.

The single reptilian adductor muscle was separated into distinct units (temporals, masseters, and pterygoids), which were arranged in pairs that formed slings around the mandible. With these slings converging onto the mandible from widely separated origins, they were able to exert fine control of mandibular position. This control permitted chewing strokes which could be customized to process each of the many different kinds of food available.

The temporalis muscles were especially useful for vertical chopping. With their long straight fibers they could perform fast snapping jaw closures from wide opening. The masseters and medial pterygoid muscles were shorter, thicker, and more horizontally oriented. From the body of the mandible the masseters extended upward and laterally, while the medial pterygoids extended upward and medially. Working in combination, these muscles formed a pair of slings that could pull the mandible forcefully from side to side for power-crushing of resistant foods.

The jaw opening muscles were much smaller. The suprahyoid and infrahyoids opened the mouth by pulling downward on the chin. In some species, the lateral pterygoids also helped to open the jaw by pulling forward on the mandibular condyles.

During chewing, the jaw opening muscles alternated with the jaw closing muscles in a series of rhythmic sequences designed to efficiently triturate food. In the brain stem, a central pattern generator initiated rhythmically alternating firings to the jaw opening and closing muscles. These firings were then modified by neuromuscular reflexes to create a characteristic mammalian chewing pattern with species specific variations.

Generally the midline of the mandible traced a pathway that was oval shaped as seen in a frontal plane. The oval was very wide in some mammals and very narrow - almost a straight line or a teardrop - in others. However its consistent lateral component, even if small, distinguished it from the truly straight vertical jaw movements of reptiles and amphibians.

THE MAMMALIAN DENTITION

To provide a working surface at the top end of the oval was a sophisticated and longlasting dentition. The highly differentiated and precisely interdigitating teeth developed crown shapes that were individualized to fit their locations, so that in each jaw it was possible to distinguish incisors, canines, premolars, and molars. Their long roots were suspended in their sockets by fibrous slings which allowed small movements to cushion the impacts generated by mastication. The crevice between each root and its surrounding socket became infiltrated with sensory nerves that allowed control of the chewing pathways according to the feel of the food.

With proprioception able to direct chewing function, the consistency of the food available determined the jaw movements that would be used for masticating it. Thus, given the same food, two different species will handle it in the same way irrespective of differences in tooth form; and a single species will show greater variation in the way it handles two different types of food than occurs between members of different species.[15]

OCCLUSAL WEAR

These mammalian masticatory systems were designed to undergo and withstand occlusal wear. The complex occlusal contours with which the teeth first erupted were designed to properly align the erupting teeth. These contours were then quickly eliminated by function. In most species, the teeth had to be reshaped by functional activity before mastication became efficient. Thus the tooth shapes which each species acquired were the ones that helped bring the teeth into proper alignment early in life and then later formed effective chewing surfaces after they were reshaped by occlusal wear.

Because occlusal wear continued throughout life, most mammalian masticatory systems took advantage of a chewing pattern that alternated between right and left sided chewing to maintain functional edges on the teeth so that chewing could remain efficient throughout life. The way this process occurred varied with different chewing patterns, so it will be discussed separately for carnivores, herbivores, rodents, and omnivores in the following pages.

Because occlusal wear continued to remove tooth structure steadily from the tops of the teeth throughout life, special compensatory mechanisms were required to maintain the stability of the bite table. The bite table was the structural platform against which the mandible was exercised. If shortening of the teeth from occlusal wear allowed that structural platform to continually become shorter as the jaws moved closer together, the jaw muscles would have to keep changing their working lengths to maintain chewing efficiency. Therefore a number of compensatory mechanisms evolved to maintain the constancy of the bite table and the supporting facial framework in spite of continuous occlusal wear.

One mammalian masticatory system trait which evolved to compensate for continuous occlusal wear was continual eruption. By means of forces that we don't yet fully understand [18], mammalian teeth (and to some extent the supporting portions of the surrounding bones) developed a tendency to continually rise up and away from their bony bases into the occlusion like a spring-loaded flint in a cigarette lighter.[19] As a result, every millimeter of tooth structure lost to occlusal wear was replaced by a millimeter of new tooth structure brought up into the bite table by continual eruption. In some species, continuous eruption was accompanied by continuous growth of the roots of the teeth so that almost unlimited eruption could occur.

A second mammalian masticatory system trait which evolved to compensate for continuous occlusal wear in conjunction with continual tooth eruption was pulpal recession. As the teeth steadily wore down and simultaneously erupted toward each other, some mechanism was needed to protect the tooth pulps from the loss of the dentin and enamel overlying them so the thermally fluctuating and bacteria-laden oral environment could be kept out of contact with the sensitive pulpal tissues. Therefore tooth pulps developed the tendency to respond to stimulation such as rapid temperature changes and mechanical vibration by receding down into the roots and leaving behind layers of secondary dentin which mineralized to become new chewing surface and thereby provide further protection for the underlying pulps. If attrition on any tooth proceeded faster than the pulp was able to recede, sensitive thermal and tactile receptors in the dentin overlying the pulp produced pain so that chewing on that tooth was avoided until secondary dentin had thickened and mineralized enough to recreate sufficient pulpal protection.

Other mechanisms evolved to maintain the health of the tissues surrounding the teeth as they continuously erupted. The joint between the teeth and the gums was a uniquely difficult area to seal off from the large numbers of micro-organisms which inhabited the mouth. The seal protecting the sterile internal tissues was provided on the outside of the body by a continuous layer of skin and on the inside of the body by a continuous layer of mucous membrane, but sealing off the areas around the teeth as they moved around during chewing and shifted to compensate for continuous wear was much more complex. It required a flexible attachment apparatus involving a sling of fibers attached between the bony sockets and the cementum covering the tooth roots, as well as a narrow sulcus through which fluid could flow outward to carry away food and bacteria.

DIVERSIFICATION OF MASTICATORY SYSTEMS

The biggest advantage of the mammalian masticatory system was its adaptability. By minor alterations in tooth shape, joint contours, and musculoskeletal features; a wealth of different chewing systems could be differentiated from the same basic musculoskeletal plan. A new mammalian species could develop a mouth suitable for grinding plant matter, grasping and holding live prey, gnawing bones, shredding roots, cracking nutshells, or crushing insects. Animals that needed grinding jaw movements developed wide skulls with large molars, animals that needed chopping jaw movements developed long skulls with pointed incisors, insect eaters developed molars suited for puncture-crushing of insect shells, and animals that nibbled food developed incisors surrounded by extensive sensorineural structures.

Soon many divergent specializations of the mammalian masticatory system arose. For each available food source, a species developed a masticatory system which made the best use of it – including its own unique arrangement, angulation, and proportional development of the same basic mammalian jaw muscles in order to enhance the vectors required for chewing the food it utilized most commonly, a skull shape which provided advantageous points of attachment for those jaw muscles, tooth shapes uniquely designed to help perform the usual masticatory tasks, and a facial framework tailored perfectly to resist the forces normally applied during mastication.

In time, a few different developments of the same fundamental mammalian masticatory system characteristics proved most successful. These divergent variations of the same mammalian masticatory system design are generally known as carnivore, herbivore, rodent, and omnivore.

CARNIVORES

Carnivores developed masticatory systems that were vertically arranged with long sharp canines for grasping prey, securely locked-in temporomandibular joints for protection during violent predatory action, and jaw movements that were almost straight up and down. Meat was such a rich food source that it didn't need much preparation before digestion. Of prime importance was wide opening and fast snapping closure.

Since these actions required long fibers, the temporalis muscles became especially well developed. An expanded temporal fossa and an enlarged coronoid process provided horizontal space for more muscle mass at the temporalis origins and insertions, and a long narrow skull provided vertical length to accomodate long temporalis fibers. Extensive development of type 2B muscle fibers provided the rapid forceful contractions that were useful in the capture of prey, although they tired easily.

The temporomandibular joints functioned like hinges which could not translate antero-posteriorly, and jaw movements consisted primarily of opening and closing by rotation around the condyles which were almost completely encircled by cylindrical bony flanges of the squamous temporal bone. Such a tightly locked-in and secure joint helped provide protection from the trauma that presents a real danger when animals being preyed upon have only seconds to fight for their lives.

Most important was bracing the mandible against retrusive forces which could drive the mandibular corpus into the airway or the mandibular condyles into the ears, so the interdigitation of the lower canines in front of the uppers with each closure served to lock the mandible forward. Since the canines were so much taller than the other teeth, this canine guided protection against retrusion functioned even with the mouth part way open.

CARNIVORE CANINE GUIDANCE PREVENTED MANDIBULAR RETRUSION

At the top of the long thin oval pattern of mandibular movement was a slight but significant lateral shifting of the mandible, as the cylindrical condyles shifted sideways in the tubular slots of the glenoid fossae. The presence of this lateral shifting during function served to keep the teeth sharp. In the molar region, the mandibular arch fit completely inside the maxillary arch so that the buccal surfaces of the lower molars faced the palatal surfaces of the upper molars. These two facing surfaces were convex, both anteroposteriorly and superoinferiorly, and hence could not be brought into contact at more than one point at a time. As the mandible shifted laterally during function, these surfaces worked together like two shears which fed each other and thereby maintained a marked mesiodistal cutting edge.[21][22]

Brodie likens the carnivore dentition in function to a pair of scissors, explaining, "Scissors have two blades with faintly concave surfaces facing each other but only one edge of these surfaces can be brought into contact with the other. The blades, when viewed from their edges, are also faintly concave in their length dimension so that only one point of the edge can be in contact with the other at one time. Thus, when the scissors are closed, the edges of their blades are in contact only at their very ends. As the scissors are opened, this point travels backward until, at full opening, it can be seen that the cutting edges cross each other. Upon closing, the contacting point travels forward and it is only at this precise point that work is done. Since the cutting edges of the blades are bevelled and their facing surfaces are concave, the scissors sharpen themselves while they work."[17]

HERBIVORES

In contrast, herbivorous masticatory systems were wide laterally instead of long vertically. Herbivore mastication was characterized by leisurely prehension followed by prolonged, forceful milling of relatively hard, resistant plant substance, so herbivorous masticatory systems were suited for slow powerful grinding rather than quick chopping. Horizontal rather than vertical motion was well developed. Maximum gape was limited, and lateral movements were wide and free.

To power such function, the pterygomasseteric slings rather than the temporal muscles became well developed. The mandibular angles where they inserted were large, and the zygomatic arches and pterygoid plates where they originated were set far apart in short wide skulls so the masseters and medial pterygoids could pull the mandible strongly from side to side. Fatigue resistant type 1 muscle fibers predominated. There was only a short, slim, coronoid process and small temporal fossa for the attachment of the much diminished temporalis muscle. The lateral pterygoids were well developed to assist in unilateral grinding movements.

For the TMJs to accommodate such a wide range of movement, both the condyles and fossae were nearly flat. With such flat joint contours, the condyles could freely slide around both laterally and antero-posteriorly during function. The joint capsules were loosely arranged to allow this wide range of mandibular movements.

The back teeth rather than the front teeth were well developed. Anteriorly, the incisors and canines were diminutive or absent where no vigorous prehension was required. Posterior teeth developed extensive chewing surfaces for milling large masses of plant matter and long roots to support extensive chewing. In most cases, the grooves on the occlusal surfaces were oriented antero-posteriorly so they would grind efficiently when the mandible moved in laterally directed power strokes. In a few herbivores, like elephants, the grooves were oriented buccolingually, and the mandible moved mesiodistally.

The complex occlusal topography of high finger-like cusps and ridges separated by deep valleys with which the teeth first erupted aligned the teeth as they came into the bite. The processes associated with tooth development and eruption could not aim the upper and lower teeth at each other with the precision they required for effective function, and misalignment of the teeth was often fatal. Therefore, as the upper and lower teeth erupted toward each other and began to fit together, their occlusal surfaces interdigitated to guide them into the precise alignment they needed for effective mastication.

After the teeth were fully erupted and interdigitation was no longer needed to align the teeth, attrition quickly reduced the cusp tips and created closely fitting irregular contours suitable for grinding. Dentin wears more quickly than enamel, so the dentin became cupped out while the protruding rings of enamel surrounding the cupped out dentin formed effective grating surfaces.[23]

As in carnivores, occlusal wear occurred in a manner which maintained functional edges on the teeth in spite of constant abrasion from grit in the foods. The articular eminence disarticulated the condyle on the non-working side each time the mandible was swung to the working side, imparting a rocking movement to the mandible during mastication. This rocking movement sharpened the edges on the non-working side during each chewing stroke of the mandible on the working side.

Extensive wear also occurred between the teeth (interproximal wear). Since occlusal contact occurs on one tooth at a time, individual teeth moved up and down and rubbed against their neighbors during chewing. The resultant continuous interproximal wear progressively narrowed the teeth mesio-distally. If such interproximal wear were permitted to open up spaces between the teeth, the spaces would form food traps leading to food impaction, periodontal disease, and tooth loss. To prevent such problems, the dental arch developed the property of continual mesial migration. Throughout life, the back teeth drifted toward the front just far enough to fill in any spaces that developed from interproximal attrition and thereby maintain contact around the perimeter of the dental arches. Animals like the kangaroo, sheep, and elephant required continuous mesial migration just to maintain an effective functional occlusion.[25]

RODENTS

A rodent masticatory system was much like a herbivore masticatory system with a large antero-posterior component. It was designed for gnawing and chewing very resistant vegetation, including nuts and seeds. Large forces had to be applied to one small area at a time, either at the front or back of the mouth, depending on the task. This required structural features that were primarily arranged antero-posteriorly instead of laterally. Thus, rodent skulls were long antero-posteriorly, and the mandible could move very far forward and backward.

Rodent lateral pterygoids were extremely well developed in order to power the extreme anterior movements which placed the incisors in an edge-to-edge position for gnawing. The masseters and medial pterygoids were also well developed to permit application of large elevator forces when the mandible was held anteriorly.

Rodent temporomandibular joints allowed the condyles to slide inside long antero-posterior grooves. Enclosed by bony medial and lateral walls, the joints were protected from dislocation laterally or medially.

Rodents dentitions were also oriented antero-posteriorly. There were long spaces between the front and the back teeth so that the anterior and posterior occlusal tables could not both be engaged simultaneously, but the mandible could move forward to engage the front teeth or backward to engage the back teeth. The molars had grooves running buccolingually so they could grind food effectively as the mandible moved forward and back.

In between functional tasks, the teeth were rubbed together in a gnawing behavior which kept their edges sharp. Brodie explains, “rodent incisors at eruption are cone-like and covered with enamel on only their labial surfaces. Chisel sharpness is imparted to this enamel and maintained by an alternate passing of the lower tooth against the lingual and then the labial surfaces of the upper - the lower sharpening the upper during one stroke, the upper sharpening the lower during the next. The rodent must engage in this tooth sharpening activity continually to adjust for the rapid and continuous growth of these teeth.”[24]

OMNIVORES

Although these highly specialized carnivore, herbivore, and rodent masticatory systems were very effective at dealing with the types of foods for which they were designed, eventually environments shifted and overspecialization became a disadvantage. Generally species that had become too dependent on the continued presence of a very specific type of environmental condition or food source were sooner or later replaced by more adaptable designs. When one particular food source became no longer available, these more adaptable organisms were able to switch to a different one. A big step in increased adaptability was the omnivore.

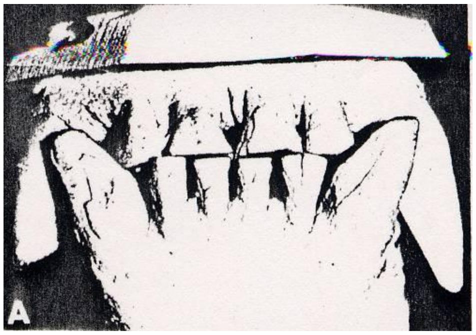
Pigs, monkeys, and bears developed masticatory systems that were able to chew a wide variety of foods. Skulls became shorter and rounder, and jaws became deeper rather than longer so that they no longer projected far out beyond the rest of the face. Locating the working portion of the mandible closer to the elevator muscles allowed jaw movements that were powerful and precisely controlled so they could be tailored to fit different food sources.

Omnivore jaw muscles were present in balanced proportions. The horizontal grinding muscles (medial pterygoids and masseters) were roughly the same size as the vertical chopping muscles (the temporals). The lateral pterygoids were well developed for unilateral grinding or protruding the mandible.

Omnivore temporomandibular joints incorporated both sliding and hinging movements. The mandibular condyles became located well above the level of the corpus so that chewing forces could be applied in a wide variety of directions against the bolus. In front of them, the articular eminentia formed slopes which allowed a range of antero-posterior and lateral movements.

Omnivore teeth were all-purpose chewing utensils which combined features of previous dentitions. In bears a basically carnivorous system lost the carnissal blades and enlarged the distal cheek teeth to form flattened crushing structures. In apes, the entire dental arcade retruded on its osseous base to a location closer to the center of mass of the elevator muscles, and the occlusal tables flattened to allow a wider range of jaw movements. Generally the canines were shorter than in carnivores, but they still interlocked during closing to protect the TMJs from retrusive forces, as can be seen in the frontal view of an ape dentition below:

APES MAINTAIN CANINE PROTECTION AGAINST MANDIBULAR RETRUSION

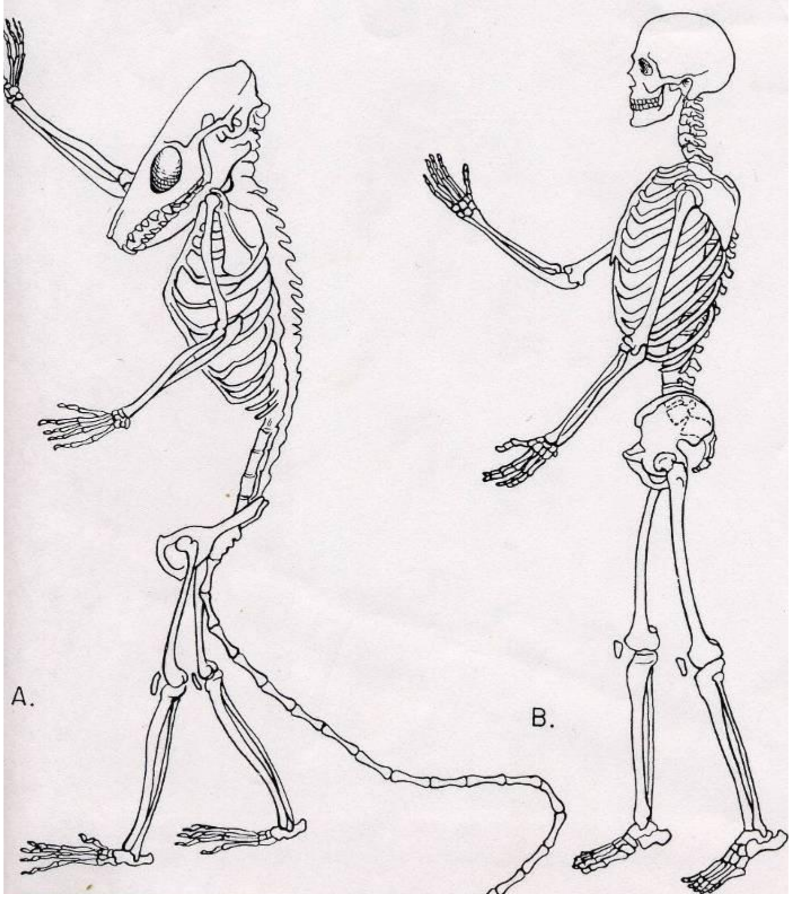


UPRIGHT POSTURE

Then, at least a few million years ago, early versions of Homo acquired habitual upright posture. This radical change, more than any other feature, distinguished us and our ancestors from other primates. It also changed the masticatory system by involving many of its components in the head posture mechanism. As DuBrul used to comment, "To understand the teeth, you need to look at the feet."

Upright posture required profound changes in the body's structural components. Previously the basic arrangement of mammalian body parts had been in a simple linear sequence parallel to the ground and supported by four widely spaced vertical struts. Structures simply hung from these struts and the beam connecting them. The forward ends of the food and air channels, hanging in sequence from the forward portion of that beam, were easily kept separate and scarcely affected by movements of the head or mandible. Simply uprighting one of these beams would create a tower with a tendency to keep collapsing forward, as can be seen below left.

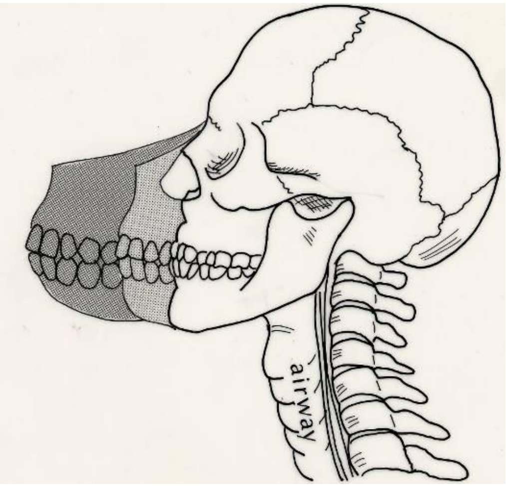
In contrast, the bipedalism shown in the hominid (below right) has more stability, because its center of mass is aligned generally on a plumb line through the center of the pelvic girdle and over the feet. This central location of the gravitational axis frees major muscle groups from their role in support and allows them to stay ready for action.



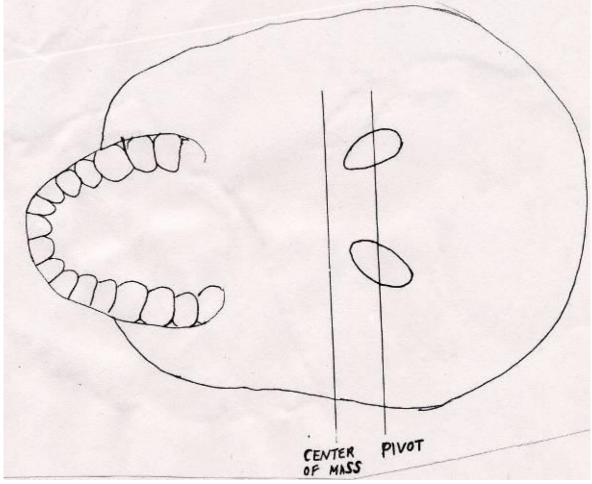
UPRIGHTING A QUADRUPED WOULD CREATE AN UNBALANCED STRUCTURE

AN UPRIGHT HOMINID CREATES A MORE BALANCED TOWER

Realigning the body’s structural features to enable balancing the head on the top of an upright vertebral column required a number of changes in head shape. The large snout, which had been receeding in homo’s predecessors, moved in as close as possible to the cranial base, bringing its weight close to the pivot where the head rested on the top of the vertebral column, as can be seen below. As the snout became smaller, its thermoregulatory function was replaced by a nearly hairless skin containing many sweat glands and an elaborate vasomotor control system for temperature control.



At the same time, the location of the pivot where the head rested on the top of the vertebral column moved more nearly underneath the center of mass of the head, as shown below. In quadrupeds, the head hung by its back end (occiput), and the neurovascular connections to the rest of the body (the occipital foramen and occipital condyles) were conveniently located at the posterior end of the cranial vault. Trying to perch this type of skull on the top of a vertebral column would require tremendous traction forces downward at the back of the cranium in order to prevent the head from rolling down onto the chest. Therefore, before posture could go habitually upright, the shape of the skull had to change to bring the occipital condyles, (where the head pivots on the top of the vertebral column), to a position almost under the center of mass of the head.



With the head relatively centered over a double condyle articulation on the top of the vertebral column, it could pivot on its base and thereby move around quite freely in relation to the rest of the body. The muscles of head rotation, the sternocleidomastoids, became better developed, and the mastoid processes to which they attached became elongated. With the head able to rotate approximately 180 degrees, the eyes could come close together in the midline and develop stereoscopic vision without losing the wide field of view that was obtained with eyes on each side of the head.

Another change in the shape of the head was required to set the stage for upright posture. If the attachment of the quadruped head to the vertebral column were not fundamentally altered as the vertebral column was tilted upright, the viscerocranium containing the sense organs would be aimed uselessly at the sky and the semicircular canals would lose the ability to maintain balance.[26] Thus for the viscerocranium to maintain its orientation with the horizon, the skull was bent sharply in its midsection.

"Bending the skull produced an effect similar to bending a bar of taffy. The top curved and the bottom buckled. The cranial effects were therefore: (1) curving of the cranial roof, (2) buckling of the cranial floor (at sella turcica), (3) extreme retrusion of snout and jaws, (4) deepening of the mandible with outward flaring of its lower border, especially at the chin, and (5) downward and forward swing of the nuchal plane carrying the foramen magnum and occipital condyles forward toward the center of the skull."[27]

The bending of the cranial base opened up the top of the skull. Once the brain no longer had to fit in between the viscerocranium and the occiput, it could expand upward and outward. Also the resulting dome shaped cranial vault provided strategic points of origin for the temporal muscles.

The bending of the cranial base compressed the underside of the skull - forcing together many of the structures of the face and creating a sharp bend in the airway where the oro-nasal airway met the pharyngeal airway. Numerous changes had to be made to accommodate this bend in the airway. The tongue became balled up and crowded back into the pharynx, a secondary palate was developed to separate the nasal passage from the mouth, and an elaborate mechanism was developed for safeguarding the entrance to the pharynx. The lower border of the mandible flared out until it came to bound the largest area of the neck to provide space for an airway trapped between the mandible and the cervical spine, and rigidity of the mandible was provided by a chin which was externally located so it would not impede the airway.

To maintain a habitual erect stance required a weight bearing alignment in which all the skeletal muscles could stay relatively relaxed and therefore ready for action. Therefore to distribute the forces generated from weight bearing evenly among its skeletal supporting structures, the chains of muscles running up the front of the body counterbalanced those running up the back of the body, and those on the right side counterbalanced those on the left side. Acting together, these myofascial chains surrounding the vertebral column formed a reciprocal tension mechanism which held the vertebral column erect much like stays hold the mast of a sailboat erect. During function, the musculoskeletal system moved away from this alignment and then back to it, guided by an almost perfectly simultaneous reciprocal inhibition in agonists and antagonists which ensured smoothness of movement.

On the sides, this reciprocal tension mechanism had inherent stability. The shoulders extended out widely to the sides, forming strategic points for muscle attachment bilaterally. Down lower, the hips also projected way out to the sides, making a stable base for the kinetic chain above. Still further down, the two feet placed side by side created a stable foundation to resist sideways tipping of the whole structure. Thus, in the frontal plane, design was symmetrical, and the output of energy required for maintaining a static equilibrium was held to a minimum.

To resist tipping to the front or back was far more difficult for a body so tall and flat. In the dorsoventral direction, symmetry was lost right from the top. The skull's center of mass was still located somewhat in front of its occipital condyles. To prevent it from rolling forward onto the chest, its occiput was anchored to the vertebral column and back of the shoulders by a thick postcervical muscle mass. These postcervical muscles had already been well developed in quadrupeds, where they prevented the snout from dragging on the ground. In humans, they were afforded especially good purchase on the back of the head by a prominent occipital protuberance and an elongated mastoid process.

A very different kind of mechanical system was needed to hold down the front of the skull. In this area flexibility was required to allow functions such as swallowing, rotation of the head, coughing, vomiting, spitting and speech – each of which depended on independent movement of parts within the total framework. In addition, the muscles at the top end of the anterior kinetic chain could not be attached directly to the front of the head, where the sense organs left little space available for large bony processes. Thus, to counterbalance the strong straight pull of the postcervical muscles, several long thin precervical muscles were attached at various angles between a series of small bones stretching from the sternum to the mandible. The long rigid mandibular body then transferred the traction of the anterior kinetic chain around the sides of the head by means of the powerful jaw closing muscles.

HOMO SAPIENS

In the succeeding lines of homo, the most successful were those with a musculoskeletal structure that was lightweight and adaptable. A large number of neural pathways to protect vital functions and more sophisticated means for acquiring food obviated the need for massive strength and structure. The superficial head of the temporalis muscle and the protruding supraorbital region diminished. The "puffed" out lateral walls of the maxillary sinuses provided support for the teeth without impinging on space needed for respiratory and sensory functions. The muscles of facial expression became highly developed for better communication.

Homo sapiens sapiens was so successful in evolutionary terms that it was able to adapt to almost any type of environment, and it soon spread all over the surface of the earth. Its genetics is basically what we inherit today and therefore is all we have to work with until we develop the technology to directly manipulate our genetics. For that reason, even though it works differently today, this is the masticatory system which we need to understand.

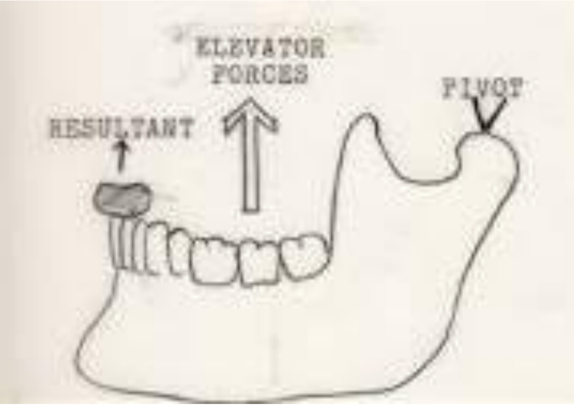
HUMAN JAW MUSCLES

In many ways, the arrangement of jaw muscles in humans was a blend of previous mammalian models. Combining the vertical components of carnivores with the lateral components of herbivores and the antero-posterior components of rodents provided a range of jaw movements that was versatile and complex.[31] The jaw closing muscles could deliver power-crushing forces in a wide variety of locations and directions so each stroke could be altered to fit the mechanical requirements of the particular chewing task at hand.

The temporal muscles controlled jaw posture. Right and left temporal muscles formed a single bilateral sling which suspended the mandible by its coronoid processes from attachments all over the side of the skull. They were multipennate muscles; with separate groups of anterior, middle, and posterior fibers. Type one fibers, resistant to fatigue and generally active in postural control throughout the body, dominated the deep portions of the muscle.[28] During chewing they acted mainly as stabilizers, and the tension they exerted depended largely on the position of the mandible.[29]

The medial pterygoid and masseter muscle of each side formed a unilateral sling which generated power for chewing. With these two muscles diverging so strongly from their common insertions on the mandibular corpus to their origins on the underside of the skull, they could pull the mandible strongly up and to either side at a wide variety of angles. Type 2 muscle fibers in their posterior sections delivered extremely powerful forces when food was brought to the back of the mouth. Gradually increasing activity leading to primary discharge during the final power-crush stroke suggests that these muscles were used for developing large loads between the teeth and were not particularly sensitive to the position of the mandible.[30]

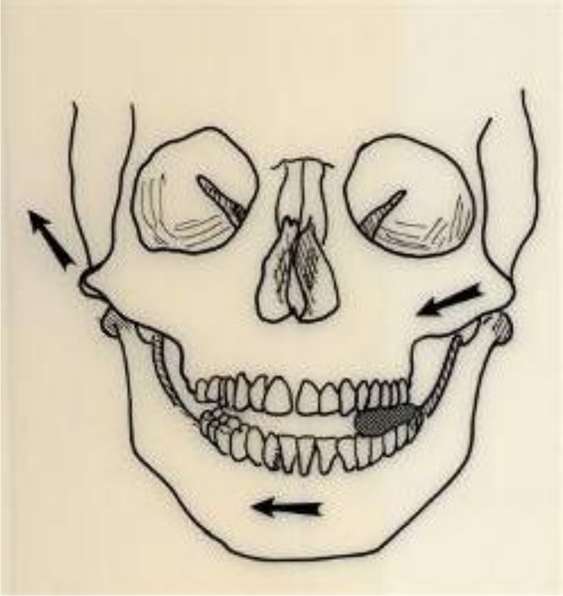
The superior lateral pterygoids, working with long inclined articular eminentia, controlled the precise position of the mandible at which the elevator muscles showered down their forces. When food was at the back of the mouth, the superior lateral pterygoids allowed the condyles to seat in braced positions at the base of the articular eminences so the center of the jaw closing muscles was located over the bolus. When food was at the front of the mouth, as shown below, the superior lateral pterygoids held the condyles down and forward on the articular eminences and thereby made the mandible a class 3 lever.



During function the superior lateral pterygoids fired independently to enhance chewing efficiency. Because of their orientation angled almost thirty degrees medially and their insertion onto the mandible at the condyles separated from the body of the mandible by a long lever arm, they could control the position of the mandible in a horizontal plane like steering a bicycle by its handlebars. During the final stages of chewing, they added a twisting motion which helped crush food much like crushing a cigarette butt with the ball of the foot. As the mandible approached the midline from the working side and the elevators applied large compressive forces to the bolus, the nonworking side posterior temporalis pulled backward and upward while the working side lateral pterygoid pulled forward and inward. These two muscles functioning together thereby formed a force couple[32] which pulled the working condyle anteriorly, medially, and inferiorly; while it pulled the nonworking condyle posteriorly, laterally and superiorly, rotating the mandible around the bolus as shown in the illustrations below.

BALANCING SIDE CONDYLE

MOVES BACKWARD



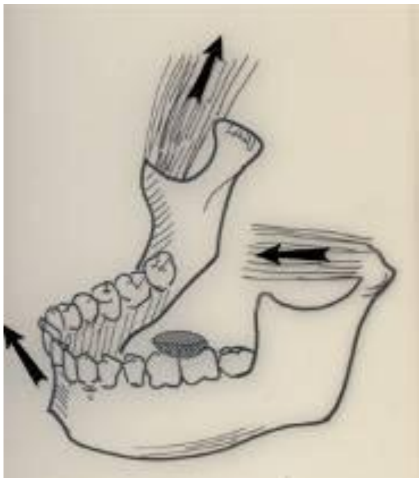
WORKING SIDE
CONDYLE
MOVES
FORWARD

MANDIBULAR MIDLINE SHIFTS FROM WORKING

SIDE TOWARD BALANCING SIDE

BALANCING SIDE CONDYLE

SHIFTS BACKWARD



WORKING SIDE
CONDYLE SHIFTS
FORWARD

MANDIBULAR MIDLINE SHIFTS FROM

WORKING SIDE TOWARD BALANCING SIDE

After reaching the central bracing position (the intercuspal area), the mandible continued its path through the midline and onto the balancing side in a follow-through phase which lengthened the power-crush stroke by bringing the lower buccal cusps in approximation with the upper lingual cusps on the working side. At the same time, the balancing side was separted by the thickness of the bolus. Then, at the end of this follow-through phase of the power-crush stroke, the balancing side condyle reached its posterior limit and started moving forward along with the working side condyle. Finally, with both condyles moving forward, the mandible smoothly transitioned into its opening phase.

Jaw opening was the responsibility of two groups of muscles which acted as a force couple to rotate the body of the mandible down and back. The inferior lateral pterygoid muscles, pulling the condyles down and forward, were relatively short and strong and therefore useful for fast opening. The digastrics and suprahyoids, pulling the front of the mandible down and back, were relatively long and thin and therefore especially useful at wide opening when their leverage began to increase just as that of the lateral pterygoids began to decrease. With the inferior lateral pterygoids pulling the condyles down and forward at the same time the digastrics and circumhyoids pulled the front of the mandible down and back, jaw opening came to consist of a cocking action with the center of rotation in the ramus instead of a hinging at the condyles which would push the lower border of the mandible into the airway structures.[76] This rotation of the mandible around the middle of the ramus prevented excessive stretching of the masseter muscle and protected the neurovascular bundle where it entered the mandible at the mandibular foramen.[77]

HUMAN JAW MUSCLE CONTROLS

Controlling and coordinating the human jaw muscles was a neural network that was uniquely extensive and complex. A tremendous amount of sensory information from both nearby and remote sites contributed to complex arrangements of facilitating and inhibiting effects that involved many different receptor types and afferent pathways as well as numerous brain-stem and higher-brain centers.[84]

Chewing was initiated by a central pattern generator which strummed a constant background of repetitive firing. "As voluntary fibers pass through the reticular formation to fire the motor nerves of masticatory muscles, their collateral branches set off special short repetitive circuits which call out the measured cadence of the chewing cycles. In doing so they coordinate the simultaneous movements of jaws, cheeks, lips and tongue."[88]

Yet, the simple repetitive firings which drummed out chewing rhythms were also subject to many influences before determining the final mandibular movement for each chewing stroke. A vast array of sensory receptors was needed to keep track of the position of the mandible in spite of rapid and unpredictable changes in the bolus, so mechano-receptors were distributed abundantly throughout the periodontal ligaments(89-91), oral mucosa[92], periostea[93], TMJs, and muscles of the jaw and face.[94] The sensory receptors surrounding the teeth are sensitive enough to detect a force of 1.5 grams or an occlusal discrepancy of .02 millimeters.(85-87) The sensory receptors in the TMJs constantly monitor the position of the mandible, even when there is no tooth or bolus contact to stimulate periodontal ligament receptors.(95-99) Electrical activity from intramuscular receptors such as muscle spindles and tendon organs respond rapidly to a constantly shifting resistance.[101] All this sensory feedback was then combined with central inputs and processed through interneurons so the resulting output to the jaw muscles was able to finely control the movement of the mandible while the soft tissues of the tongue, cheeks and lips continually pushed the food onto the bite table and then darted out of the way of the teeth.(100)

The jaw muscles were armed with extensive neuromuscular reflexes to protect the TMJs. Monkey experiments have shown that, even when mechanical forces applied to the mandible result in great pressure on the teeth, the joints are generally spared.[102] Reflex protection of the TMJs by preventing the application of lateral forces at the condyles is probably the reason that adding steep incisal or canine guidance to a dentition automatically decreases the functional forces applied by the jaw closing muscles.

The jaw muscles were also armed with extensive neuromuscular reflexes to protect the teeth and their supporting tissues.[103] Sensitive mechanoreceptors in the periodontal ligaments which covered the roots of the teeth like the fingers of a glove were able to alter the pattern of jaw muscle firing so rapidly that, in response to striking a stone in a bolus, the path of the mandible could be changed within milliseconds.(104-106) Even acoustic signals, mechanical vibration, electrical stimulation of pulpal nerves, and pain from almost any area of the face are able to alter the firing pattern of the jaw muscles, and larger forces also activate the jaw opening muscles.[107-111] Because of these protective reflexes, a cantilever bridge receives less force during chewing than a tooth borne bridge[112], and a tooth made tall enough to theoretically receive the full force of the mandible actually experiences surprisingly small forces during function due to altered muscle firing.[113]

At the same time, positive feedback loops prevented the jaw muscles from being able to shower down strong forces unless the periodontal receptors signaled widespread stable occlusal contacts.[116-118] For that reason, maximal voluntary bite force is positively correlated with occlusal stability[119-120], and even simply anaesthetizing the teeth causes a significant reduction of maximal voluntary bite force. [121]

There were so many protective mechanisms able to inhibit the functional movement of the mandible that the central nervous system had to be able to limit their influence or they could prevent the necessary application of power on the working side during chewing by creating a kind of central nervous system gridlock. To prevent such gridlock, throughout each power-crush stroke, inhibitory neurons diminished the responses to sensory stimulation on the working side so that basic chewing strokes could continue unhindered.[114]

Although an enormous number of neuromuscular reflexes were able to protect the masticatory system, few were active during normal function. The neuromuscular system had a way of incorporating mechanical irregularities such as crooked teeth or spinal injuries into the pattern of habitual functional movements so that protective reflexes would not be constantly activated and interfere with efficiency. The adaptive movement patterns which resulted from this ability of the neuromuscular system to dance around obstacles are called engrams.

A simple analogy has been used to explain engrams. "Imagine that your job requires you to walk constantly through a very narrow hallway that has a series of boards protruding from the wall every two feet. These boards are so situated that the top of your right shoulder hits each one as you walk by. Your choice is then to allow your shoulder to hit the boards or learn to reposition your shoulder slightly lower so that it is below the level of the boards as you pass by. Of course, your choice would be to learn quickly to walk with your right shoulder slightly lower than your left to avoid any trauma from the boards."[123]

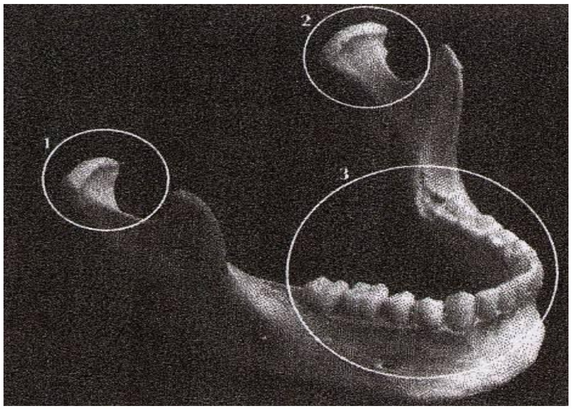
Just as engrams in the leg muscles allow us to walk on a hurt foot with a limp which protects the foot from further damage, engrams in the jaw muscles minimized loss of functional capacity from injured or irregular teeth by incorporating slight modifications into the same overall muscle firing which optimized efficiency in chewing and swallowing. When an obstacle to normal jaw function is experimentally placed in the dentition, the neuromuscular firing pattern is very much altered initially, but eventually reestablished itself almost completely in spite of the continued presence of the obstacle.

Postural muscle controls were integrated with jaw muscle controls. The jaw muscles and the craniocervical muscles recruited each other frequently, and most had roles in both mastication and posture. The postcervical muscles fired to stabilize the head by pulling down on its back end during swallowing when the anterior kinetic chain was contracting, and the neck muscles fired rhythmically to prevent the head from rocking during chewing.

THE HUMAN MANDIBULAR ARTICULATION

The template against which the jaw muscles functioned, (like the shape of the hallway used by the muscle engrams controlling the mandible in the analogy above), was a tripod of support simultaneously at the bite table and the two TMJs. (133) Wherever the mandible moved, it was supported at each of these three areas by platforms which provided stable support for the mandible to rest on and to work out against. With all three areas of the mandibular articulation functioning cooperatively to provide continuous solid support for the mandible, the whole mandibular articulation functioned with the harmony of a single joint.

THE TRIPOD OF SUPPORT AT THE MANDIBULAR ARTICULATION



An important role of the mandibular articulation was to provide a means for bracing the mandible. The mandible was braced when the jaw closing muscles immobilized it by locking it up against the teeth and the TMJs in a fully seated central location.

Bracing the mandible was needed for postural stability, because the jaw closing muscles needed a great deal of flexibility for functional tasks, but a mandible that was free floating could form a weak link in the anterior kinetic chain. A braced mandible provided a solid handle for the anterior myofascial chain to exert downward traction directly on the front of the skull.

Bracing the mandible was also needed during swallowing. At the onset of each swallow, a braced mandible was needed to provide a stable platform against which the tongue could push its tip forward to collect the food at the front of the palate. Then, later in the swallowing process, a braced mandible was needed to provide a fixed base against which the suprahyoid muscles could pull the hyoid bone upward and thereby allow the food to pass behind it.

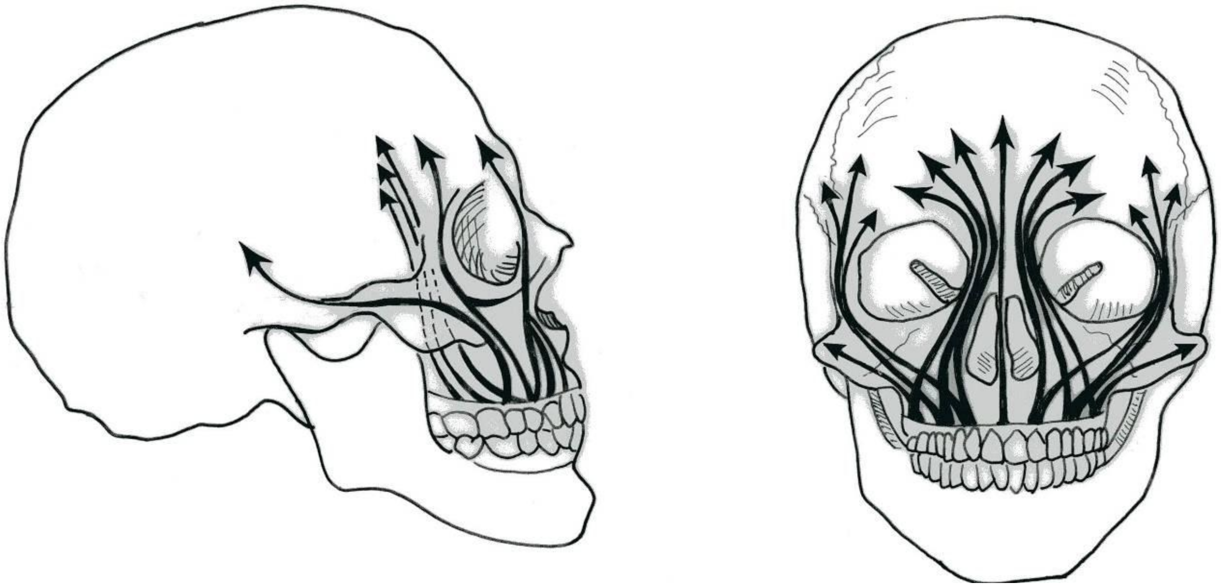
Bracing of the mandible was also needed for protection. The mandible was a heavy bone which hung freely below the skull with its back end close to many vital structures including the hearing and balance centers, the temporomandibular joints, and the temporal lobes of the brain. A blow to the mandible could impact it like a hammer against these structures. Thus the first reaction to danger was to protect the vital structures in the area by bracing the mandible.

THE HUMAN BITE TABLE

The support at the front of the human mandibular articulation was provided by the bite table. In many ways the bite table was a unique type of joint between the upper and lower jaws. Unlike other joints, this maxilla-mandibular joint had a fixed end point and rock hard articular surfaces.

The members of the bite table were well designed to absorb shocks. Each tooth was individually suspended by a circumferential fibrous sling embedded in a layer of collagenous ground substance with interstitial fluid and an elaborate system of vascular plexes.[48] Pressure which intruded a tooth root into this structure tugged on the sling, drove fluids into nearby vessels, bent out the walls of the socket, and thereby provided resistance which increased steadily as the tooth moved further from its rest position.[49] Release of pressure then permitted rebound of the tooth, first by elastic recoil and then by a slow hydrodynamic phase with superimposed pulsation.[50-52]

The bones supporting the teeth also had shock absorbing capacity. Laterally, at the canine and premolar areas, the walls of the maxillary sinuses and nasal cavity transferred chewing forces up to the supraorbital ridge. Further laterally and back in the molar areas, the zygomatic arches transferred chewing forces to bone diverging out along most of the sides of the head. Deeper in the face, the wings of the sphenoid bones transferred medially directed chewing forces up to the cranial base. Endo showed that chewing forces compress the frontonasal region and cause bending stresses in the middle and upper portions of the maxillae and the nasal bones. Benninghoff loaded skulls coated with a stress sensitive paint to illustrate the distribution of compressive forces during chewing. His findings are shown below.



During function, all of these bony supports flexed, the mandible and the alveolar processes bent, and the maxillae were intruded into a set of circum-maxillary sutures which remained open throughout life. Even the bioelastic pressure-bearing synchondroses of the cranial base and the neurocranial sutures helped to dissipate the high-magnitude strains produced during mastication.(10, 145-146)

Human teeth combined elements of the preceding mammalian masticatory systems to form a highly adaptable hybrid. Incisors, canines, premolars, and molars were all moderately well developed. The canines only projected slightly past the occlusal plane so they no longer restricted the range of motion of the mandible (and no longer provided protection against mandibular retrusion).

Each tooth acquired a position which made it an integral part of a smoothly functioning dental arch by erupting just until bite forces stopped its eruption when it began to impinge on the normal mandibular range of motion. Spreading chewing forces out laterally produced wide flat bite table contours. Spreading chewing forces out antero-posteriorly created a curve of Spee that rose at a gradual angle in the front and back of the dental arch.

Once all the teeth had erupted, upper and lower dental arches articulated as a single joint - with a central bracing position (characterized by one area where all the back teeth fit together simultaneously and the mandible was as close to the midface as possible) surrounded by gradually sloping walls which acted like the walls of a bowl surrounding the mandible. In which ever direction the mandible moved from this central bracing area, it ran into the overhanging sloped wall of tooth structure located in that direction. When the mandible moved forward, the lower front teeth rode up on a wall of upper front teeth while the back teeth separated. When the mandible shifted to one side, the lower teeth of that side rode up on a wall formed by the buccal cusps of the upper teeth of that side while the teeth of the opposite side separated. When the mandible moved backward, it rode up on the palatal cusps of the rearmost molars of both sides while all the other teeth separated.

During the power-crushing of food, the buccal cusps of the lower teeth were driven into the fossae of the upper teeth like a pestle against an upside down mortar. Contact began at the back of the arch and moved steadily forward. Then, as the mandible followed through to the balancing side, contact on the balancing side was eliminated because of the thickness of the bolus on the working side. Thus the balancing side contacts were non-articular facets. The congruence between them was obvious, but they rarely participated in the guidance of the mandible during function.

GROUP FUNCTION OF THE TEETH

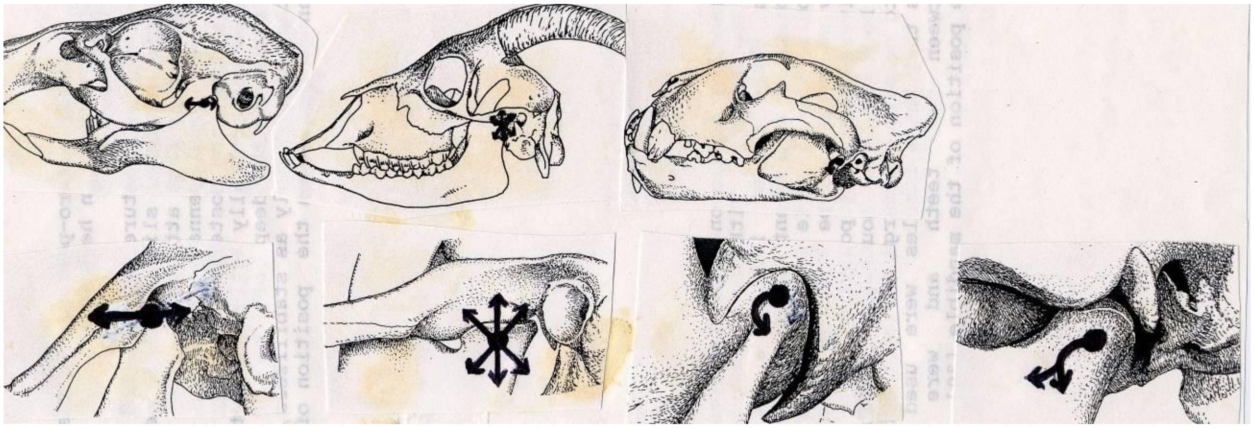
Eventually the best fit of the biting surfaces to mandibular pathways created an arrangement of opposing teeth known as group function. Adjacent teeth formed a continuous arch which delivered, absorbed, and transmitted forces as a single unit - much like stones in a wall. By this sharing of articular forces, each tooth was protected from the danger of receiving the full impact of the mandible, and functional capacity was maximized. Chewing forces were applied along the arch in a wavelike fashion, with a single point of tooth contact moving up and down and even across the dental arches.[16] As the mandible rocked back and forth from side to side in this fashion, it created a shearing action between the upper and lower dental arches.

By spreading out these forces among a large number of contacting surfaces, group function also maximized longevity of the masticatory system. Throughout human evolution, rapid attrition was the most frequent cause of dental disease and the primary threat to the stability of the masticatory system. In group function, attrition was shared by all the teeth and thereby resisted as effectively as possible and for as long as possible. Teeth didn't wear out in one area until they were almost worn out everywhere.

Group function was so important for the health of the masticatory system that it was established even when a single intercuspal area was not. After studying aborigines still living in their native environments, Barrett noted that a number of them lacked a single position of bilateral maximal intercuspation - instead having stable unilateral intercuspal positions on each side. These two unilateral intercuspal positions could not be used simultaneously, but alternated providing a solid platform for the mandible during function.[127] This same type of occlusion, without any bilateral intercuspal position, is found in many other mammals[128]; and, in the humans studied by Barrett, it was not associated with any pathology.

THE HUMAN TMJS

Human TMJs were a highly adaptable blend of previous mammalian TMJs. The posterior slopes of the articular eminentia formed an inclination of about 45 degrees to the occlusal plane[33] - less than the vertical temporal bone walls of carnivores and more than the flat articular areas on the undersides of the temporal bones of herbivores or rodents. As the condyles slid around against these slopes during function, they rotated like carnivore condyles while sliding laterally like herbivore condyles and antero-posteriorly like rodent condyles.



RODENT TMJ HERBIVORE TMJ CARNIVORE TMJ HUMAN TMJ

Each TMJ consisted of two compartments. The upper compartment allowed sliding of the condyle, and the lower compartment allowed rotation of the condyle. The two compartments were separated by an articular disk held in place by a surrounding ligamentous sleeve which served to limit movement and bind the bones and disc into a single working unit.[34][35]

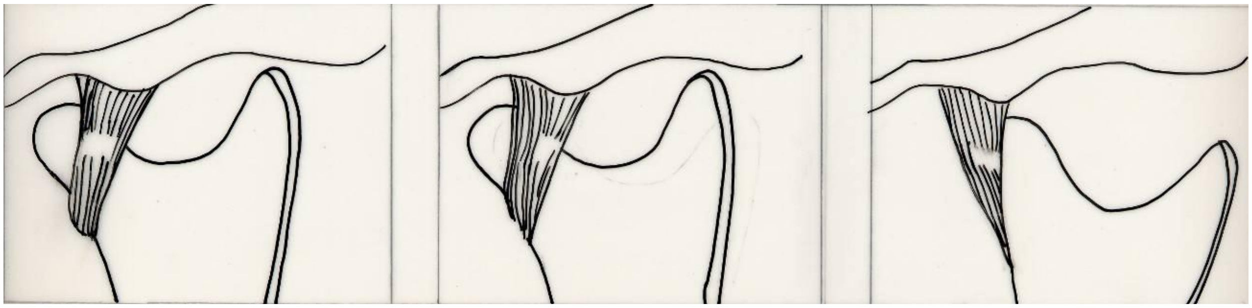
Like the dentition, the TMJs were also designed to absorb shocks. Proteoglycans within the load-bearing areas responded to compressive force by expressing water molecules and deforming. Then, when the compressive force is released, they reabsorb water molecules and expand again. The resistence of the tissues increased progressively as the force increased.

"Vigorous chewing sends sudden waves of impacts from the articular surfaces to the bodies of the bony components. These waves are effectively dissipated by a graduated increase in resistance provided by the elegant design of the underlying architecture. Thus thrusts are first met by layers of maximum flexibility in the plastic lubricating film and fibrous articular covering. The wave then flows through increasingly more rigid regions, - the calcified cartilage, the thin subchondral bone, multiple, stiffer, vertically oriented, bony trabeculae in the spongiosa - finally to end in the hard cortex of the body of the bone. This action can be likened to the softening of impact by the studied recoil of the athlete's arm when catching a fast ball with a bare hand."[44]

Cushioning of the joint components was also provided by the rapid filling and emptying of the vascular retrodiscal plexus. Each time the condyle moved backward, the loose vascular plexus behind the condyle was compressed and emptied. Then, each time the condyle moved forward, the retrodiscal plexus had to fill as fast as the condyle could move so that a vacuum would not be created. During chewing the rapid anteroposterior movements of the condyle pumped the retrodiscal plexus like a piston in a cylinder, and the hydraulic forces produced by such pumping helped to cushion the violent movements of the condyle during mastication.

Further cushioning of the joint components was provided by maintaining a point of contact across each TMJ at all times. If the articulating bones could separate during function, they could come back together with an impact that could damage their specialized bearing surfaces.

One mechanism that helped maintain intrajoint contact was the network of ligaments that suspended the condyle up against the articular eminence. When the condyle translated forward, these temporomandibular ligaments functioned like the radius of a circle to keep the condyle pressed firmly against the slope of the articular eminence.



CONDYLE IN CENTRAL BRACING POSITION

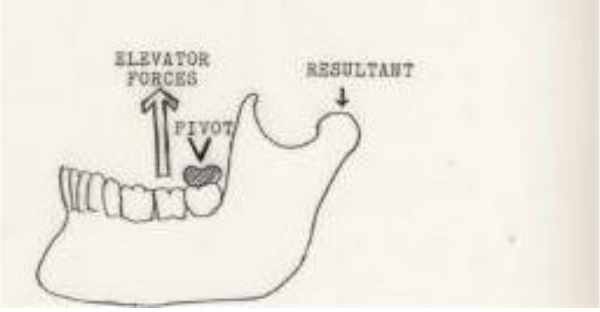
CONDYLE MOVING FORWARD AS MOUTH OPENS

MOUTH FULLY OPEN CONDYLE AT CREST OF ARTICULAR EMINENCE

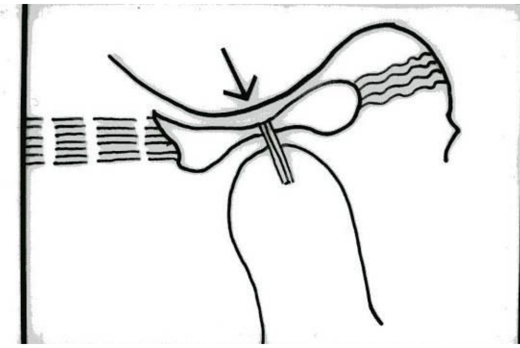
THE TMJ ARTICULAR DISKS

Also helping to maintain contact across the TMJs was the mechanism which positioned the articular disks. When the condyles were fully seated, the disks filled most of the space between the condyles and the glenoid fossae to provide effective cushioning of compressive forces. As each condyle moved around during function, a set of collateral ligaments (composed of medial and lateral thickenings of the TMJ capsule) held its disk down on its top end like chin straps holding a hat down on a head. As a result, the disc could roll around forward and backward on the rounded condylar head, but it could not be pulled laterally or superiorly out of contact with the condyle without stretching or tearing these ligaments. Because the disk was a biconcave structure composed of a central thin zone surrounded by peripheral wedges and bathed in lubricant [42], compressive forces from biting served to center the disk between the bones of the TMJ.

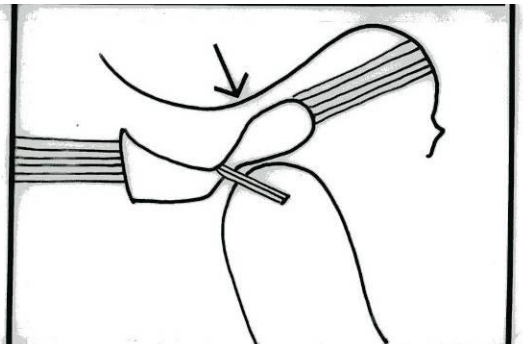
At times during function, a condyle was distracted because a very resistant bolus was placed between the rear teeth behind the center of the jaw closing muscle mass. The resultant force downward on the working side condyle (shown below) served to increase the disk space.



At such times, anterior traction of the superior lateral pterygoid muscle on the anterior aspect of the disc and capsule maintained intrajoint contact by ensuring that the disc occupied a position on the condyle which was rotated as far forward as was permitted by the width of the articular disc space.[39] The space created between the condyle and temporal bone was immediately filled in by as much of the posterior band of the disc as could fit in there, and the joint was still able to maintain a point of contact as seen below.



COMPRESSIVE FORCE IN TMJ
KEEPS THIN PORTION OF DISK
BETWEEN THE BONES



CONDYLE DISTRACTED DURING FUNCTION
BRINGS THICKER PORTION OF DISK
(POSTERIOR BAND) BETWEEN THE BONES

For the disks to be able to move their wedge-like contours rapidly back and forth on the condyles in response to the many different degrees of loading and the rapid fluctuations in the width of the articular spaces during chewing required great flexibility. Unlike the disks in other joints, the TMJ disks had to be able to rapidly and repeatedly change shape between concave up and concave down. As a result, the TMJ disks were made of fibrous connective tissue rather than the more brittle cartilage which comprises other articular disks.

TMJ CONTOURS

As members of the mandibular articulation, the bony contours of the TMJs were shaped by function to provide support for the back of the mandible much like the dentition was shaped by function to provide support for the front of the mandible, however the mechanisms responsible for shaping the two types of articular surfaces were very different. While the teeth could be directly reshaped by wear, the joint surfaces were composed of a specialized lining which had to be protected. Thus, beneath the specialized joint lining, remodeling occurred by resorption of bone in areas of high compression and apposition of bone in areas of low compression until the shapes acquired by the condyles, glenoid fossae, and articular eminentia became a reflection of functional forces.

In function, the TMJs operated like fourth molars. Each mandibular condyle articulated in a glenoid fossa like the buccal cusp tip of a mandibular molar articulated in the central fossa of a maxillary molar. On the working side during power-crushing, when the working side buccal cusps of the mandibular teeth slid anteriorly and medially up the posteriorly and lingually facing inclines of the maxillary buccal cusps, the working side mandibular condyle slid medially and anteriorly up the lingually and posteriorly facing incline of the lateral aspect of the glenoid fossa. In these areas functional forces produced articular facets in the layers of thickened avascular fibrous connective tissue on the posterior and laterally facing slopes of the articular eminentia and the anterior and medially facing surfaces of the condyles. The area occupied by these working side facets was positively correlated with the range of jaw movements in function. Broad concavities on the posterior slopes of the eminentia and matching flattened areas on the opposing surfaces of the condyles were formed in response to chewing forces with a strong horizontal component.

Then, when the mandible continued in a follow-through to the balancing side, the balancing side condyle moved backward until it reached or almost reached the nonarticular facets on the posterior facing slope of the condyle and the anterior facing wall of the postglenoid process.[61-62] These balancing side facets in the joints, (like the balancing side facets in the teeth) were border areas rather than functional areas, so they did not become avascular and did not participate in the passive mechanical guidance of the mandible. However, they were still shaped to fit the same mandibular range of motion, as indicated by the obvious congruence between facets on the back of the condyles and those on the front of the postglenoid processes.

FUNCTIONAL HARMONY

With the TMJs (by remodeling) and the dentition (by direct wear) both undergoing a constant adaptation to the same mandibular range of motion, the TMJs and the dentition acquired a harmonious fit with each other. Studies show that form and surface changes of the joint components were well correlated with dental attrition [129-131] rather than with age or sex.[132] The harmony of form and function between the teeth and the TMJs protected these components of the mandibular articulation by enabling them to share functional loads and also contributed to the health of most of the involved tissues by providing an accessory source of circulation.

Functional harmony provided effective weeping circulation in the TMJs by maintaining a broad range of mandibular movements which ensured distribution of synovial fluid all around the articular surfaces. Long smooth mandibular chewing strokes with sufficient variability to provide alternate compression and release in all portions of the articular zone kept the avascular tissues of the articular zone supplied with oxygen and nutrients and free from accumulations of waste products. For that reason, weak jaw function leads to a thinning of the condylar cartilage[136], immobilizing a synovial joint produces atrophic degenerative changes characterized by reduced proteoglycan content and alteration of proteoglycan structure[137-

138], and remobilizing an injured joint with continuous passive motion dramatically enhances its rate of healing[139].

Functional harmony supported muscle health by minimizing the need for protective reflexes. Thinking back to the hallway analogy used to describe engrams, functional harmony was acquired when no boards were left sticking out, and the hallway acquired a shape that perfectly fit your body as you walked through it. During masticatory function, a cadence of strong, smoothly alternating, and relatively uninterrupted firings corresponded with a steady repetitive pattern of sensory feedback as control shifted smoothly back and forth between muscles and articular structures. Each closing movement was guided by the jaw muscles and the temporomandibular joints until the dentition or the bolus was engaged. Then, as the elevator muscles showered down their full forces for power-crushing, guidance was transferred to the teeth and bolus. Finally, as the power-crush stroke followed through and merged with the opening stroke, guidance was transferred back to the muscles and joints. Agonists and antagonists alternated firing in strokes that frequently used only slightly less force than was permitted by the physiology of the system. When one group fired strongly, the other group relaxed fully. There was no unnecessary overlapping of opposing muscle groups so that little energy was wasted by muscles pulling against each other.

Functional harmony supported the periodontal tissues by providing a rhythmic physiologic loading of the teeth which probably enhanced circulation. The teeth were loaded primarily in an axial direction, with a small and variable range of movement horizontally, especially bucco-lingually. With each loading event, some fluids in the direction of compression through the bony socket out of the surrounding periodontal ligament space and into venous circulation, followed by a subsequent rebound of the tooth which brought in new fluids. This accessory circulation is likely the reason that teeth with occlusal wear have better periodontal health than those without wear.[141] When loading of the teeth is aberrant or excessive, it probably exacerbates periodontal disease by decreasing blood supply to the periodontal ligament.[142-144]

Functional harmony probably also supported the health of other craniofacial tissues by providing a source of accessory circulation. In the vascular plexus behind the temporomandibular joint, condylar movements acted like a piston to pump waste products from the synovial tissues into main circulatory channels and to bring in the extensive supply of fresh oxygen and nutrients that was needed in such a metabolically active area.[140] In other areas, the long lever arm formed by the mandible functioned much like a pump handle which was driven up against the cranium with huge forces thousands of times each day and thereby provided rhythmic compressions and releases which moved fluids in and out of the tissues. Functional forces tugged on ligaments and tendons, bent membrane bones back and forth, and alternately compressed and released enclosed soft tissues. All of these rhythmic movements probably pumped blood in and out of the involved tissues.

AGING

With age the character of the mandibular articulation changed in a way that made it more compatible with the changes that naturally take place in aging tissues. The flattening of the dental contours by occlusal wear and of the TMJ contours by remodeling which accompanied a shallower and steadier mandibular range of motion occurred as the tissues became progressively less able to withstand the stresses associated with irregular vertical chewing on jagged occlusal contours. In this manner, the functional harmony in the chewing system gradually transformed in a way that maximized its longevity.

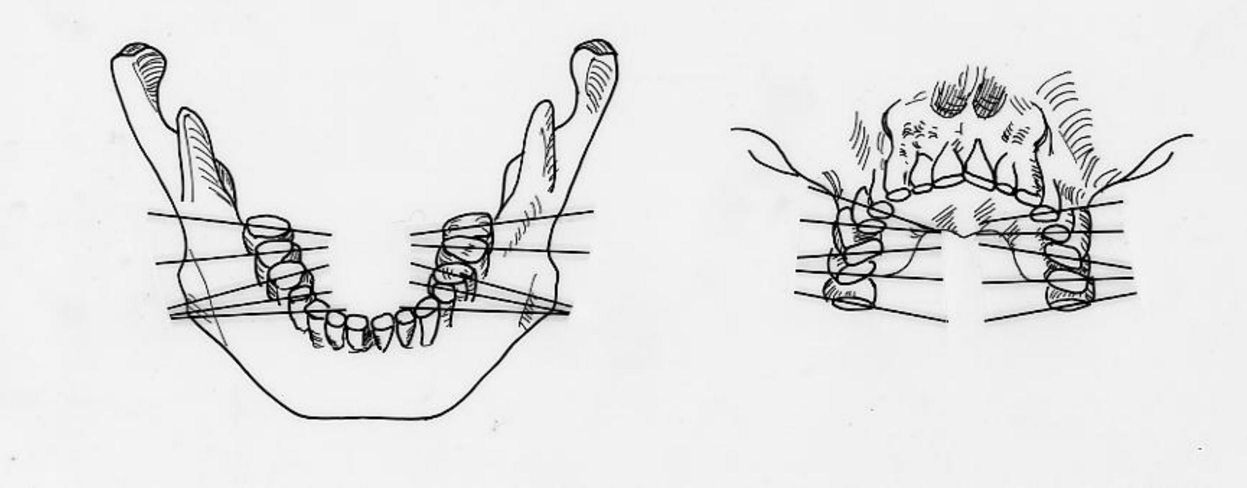
In childhood and adolescence, lateral masticatory patterns delivered against a vertically oriented and often irregular occlusal table were well tolerated. Newly erupting teeth had sharp lines and angles. The incisors came into the mouth with chisel-like edges and a steep overbite that quickly developed a cutting edge, and the newly erupting canines were pointed and sharp. Unworn premolars and molars had tall pointed cusps which interlocked at a single, clearly defined, intercuspal position. The dentition was most effective at incising, puncturing, and ripping food.

During those early years, the tissues were well equipped to function against such a dentition. They were full of water, enzymes, and elastic fibers which enabled them to withstand diverse articular stresses and unanticipated impacts. Bones easily bent, and teeth easily shifted. Protective neuromuscular reflexes were fast and hyperactive. Chewing strokes could bring the mandible laterally across a steep intercuspation and then in and out of a sharply determined intercuspal position while still avoiding traumatic collisions between tall overlapping cusps. The muscles were versatile and could cope with frequent sudden changes in firing patterns or forces applied. They could move the mandible for prolonged periods in intricate neuromuscular dances to avoid occlusal interferences. In case of injury to any of the tissues, extensive blood supply was readily available where it was needed.

As people got older, soft tissues became more like leather, and hard tissues became more like stone. Elasticity and flexibility decreased as water and enzymes got replaced by fibers and fat. Collagen fibers underwent increases in number, size, density, tensile strength, and degree of cross linking along with a decrease in solubility and extensibility.[147][148][149][150][151][152] Cartilage developed fatty inclusions within cells, thickening and clumping of fibers, calcification by deposition of calcium salts, and increased mineralization of the extracellular matrix, converting it to bone.[153] Articular cartilage underwent calcification and dehydration with chondroid changes of the discs[154], and exhausted its supply of undifferentiated mesenchymal cells. Articular discs became dehydrated, fibrotic, and sometimes calcified.[155] Bones underwent a decrease in water content[156] and an increase in the amount and size of apatite crystals.[157] Vessel walls became more rigid, and collateral circulation became less abundant – anastomoses becoming confined to thick-walled less physiologically active vessels rather than capillary beds.[158] In bones, nutrient canals became blocked.[159] In teeth, blood supply to the pulps decreased through reduction in numbers and internal diameter of arteries as a result of calcification, intimal thickening, and elastic hyperplasia.[160] The body became less able to rapidly increase blood supply to any area where it was needed, thereby diminishing the intensity of its inflammatory responses. The intensity and effectiveness of neuromuscular responses diminished. In muscle tissue, the availability of ATP for fuel dwindled, the number of contractile fibers declined at the rate of about 5% per decade, and the number of noncontractile elements within them increased.[161-162] In nerve tissue, there were age related declines in several different abilities[163], while reflexes became slower due to a delay in processing rate and conduction velocity.[164-165] In the performance of tasks, there was a loss of coordination, precision of movement, and strength.[166]

These progressive losses in strength and adaptability of the tissues with age were accompanied by changes in the form of the mandibular articulation which made chewing more easily accommodated by the tissues. Anteriorly, the overbite was eliminated so that the incisors and canines no longer extended beyond the occlusal plane. Posteriorly, tall sharp cusp tips that once fit together with pinpoint precision became rounded and then flattened until they met along wide areas with significant lateral freedom of movement. The enamel was completely worn off from the occlusal surface of the first molar by the time the second molar erupted, and that of the second molar was largely gone by the time the third molar erupted.[54] Chewing strokes acquired progressively longer medial and anterior gliding strokes with a biphasic masticatory pattern that maintained functional edges much like in herbivores. Evidence of that pattern can be seen in the scratch marks oriented in two distinctly different directions on the molars of museum skulls[55], as well as the separate balancing side and working side facets found on their teeth and their condyles.[56] The entire occlusal table became more like one long smooth curve than a collection of individual teeth, and the area of maximal intercuspation enlarged so that the mandible could be comfortably braced in a wide variety of positions against the occlusal table.

The smooth flattened curve usually acquired by the human occlusal table has been described as helicoidal.[57][58] The occlusal surfaces of upper and lower dental arches formed long continuous walls with longitudinal twists somewhat like a propeller blade. The plane of the occlusal table relative to a horizontal plane was relatively steep at the central incisors and flat at the second molars. At the first molars the maxillary occlusal surfaces sloped slightly lingually, and at the third molars the maxillary occlusal surfaces sloped slightly buccally. Contours in the mandibular arch were opposite and complementary.[59]



Such a curve was not at all in line with the curves along which the teeth first erupted. The steep curves of Spee and Wilson, which were always quickly eliminated by function, served only to supply working surfaces for mastication. They were not designed to dictate the pathway of the mandible. Even in the few tribes who experienced minimal occlusal wear, masticatory function still shaped the occlusal surfaces into a helicoidal curve.[60]

As the end product of modification of the occlusal surfaces by function, the helicoidal curve was the terminal occlusal platform. It was the imprint in tooth structure erupting all around the mandible of the functionally generated pathways of the mandible. Tooth structure that was in the way of these pathways was removed by attrition or minor tooth movement. The result was a three dimensional registration of the envelope of motion acquired by the mandible after the jaw muscles had overcome the resistance posed by the dentition.

As the mandibular articulation flattened, jaw movements became wider and steadier. Within the muscles, fluid pressure rose and fell more gradually with each stroke. At the articular surfaces, the smoother bite table supported long steady strokes that enhanced the effectiveness of weeping circulation. The less ballistic state of masticatory function obviated the need for extensive shock absorbing capacity in the dentition, the temporomandibular joints, and the basal bones supporting the maxillary bite table just as these areas were already losing their shock absorbing capacity and also obviated some of the need for protective reflexes while the aging nervous system became progressively less able to maintain a continual state of alert. With age, the more smoothly curved occlusal table allowed a relatively quiet and smooth neuromuscular system by feeding it sensory stimuli in a uniform manner that allowed easy tracking of mandibular position. Pressure passed evenly down the arch from each tooth to its neighbor, putting similar forces on each sensory receptor bed and allowing a simple and repetitive pattern of motor impulses to drive the system. The jaw muscles were able to fire in long steady strokes that gradually built momentum and came to a smooth end, uninterrupted by protective reflexes producing silent periods or the firing of antagonists during active phases of contraction. Mesio-distal tooth wear (between the teeth) shortened the dental arch while bucco-lingual wear (on the sides of the teeth) made the bite table narrower.

With all these changes taking place simultaneously, the human masticatory system was able to maintain its harmony of form and function well into old age. The articular disks stayed in place but wore out along with the other TMJ components. Eventually, even with the teeth worn down to the root surfaces and the condyles flattened to their necks, the masticatory system of our ancestors was able to sustain healthy strong chewing function. If the system finally failed it was usually because the articular components exhausted their reserves, and there were no tooth surfaces or condylar heads left to chew on.

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CHAPTER 2) EVOLUTIONARY HUMAN CRANIOFACIAL GROWTH

These evolutionary human masticatory systems did not just start out with a functional harmony that enabled them to adapt to all kinds of diets and extreme environmental conditions. They attained a functional harmony which was customized to fit their needs as the result of a long and multistaged postnatal development process in which genetics interacted with functional stimuli to build a masticatory system optimally suited to withstand those functional stimuli. Genetics provided the motive forces, the raw materials which were bound to cause proliferation of tissues according to a pre-determined sequence. However, the final form taken by the tissues was also very much determined by the system's adaptation to the environment in which the genetic tendencies were expressed.

POSTNATAL GROWTH OF THE HUMAN MASTICATORY SYSTEM

The human masticatory system developed most of its form postnatally. At birth, the masticatory structures were either rudimentary or nonexistent. The head consisted mostly of the brain, the eyes, and a thin shell of bones surrounding them. The cranial base was still flexing. The articular eminence, styloid process, coronoid process, and articular disc had not yet formed. The squamous portion of the temporal bone was essentially flat. The mandible was no more than a bulbous tube enclosing the crowns of the teeth. With an unfused symphysis, it was not yet capable of receiving or transmitting significant forces. The elevator muscles were still poorly developed. The spine had not yet developed its curves.

Shortly after birth, some of the structures which would later constitute the masticatory system began developing under the influence of functional stimulation. The temporomandibular joints began to form between the condyles and the temporal bones where opposing periosteal envelopes rubbing against each other produced secondary cartilage on the surfaces of the bones and a fibrocartilaginous pressure-bearing disc from the tendon of the lateral pterygoid muscle. Soon the pressure-bearing articular surfaces became avascular, the disc acquired a thin central zone surrounded by peripheral wedges, and an articular eminence formed in response to loading by the immature condyle against the temporal component of the joint.

Still, sucking and swallowing stimulated a different growth pattern than mastication did. In sucking behavior, the tongue was the primary functional organ, working like a plunger against the strong lips tightly surrounding it. Swallowing occurred with the jaws apart, the tongue resting between the gum pads, and the mandible stabilized by the facial muscles. If solid food was introduced into the mouth, it was spit out by the functional movements used for sucking. In resting posture, the tip of the tongue maintained contact with the lips.

The arrival of teeth established a whole new set of neuromuscular reflexes which profoundly changed the behavior of most of the muscles in the craniofacial area. An occlusal table replaced the tongue as the platform against which the mandible was braced, and the elevator muscles replaced the facial muscles as the source of mandibular stabilization during swallowing. Freeing the muscles innervated by the seventh cranial nerve from their crude infantile suckling and swallowing functions allowed these muscles to take on the more delicate and complicated functions of speech and facial expression. Experiments have shown that the consistency of the food is at least partly responsible for the change in neuromuscular control. Older children given a bottle revert to the same suckling, swallowing, and respiratory rhythms that they manifested in infancy.

By changing muscular activity in the craniofacial region, chewing stimulated a new pattern of growth and development. The zygomatic processes thickened and began to bow outward, the glenoid fossae deepened, and the articular eminentia began to develop their characteristic S-shaped profiles. By the time the primary dentition was completed, the temporomandibular joints were well established and the articular eminence had gained more than half of its adult form.

While chewing forces were molding craniofacial form, postural forces were molding craniocervical form. Learning to hold the head upright leading to sitting behavior at the age of 5 months gave the cervical spine much of its lordosis. Soon afterwards the primary teeth provided a means to stabilize the lower border of the mandible so the anterior myofascial chain could hold down the front of the head, the child learned to stand up by coordinating opposing muscle groups to maintain physical balance, and the lumbar spine acquired its lordosis. In this way, the forces of gravity acted in concert with the expansion of cartilage against compression to create a system of vertebral curves in response to bearing the weight of the head over the long axis of the body.

Thus most aspects of the craniofacial region were shaped during postnatal growth as they were exposed to function, allowing the region to customize its growth to fit the functional environment. This process created great adaptability and therefore selective advantage, but it required coordinating a number of different growth mechanisms into a single sustainable growth pattern.

COMPLEXITY OF POSTNATAL CRANIOFACIAL GROWTH

The postnatal growth of the craniofacial area is uniquely complex. It involves at least four distinct growth processes, - neurocranial expansion in response to enlarging enclosed neural structures, cartilaginous elongation against resistance, maintenance of external form and key internal structural components in response to resting muscle forces, and functionally stimulated growth of the portions of the face directly involved in chewing. Each of these processes operates on its own vectors and its own time scale. Enlow says, “Different parts have different schedules in which changes in growth velocities occur at different times, by different regional amounts, and in different regional directions.”(1) These four skeletal growth mechanisms were weaved together along with a number of adaptive mechanisms to coordinate them into a single steady integrated growth pattern.

Even some areas of the craniofacial skeleton very distant from the jaws are also affected by masticatory forces. In monkeys, biting forces are able to separate the parietal bones and open the sagittal suture at the top of the head.(50) Eskimos, who have very strong jaw muscles, develop a distinct thickening along the sagittal suture.(49) Researchers have concluded that the presence of significant strains at the sagittal suture indicates that the braincase is loaded by chewing forces.(14) In fact, much of postnatal craniofacial growth and development may have been simply an adaptation to this complex pattern of forces during mastication. The density of all the bones of the cranial vault varies according to jaw muscle strength as well as cervical muscle strength. Moss pointed out, "The external form of the human skull... is related directly to imposed loadings, a point verified experimentally in miniature swine skulls. It is known that unit strains are greatest in infant skulls, less in adolescent skulls and least in adult skulls, suggesting that the growing skull increasingly adapts its structure to masticatory loadings."(20)

The face was the part of the craniofacial area most loaded by mastication, and its growth was profoundly influenced by the forces produced during mastication. One researcher summarized the complex distribution of forces experienced during chewing, “First, mastication generates a gradient of strains in the face with highest strains experienced near the occlusal plane, moderate strains in the middle face, and very low strains in the upper face. Second, regions of muscle attachment and insertion such as the zygomatic arch and the coronoid process probably experience locally high strains. Finally, during unilateral mastication, the retrognathic face is likely twisted in the coronal plane and both bent and sheared in the sagittal plane."(145) In response to the complex array of forces produced during chewing, the face grew in a manner which structured it to best withstand those forces.

Many components of the craniofacial area depend on functional forces for their very existence. The articular eminentia and glenoid fossae do not form when there is no condyle(2-3) , and even after they are fully formed will lose their contours if the condyles are removed or fractured.(4-6) The size of the chin is proportional to the bite force, the existence of a coronoid process depends on the presence of the temporal muscle, the existence of a bony prominence at the angle of the mandible depends on the presence of the internal pterygoid and masseter muscles (7-8), the size of the angle of the jaw varies as a direct function of the size of the masseter and internal pterygoid muscles, the thickness of the condylar cartilage is determined by the activity of the lateral pterygoid muscles(9-10), and the thickness of the condyles is determined by the functional loads it receives (11-12) The zygomatic region is largely formed as a buttress to resist the twisting that results when forceful contraction of the masseter muscle on the biting side draws the zygomatic arch downward and inward. (19) In fact, there is evidence that the thickness and breadth of every part of the facial skeleton varies according to the masticatory forces it receives during function.(15-17)

Other components of the craniofacial skeleton are partially dependent on functional forces and partially dependent on genetics, with the two combined in various proportions in different areas. For example, the shape of the mandibular corpus, the lingual symphysis, the lateral surface of the ramus and the frontal curvature of the mandible are largely dependent on genetics; while the thickness and density of the mandible, the size of the gonial angle and the antegonial notch, the coronoid processes, and the alveolar processes are profoundly influenced by function. The supraorbital ridge is partly formed as a buttress to resist compressive forces in its middle segment and tensile forces on its lateral segments. In monkeys a new layer of bone forms there just after the arrival of each new molar.(18)

The importance of masticatory forces in normal cranial growth has been dramatically demonstrated by animal experiments in which unilateral alterations of the masticatory system by generalized muscle disease (36), unilaterally or bilaterally impaired jaw muscles(37-46), or unilaterally extracted posterior teeth produce a deviation of facial growth to one side and a scoliosis of the whole cranium.(21, 47-48, 144) To understand the way masticatory forces affect craniofacial growth requires understanding how the various components of craniofacial growth interact.

NEUROCRANIAL EXPANSION

The human craniofacial structure that was completed earliest in postnatal life was the cranial vault. It was already about 90 percent complete at birth and virtually 100 percent complete by the age of 7. Its expansive force was determined completely by the genetically controlled expansion of its enclosed neurocranial contents. We can see how easily it expands to accommodate hydrocephaly,

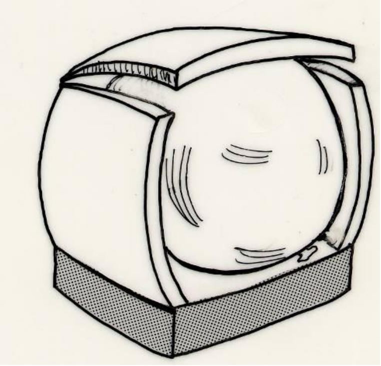
The cranial vault was a tabular structure of membrane bones connected by cranial sutures to form a continuous shell which encloses the brain and eyes. As the enclosed neural contents enlarged, the shell expanded. All bones drifted away from the center, inner areas less rapidly than outer areas where extensive myelinization was occuring. Thus the sutures running from the cranial base outward into the calvarium demonstrated higher growth rates peripherally than centrally. Lateral and frontal serial X-ray tracings of a growing head look like a slow motion picture of an explosion.

Between the individual cranial bones, growth to accommodate the enclosed expansion takes place at the cranial sutures - interdigitating margins composed of two periosteal growth centers placed back-to-back. Rapid growth at these sutures, triggered by mechanical separation of the cranial bones bordering them, allows the cranial vault to always expand just enough to perfectly fit the periphery of the brain. Even when the cranial contents occasionally expand much more quickly than normal in hydrocephaly, the sutures were still able to produce enough bone to maintain a continuous shell around them.

While the cranial vault's size was determined genetically, its shape was at least partly determined by its functional environment. The susceptibility of cranial shape to external forces can be seen in the skeletal remains of some tribes who molded the heads of their infants by means of cloths or boards and thereby permanently altered the shape of the head without inhibiting the volume or the functional capacity achieved by the brain. The importance of jaw muscle forces in this process has been highlighted by experiments in which cutting the temporal muscles in rabbits changes the length and width of the braincase.(81) Generally compression of the cranium by muscles acting in one direction produces compensatory growth in other directions.   Since the powerful jaw closing muscles are vertically oriented, their force limited the growth of the cranium vertically. Compensatory growth took place laterally and antero-posteriorly. As a result, individuals with very strong overall musculature had cranial vaults that were short and wide, while individuals with weak overall musculature developed cranial vaults that were taller and rounder.(23-24)

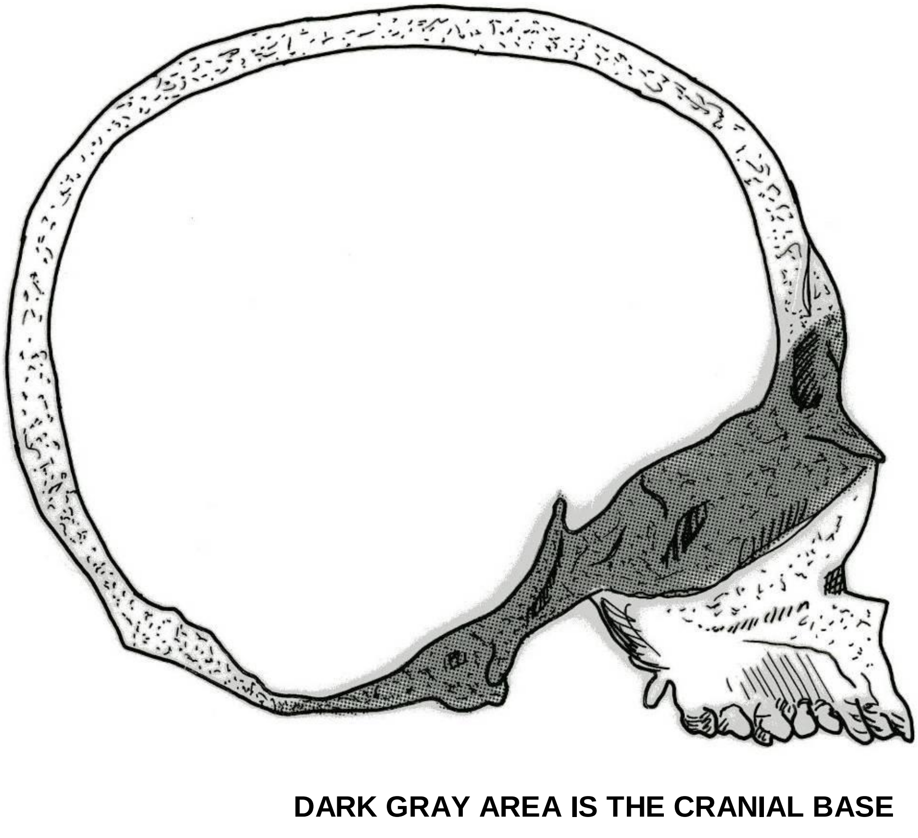
CARTILAGINOUS ELONGATION

A different growth mechanism was responsible for lengthening the spine and its extension into the cranium all the way to the front of the face. This growth was powered by the ability of cartilage to elongate against resistance. Just as it pushed the vertebral column upward and lengthened the long bones, cartilaginous elongation pushed the middle of the face forward and also made the face longer by pushing the cranium up and away from the shoulder girdle.



The main source of cartilaginous elongation in the craniofacial region was the cranial base -a sagittal ridge of bone at the bottom of the cranial vault which was so thick that it did not burgeon out in response to neurocranial expansion as readily as the thin plates of membrane bone bordering the other sides of the vault. The cranial base responded to growth of the neurocranium much like the reinforced bottom of a box which contains an expanding mass, as seen in the illustration on the left. The relative independence of cranial base growth from neurocranial expansion can be seen in the way it is only slightly affected in microcephaly and hydrocephaly, while the rest of the cranial vault becomes grossly distorted.

The cranial base grew like a part of the spine or the long bones of the skeleton, with a directional vector and a time scale much later than neurocranial expansion. The two primary components of the cranial base, the basi-occiput and the baso-sphenoid, were phylogenetically cephalized vertebrae (22), so that the cranial base was structurally and functionally the cranial extension of the vertebral column. Epiphyseal plates arranged back to back at the spheno-occipital synchondrosis, the intersphenoid synchondrosis, and the spheno-ethmoidal synchondrosis were able to elongate the cranial base in a sagittal plane much like the long bones of the body were able to elongate against gravity - exhibiting a spurt at puberty and continued lengthening until the late teens.(23)



DARK GRAY AREA IS THE CRANIAL BASE

As the cranial extension of the vertebral column, the cranial base was very much affected by postural forces. In a natural experiment, a patient with bilateral palpebral ptosis learned to hold his head in extension to maintain a visual axis and thereby produced a flattening of his cranial base.(48, 57)

In addition to serving as the floor of the brain, the cranial base served as the base of operation for facial growth. From the front of the cranial base, the wings of the sphenoid bone spread out laterally above and behind the maxillary bite table to brace it against the forces of mastication. From the rear portion of the cranial base, the petrous ridges of the temporal bones spread out laterally above and behind the articular eminentia to absorb compressive forces from the mandibular condyles. From the angle in the midsection of the cranial base, the pterygoid plates and ethmoid bone hung down like structural brackets.

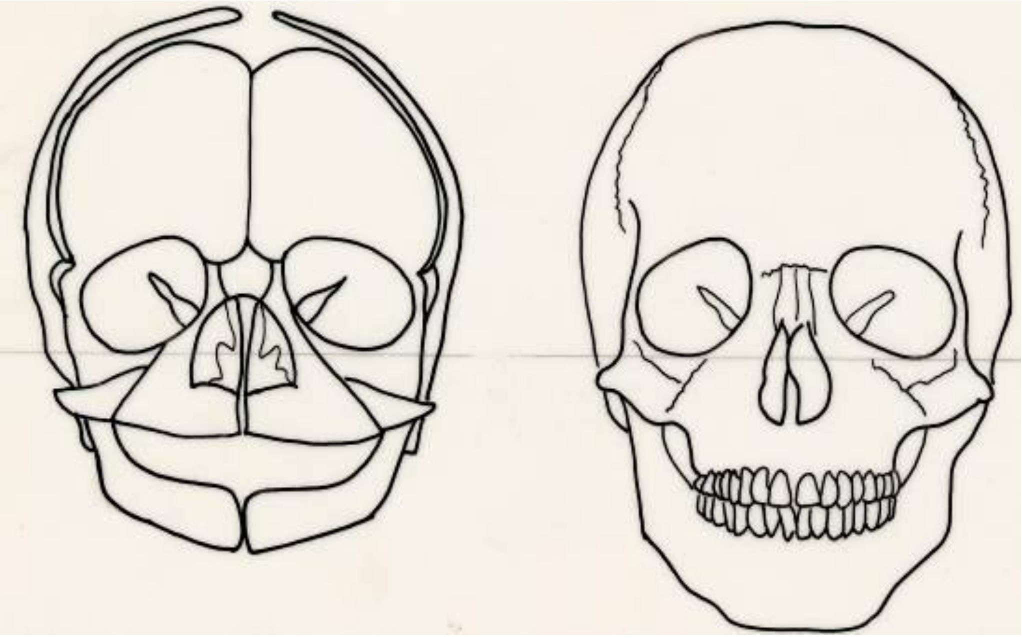
As elongation of the cranial base pushed the middle of the maxillary complex forward, the cartilage of the nasal septum functioned much like the final extension of the cranial base and pushed the front of the nose forward. Some researchers believe that this elongation of the cartilage of the nasal septum pulls the rest of the face forward.

Cartilaginous elongation also seems responsible for at least some of the forward translation of the mandible. Although growth at the mandibular condyles is an extremely adaptive process, especially later in life, the cartilage of the mandibular condyles appears to have some independent growth potential, especially early in life when other areas of cartilage are also producing rapid growth. The effect of this independent growth potential at the mandibular condyles can be seen in a condition called acromegaly where growth hormone stimulates excessive elongation of cartilage. In contrast, when ankylosis of a TMJ prevents it from growing normally, the gonial angles to fail to descend and the back of the face grows remarkably short with a steep mandibular plane angle.

All of this elongation in the center of the face was needed to increase airway space as the growing body needed more air. Mandibular translation and cranial base elongation diminished airway resistance by making the bend in the upper airway more obtuse. Nasal septal elongation diminished airway resistance by moving the front of the nasal airway further forward.(25) Significant increases in the cross sectional area of respiratory passage had to accompany increases in body size; because respiratory needs are a function of body volume which increases in proportion to the cube of any increment in linear dimension, while cross sectional area of the airway only increases as the square of any increment in linear dimension.

INCREASES IN FACIAL HEIGHT

On the same time course of cartilaginous elongation, the increase in overall skeletal height, (possibly with the help of extrusive forces in the teeth and their surrounding bones), produced increases in facial height. As the individual grew taller, the lengthening of the vertebral column pushed the cranial base upward relative to the sternum and clavicles which were tied by a thick myofascial curtain to the mandible. Thus, relative to the rest of the cranium, the mandible lowered with skeletal age. The rest of the facial structures, filling in the space between a lowering mandible and a stable forehead, followed part way. The resulting increases in facial height, long after neurocranial expansion had ceased, led to a change in proportions of the face between childhood and adulthood, as can be seen below.



Generally this increase in facial height continued only as long as skeletal growth. Once adulthood was achieved, skeletal height and facial height (vertical length at the front of the face) were stable. Stability of facial height provided important selective advantages. If the jaw closing muscles had to keep changing their resting lengths, they could not operate with maximal effectiveness.

RESTING MUSCLE FORCES

The stability of adult facial height was primarily due to the resting tonus in the craniofacial muscles. The constant light tension produced by the passive tension of relaxed muscles is a very effective way to reshape bones, as seen in orthodontics and some orthopedic work. In habitual posture, a constant light tension is provided by a myofascial curtain which holds each bone in a kind of neutral zone between opposing forces. Any shift of a bone away from its neutral zone creates an imbalance between opposing myofascial pulls and therefore a resultant force which causes resorption of the portion of the bone intruding into the pattern of resting tensions. Surgeons have found that rapid resorption occurs in any part of a bone graft which is located beyond the tension zone controlled by the musculature.

In the craniofacial region, the passive tension of the myofascial curtains draped from the cranium down onto the shoulder girdle and sternum in rest posture maintain the constant positions of the mandible and hyoid bones embedded within those myofascial curtains. Experiments in animals have shown that the craniofacial growth pattern can be changed by altering the rest posture of the head, the mandible, or the tongue.(26-31) Solow found that children with forward head posture (determined by a large craniocervical angle) subsequently developed reduced facial prognathism and decreased forward rotation of the face, while children with a small craniocervical angle subsequently developed increased facial prognathism and increased forward rotation of the face.(34) Experiments have also shown that mechanically intruding on the resting tonus of the jaw closing muscles (by increasing the height of the bite table) is a rapid way to intrude teeth and their supporting bones. The ability of the anterior myofascial curtain to fix the mandible's position in space has been demonstrated by experiments in which isolation of the temporomandibular joint region with its surrounding bone in fresh cadavers leaves the condyle still seated in the glenoid fossa with only the peri- and intra-articular structures maintaining its position. The ability of resting temporalis muscle forces to maintain superior traction on the mandible has been demonstrated by the immediate shortening of temporalis fibers which results from detaching them and from the resistance to wide opening of the mouth which is experienced in the anesthetized rat or in the relaxed human.(32)

The influence of postural forces on the position of the mandible can be seen in the way head posture causes a change in mandibular position. When the head is tipped back, the mandible moves back in relation to the maxillae; when the head is tipped forward, the mandible moves forward in relation to the maxillae. Similarly when the head rotates to the right or left, the mandible moves at least part of the way in the same direction. Resting tensions which positioned the mandible also affected the growth of the mandible.

Controlling craniofacial and craniocervical resting muscle tensions was a hierarchy of neuromuscular reflexes, and protection of the airway was at the top of that heirarchy. The craniofacial area literally grew around its airway. In the pharynx, the airway was bounded in front and on both sides by the inner borders of the mandible (and the hyoid bone suspended from it) and in back by the cervical spine, To maintain airway passage in this area, neuromuscular reflexes controlled the resting tensions of the intrinsic musculature of the pharynx, the muscles able to pull the mandible forward (the lateral pterygoids, anterior temporals, and superficial masseters), the muscles able to pull the tongue forward (the genioglossus, geniohyoid, and transverse and vertical intrinsic muscles of the tongue), and the postcervical muscles.(78) The actions of these muscles in the service of airway protection can be seen when congenital defects which result in posterior positioning of the mandible evoke a conditioned reflex to hold the mandible protruded sufficiently to permit breathing, even if the condyle must be held far down on the eminence. (36-39, 81) Similarly, after orthognathic surgery to retrude the body of the mandible, the neuromuscular system still maintains a constant minimal antero-posterior distance between the back of the hyoid bone and the cervical vertebrae as well as between the back of the hyoid bone and the anterior pharyngeal wall.(40) Even the effect of gravity on the mandible during back sleeping evokes increased tonus of the lateral pterygoid muscles.(82-83]

As primary guardian of the pharyngeal airway space and the most flexible organ in the body, the tongue also acquired whatever posture was necessary to ensure adequate space for respiration. The tongue's versatility in the service of airway protection can be seen in situations where growth does not naturally provide sufficient airway space and the tongue acquires unusual postures to create an oral airway - lying low in the floor of the mouth, curling longitudinally, squeezing in between the teeth, or even pulsing forward and backward in synchrony with breathing.[79] Blocking the nasal airway in monkeys produces a lowered mandibular rest position, protrusion of the tongue, rhythmic activity of the geniohyoid and jaw closing muscles in synchrony with the diaphragm, and a reshaping of the tongue and lips to form an oral airway passage.(44-47)

Many researchers have commented on the apparent growth effects of airway protective reflexes. Moffett said, "When we examine cephalometric landmarks in individuals affected by mongolism and achondroplasia, we see that respiratory function has been protected by different kinds of facial adaptation in each group. The adaptive changes in mongoloids have been described earlier as very localized effects on parts of the skull that spare the respiratory passages but reduce the size of the olfactory and masticatory components. In achondroplastics nasal airway volume is protected in spite of the mid-face deficiency and the increased cranial base flexure by an adaptive counter-clockwise rotation of the palatal plane. The biologic problem of respiratory survival is solved by a shortened palate in one group and by downward or counter-clockwise palatal tipping in the other."(41)

Proffit said, "Consider what must happen when a prognathic lower jaw is sectioned and moved distally reducing oral volume significantly. Since the tongue is attached to the mandible, as the mandible is moved distally the tongue moves distally with it. A logical consequence of this could be that the tongue is carried into the airway, blocking it and the unfortunate patient therefore immediately dies of suffocation. Of course, this does not happen. Examination of cephalometric tracings reveals the physiologic adaptive mechanisms by which the airway is maintained. The mandible is moved backward, but the tongue repositions downward. In some instances, the base of the tongue actually moves forward as the mandible is moved back. Moving the mandible into a different position requires an immediate physiologic adaptation to produce a different tongue posture. The hyoid bone assumes a new position which reflects an alteration in resting length of both the supra and infra hyoid musculature. Muscular adaptations occur all the way down to the level of the clavicle. In fact, careful observation reveals that the posture of the head on the neck is altered by mandibular surgery."(42)

Resting muscle tensions also maintained the stability of the bite table. Its position and orientation remained remarkably stable, even during childhood and adolescence when a number of varied growth processes are shifting the bones supporting the bite table.

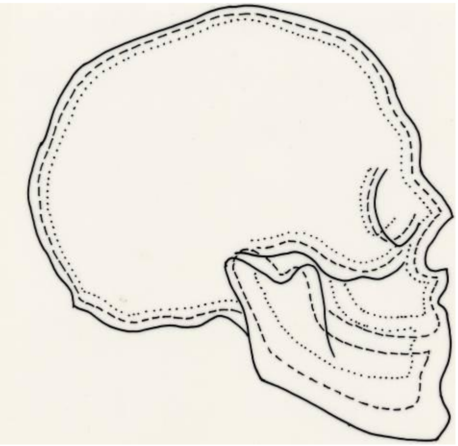
The bite table is a stable landmark in the craniofacial growth of other mammals. In growing primates it changes little while the orientation of the facial skeleton to the anterior cranial base is characterized by a wide range of variability.(82) In growing rabbits, experimentally altering the plane of the bite table produces a scoliosis of the entire craniofacial skeleton.(83)

The constancy of the bite table can also be seen in growth studies of humans. One researcher noted, "Data from standardized lateral cephalographs of caucasoid children and adults indicate that the occlusal aspect of the normal human maxillary dentition relates within the facial complex in a relatively invariant manner. For instance, the angular relationship between the occlusal plane and facial plane is characterized by small variability when judged by the size of its standard deviation as compared with those of other cephalometric angular values. Also linear measurements reveal that the occlusal surface reference points used in the construction of the occlusal plane are themselves orientated to the nasion, so that their relative distances to this skeletal point show small absolute variability. This linear occlusofacial relationship of small variability was found in a variety of occlusal types, suggesting that it is a primary attribute determining the angular constancy of the occlusal plane to the facial plane evident in occlusal normals."(84)

Finally, resting muscle tensions maintained surface contours. The large number of superficial facial muscles were weaved together to form a mat which was broadly attached to the superficial surfaces and thereby maintained the superficial shapes of those surfaces.

All these craniofacial muscle resting tensions provided a regulating influence on growth by ensuring steadiness and symmetry of the overall growth pattern. Longitudinal studies of children have shown that annual increments are not at all evenly distributed among the various bony elements. Some portions grow faster one year, others grow faster the next year, and diminished growth of any one bone is always compensated for by increased growth in neighboring bones so that the steadiness of the overall growth pattern is preserved. Even after an experimental occlusal interference has caused a growth deformity, removal of the interference is followed by compensatory growth which reestablishes symmetry. (85) Studies have also shown that facial symmetry is diminished in animals with jaw muscles weakened by experimental softening of their diets.

In looking at longitudinal growth studies of children Brodie remarked on the stability in the spatial relationships between craniofacial bones and concluded, "The only agent that could be responsible for such stability was the musculature that connected the mandible with surrounding parts. It was apparent that this musculature grew in the same orderly fashion as did the bony skeleton of the head and led to a stable relationship of the mandible in each person."(33) The steadiness of a typical craniofacial growth pattern can be seen below:



FUNCTIONALLY STIMULATED FACIAL GROWTH

In the middle of this steady growth pattern maintained by muscle resting tensions, on a time course which continued far beyond cartilaginous elongation and indeed throughout life, was a surprisingly independent pattern of growth in the portions of the face supporting the teeth. This facial growth pattern included forward translation of the mandibular corpus, counterclockwise rotation of the mandibular corpus, and expansion of the midface.

Functionally stimulated facial growth includes the thickening and reshaping of craniofacial bones in response to imposed forces. All over the body, vigorous muscle function produces heavy bones with large protuberances for muscle attachments. Experiments have demonstrated a 17 percent increase in the thickness of the femur in exercised young pigs compared to unexercised young pigs.(22) Paralysis of muscles produces extremely thin abnormally shaped bones. Clinical and experimental evidence has shown that the skeleton is morphologically and mechanically deficient when normal functional loads are not present during ossification and growth.(25-27) In the craniofacial region, the forces of the jaw closing muscles stimulated osteogenesis at the origins of the muscles on the cranium and at the insertions of the muscles on the mandible. Eskimos (who had particularly strong jaw muscles) developed everted prominences of bone at the gonial angles, large flared zygomatic regions, and unusually thick postglenoid processes.(13)

Functional forces may produce localized bone growth by increasing circulation. The rhythmic pattern of alternating tension and release created by strong chewing probably helped flush out waste products and bring in fresh oxygenated blood. Oxygen seems to be a "master controlling switch" – affecting osteoblast metabolism, osteoclast metabolism, and osteoid calcification.(29-30) Increased bone growth takes place in areas of hyperemia, and decreased bone growth takes place when blood supplies are interrupted. (28) In addition, experiments have shown that the stimuli which produce osteogenic activity are frequency-specific (31) and that repetitive loading is osteogenic while constant loading is not. (32) It seems plausible that the frequencies which stimulate osteogenesis in bone are similar to those produced by vigorous mastication. One researcher concluded, "Cyclic stress is important in inducing intracortical bone remodeling... Variations in bone strain levels of a physiologic magnitude influence the rate of intracortical remodeling... This phenomenon is not confined to bone of endochondral origin but applies to bone of endosteal and periosteal origin as well."(33)

Superimposed on the reshaping of bone in response to functional forces and the steady growth pattern of the craniofacial area was the distinct pattern of functionally stimulated facial growth involving forward translation of the mandibular corpus, counterclockwise rotation of the mandibular corpus, and expansion of the midface. Because these three facial growth patterns were stimulated by function, people with strong overall musculature experienced more growth in these directions. As a result, they grew short wide prognathic faces to go with their short wide crania. In contrast, people with weaker jaw muscles grew longer, narrower, and more retrusive faces to go with their more globular crania.

These same effects have been demonstrated experimentally. Animals (including rats, ferrets, hyrax, minipigs, rabbits, and monkeys) raised on soft food develop weak jaw muscles and experience diminished growth in the regions supporting mastication.(86) They show narrow palates, reduced counter-clockwise rotation of the mandibular corpus, and retrusion of the mandibular corpus. Animals with jaw closing forces that have been increased by raising their teeth or electrically stimulating their jaw closing muscles experience increased counterclockwise facial rotation.(87-88) In humans, increasing jaw closing forces by means of a Milwaukee brace produces increased maxillary expansion and counter-clockwise rotation of the mandibular corpus, and diseases which weaken jaw muscles have the opposite effect, producing growth changes similar to those resulting from softening of the diet. Human jaw muscle size is well known to be highly correlated with facial width and prognathism. (89-95)

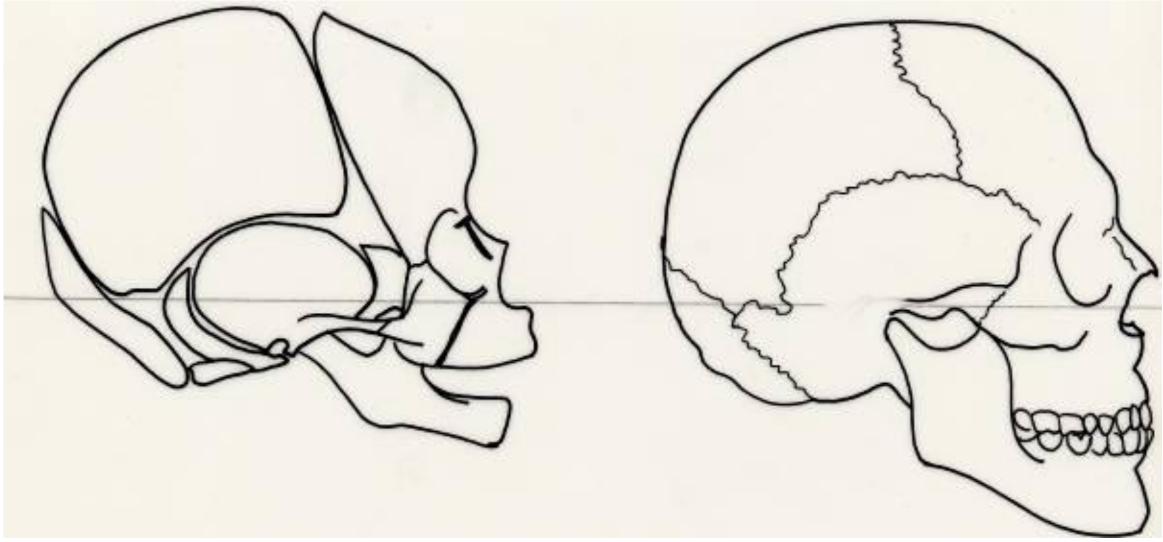
At the borders of this functionally stimulated facial growth process, wherever the bones influenced by functionally stimulated facial growth met areas controlled by the resting tensions of the jaw muscles, remodeling masked much of the functionally stimulated facial growth. Thus functionally stimulated facial growth had little effect on the overall craniofacial growth matrix. For example, rotation of the midface almost completely stopped at the floor of the nose, and extreme counter-clockwise rotation of the mandible was largely masked on the underside of the mandible by resorption of bone at the back of the corpus and apposition of new bone at the front of the corpus. In fact, it was only when orthodontists used implants in longitudinal studies that we learned about the functionally stimulated rotation of the mandible.

TRANSLATION OF THE MANDIBULAR CORPUS

The mandibular corpus led the face in forward translation. This front portion of the mandible maintained its shape while shifting forward further and faster than structures above it. Behind the corpus, the condyles and the posterior borders of the rami functioned like rapidly elongating handles, growing just as much bone as necessary to hold the corpus continually out under the front of the face. At the same time, resorption occurred on the anterior borders of the ascending rami. In this manner, the rami continually pushed out new corpus in front of them, and the anteriormost parts of the rami continually became the posteriormost parts of the corpus.

Forward translation of the mandibular corpus probably served to ensure the longevity of the chewing system by helping to compensate for occlusal wear. The forward translation of the mandibular corpus continuously carried the lower dentition forward into the upper dentition which enclosed it in front and on both sides. In addition, because this functionally stimulated facial growth processes and the rate of occlusal wear both occurred in proportion to the amount of chewing forces they experienced, they occurred in some proportion to each other. In this manner, the functionally stimulated forward translation of the corpus served as a self-regulating mechanism to compensate for occlusal wear. People with stronger jaw muscles and more vigorous chewing experienced more wear from abrasives in the food and also more forward translation of the mandibular corpus, and people with weaker jaw muscles and less chewing force experienced less occlusal wear and less forward translation of the mandibular corpus.

As a result of the forward translation of the corpus, the face flattened with age due to its lower portion swinging out from under the forehead. The forward translation of the corpus usually eliminated overbite and overjet by early adulthood, and most older dentitions were either end-to-end or in a class 3 relationship.



CHILD FACIAL PROFILE IS CONVEX **ADULT FACIAL PROFILE IS FLATTER**

ROTATION OF THE MANDIBULAR CORPUS

While the corpus translated forward, it also rotated in a counterclockwise direction. The center of the corpus, best defined as the inferior alveolar neurovascular bundle and the surrounding bony canal, rotated as the portion of the mandible in the chin area moved up toward the nose and the portions of the mandible at the back of the corpus (the gonial angles) lowered.

The rotation of the corpus of the mandible can be seen most clearly relative to the ramus of the mandible, an area of bone which is located just behind the corpus and is a steady architectural landmark because it is controlled by the resting tensions of the postural temporalis muscle. (96) The gonial angle is the area where the corpus and ramus meet. People with strong overall musculature and strong jaw muscles in particular experienced a large degree of counterclockwise rotation of the corpus and developed more acute gonial angles, while people with weaker muscles experienced less counterclockwise rotation of the corpus and developed more obtuse gonial angles. (97-103) Men, who have stronger average bite forces than women, also tend to have more acute gonial angles. Similarly young adults, who had the strongest average bite forces, have more acute gonial angles than children or older adults. Longitudinal studies have shown that the gonial angle is obtuse in youth when masticatory forces are small, it becomes more acute with adulthood and increasing jaw muscle strength, and it becomes more obtuse again later in life when the jaw muscles become weak from the effects of aging.

By continuously carrying the lower dentition up into the upper dentition, the counter-clockwise rotation of the mandibular corpus also probably served to ensure the longevity of the chewing system by providing a self-regulating mechanism to help compensate for occlusal wear. People with stronger jaw muscles and more vigorous chewing experienced more wear from abrasives in the food and also more counter-clockwise rotation of the mandibular corpus, and people with weaker jaw muscles and less chewing force experienced less occlusal wear and less counter-clockwise rotation of the mandibular corpus.

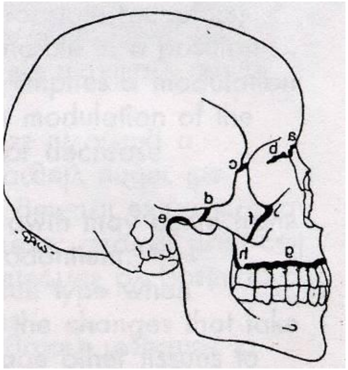
EXPANSION OF THE MIDFACE

The functionally stimulated dynamic pattern of growth in the mandibular corpus moved the midface in the same direction -, just a little less far and less fast. In many ways the bite table acts as a frictional joint between the corpus and the midface. Thus, as the corpus moved forward, the mandibular alveolar process moved less far forward than the corpus (thereby shifting backward on its bony base), the mandibular (lower) teeth moved less far forward than the mandibular alveolar process (thereby tipping backward), the maxillary (upper) teeth moved less far forward than the mandibular teeth (thereby shifting toward an Angle class 3 relationship), the maxillary alveolar process moved forward less far than the maxillary teeth, and the bony framework of the midface moved forward still less far so that the upper teeth shifted forward relative to their bony base.(104- 107) Similarly, the counterclockwise rotation of the corpus affected the midface in proportion to its distance from the occlusal (bite) table. The face grew down and forward as parallel planes - the mandibular corpus, the alveolar processes, the basal bone of the maxillae, the floor of the nose, the suborbital bones, and the supraorbital bones. As the midface followed the counter-clockwise rotating corpus, these planes diverged posteriorly and converged anteriorly. Vertical increases in the height of the face were greater posteriorly than anteriorly.(108-112)

As the midface followed the mandibular corups, adaptive bone growth to fill in structure behind it occurred at the interface between the face and the rest of the cranium. This fill-in growth probably affected all the bones involved in that interface. For example, in strong chewers like Eskimos, the postglenoid processes and the tympanic plates became thick as the glenoid fossae followed the corpus anteriorly.(120) However, the areas where fill-in growth behind the midface is most visible are at the cranial base (24), the maxillary tuberosities, the maxillary alveolar processes, and the circum-maxillary sutures.

The circum-maxillary sutures were almost perfectly aligned to follow the movement of the upper jaw down and forward. They are shown below, along with the maxillary alveolar processes, where the upper teeth meet the maxillary bones.

THE CIRCUM-MAXILLARY SUTURES ALIGNED TO CONTINUOUSLY FILL IN BONE BEHIND MOVEMENTS OF THE FACIAL BONES DOWN AND FORWARD



Unlike the other cranial sutures, the circum-maxillary sutures stay open throughout life and thereby remain growth centers, and there is good evidence that chewing activity contributed to their continued patency and capacity for adaptive growth. Experiments have shown that the small movements at sutures caused by function produces continued slight interosseous movements which can maintain patency, while immobilization of sutures leads to ossification and suture closure.(139-141) Even merely softening the diet has been shown to produce some premature obliteration of facial sutures in experiments with rats.(142) Since this adaptive growth at the circum-maxillary sutures was stimulated by function, it also occurred in some proportion to occlusal wear and thereby provided another self-regulating mechanism for adapting to occlusal wear.

With so much of its growth an adaptive response to functional forces, the midface grew to become a platform almost perfectly designed to resist the complicated synthesis of bending stresses produced by chewing. During incisal biting, the nasal processes of the maxillae carried compressive forces to the medial aspects of the supraorbital ridge through the nasal process of the frontal bone. (113) During power-crushing, the maxillary bite table transferred compressive forces to the cranial base via the walls of the maxillary sinuses and to the lateral borders of the cranial vault via the zygomatic arches. The bony prominence over the canine transferred biting forces directly up to the side of the orbit and the anterior root of the zygomatic arch (114), the bony prominence over the first molar transferred biting forces directly up to the posterior root of the zygomatic arch, the zygomatic arch transferred biting forces to the zygomatic sections of the maxillary and temporal bones which in turn transferred biting forces anteriorly to the lateral wall of the orbit and posteriorly to the temporal bone, and the superiorly and anteriorly directed forces from the condyles during chewing were transferred to the articular eminentia and then to the rest of the cranium by the bone of the temporal squama which converged into the articular eminence from above.(115) Wherever the jaw muscles compressed bones, those bones developed an architecture of struts and beams well suited for resisting compressive forces. External form as well as thickness, density, and orientation of the internal cancellous structure were affected.

However, while the corpus grew by maintaining its shape and shifting its position, the midface grew primarily by changing its shape. The midface was comprised of a number of paired membrane bones. In response to the persistent hammering against them by the mandible, these bones spread like wings.

One direction in which the maxillae rotated in relation to each other was in a frontal plane around an axis through the midpalatal suture. As elevator forces drove the lateral components of the maxillary bones upward and outward around their midline connection, they flattened the roof of the palate. Very strong chewers even developed palatal roofs with a slight downward facing convexity.

Another direction in which the maxillae rotated in relation to each other was in an axial plane around a vertical line drawn through the anterior nasal spine. The posterior portions of the maxillae moved apart farther and faster than their anterior portions, swinging the two maxillae out laterally around their anteriormost attachment. Strong masticatory forces may have helped promote this swinging by driving the lateral portions of the maxillae anteriorly during the working side phase of the power-crush stroke, by driving the posterior portions of the maxillae directly outward during the follow-through phase of the power-crush stroke, or simply by exerting vertical forces against an outwardly inclined maxillary posterior dentition. The effect of superiorly directed forces from the mandible on the widening of the maxillary bite table can be seen in the way a Milwaukee brace produces a splaying of all the maxillary teeth.(116)

As a result of these rotations of the lateral portions of the face around midline portions, in the presence of vigorous mastication, there was more anterior movement laterally than there was medially, and the face became flattened frontally. For this reason, small zygomaxillary angles, large nasomalar and zygomaxillary angles, and flared zygomas were prominent features of adults in tribes who made extreme use of their masticatory muscles.(117) Thus the faster translating mandibular corpus occurred against a faster expanding midface and thereby kept the upper and lower teeth in close proximity.

Not only was bone in the craniofacial region deposited wherever it was needed, it was also resorbed wherever it was not needed. In the upper half of the face, resorption produced an enlargement of the sinuses which filled the spaces between structurally important areas. Thus a frontal sinus formed behind the anteriorly migrating frontal bone, and maxillary sinuses grew to occupy large areas between the structural buttresses of the expanding midface. The anterior translation of the mandibular corpus, supported by apposition at the back of the rami, was also accompanied by resorption at the front of the rami, because additional ramal bone was not needed to support masticatory function - especially after maturity when elevator forces stopped increasing but the corpus kept translating.

The product of this pattern of apposition and resorption stimulated by masticatory function was a lightweight and efficient honeycomb of thin membrane bones arranged in a series of trusses and buttresses which provided just enough structure to effectively resist the forces received. (118) Each membrane bone acquired and maintained a thickness and alignment to best withstand the forces applied to the upper bite table by mastication and to distribute those forces widely against the underside of the front of the cranium. (119) The distribution of bone became virtually identical to the stress distribution experienced during loading. Furthermore, because of constant remodeling activity, the distribution of bone remained identical with the stresses experienced during loading, even as chewing patterns changed with age.

ADAPTATON AT THE TMJS

To coordinate these diverse growth patterns in the lower and middle face so that they maintained the stability of the bite table required extreme adaptability at the TMJs. The mandibular condyles were uniquely designed with a layer of undifferentiated mesenchymal cells in the proliferative zone covering them, therefore they could grow in almost any direction.(121)

In unusual growth situations, such as in facial growth affected by injury or disease, the condyles can make extreme accommodations to maintain contact with the temporal bones at the TMJs, often making a sharp bend at the condylar neck.

The remarkable adaptability of condylar growth has been demonstrated experimentally. Studies using functional appliances, biteplates, chin cup appliances(122), trauma, and loss of occlusion have all demonstrated that changing the position of the mandible leads to rapid adaptative bone growth at the condyles and rami. Condylectomy is routinely followed by spontaneous regeneration of a new condyle with a functional articular head and condylar neck contained within a normal synovium and in some cases with a fibrocartilaginous cap. Surgery to alter the position of the maxillae triggers adaptive processes in the mandible and the temporomandibular joints. (123-126) Manipulation of the mandible produces changes in the location and thickness of the layers of condylar cartilage.(127) Removal of the articular disc and zygomatic arch produces some very unusual condyle shapes.(128) In rats removing and/or trimming the teeth leads to a reduction of condylar cartilage thickness (129), softening the food leads to a reduction in all condylar dimensions (130), and rotating the mandible posteriorly redirects condylar growth backward until contact with the glenoid fossae is reestablished.(131) In rabbits moving the glenoid fossae posteriorly triggers an increase in condylar growth until contact between condyles and fossae is reestablished.(132)

Adaptability at the condyles plays a critical role in growth. Enlow says, "The variable capacity of condylar growth thus provides adaptation to different facial types, different articular patterns between the individually variable configuration and dimensions of the cranial floor and maxilla, different occlusal patterns, and normal structural changes occurring in conjuction with progressive growth. As the whole mandible becomes displaced in whatever vectors are involved at different ages and in whatever variations occur among different individuals, the condylar cartilage and the contiguous membranes forming the intramembranous bone of the condylar cortex and the condylar neck grow in whatever directions and in whatever amounts are required to sustain constant functional position and articulation with the cranial floor.” (133) Petrovic says, “The condylar cartilage growth is integrated into an organized functional whole having the form of a servosystem, which is able to modulate the lengthening of the condyle in such a way that, through postnatal growth, the lengthening of the lower jaw adapts to the lengthening of the upper jaw.” (143)

DENTO-ALVEOLAR ADAPTATION

To coordinate the diverse growth patterns in the lower and middle face so they maintained the stability of the bite table also required dento-alveolar adaptability. The teeth needed to be able to maintain the stability of the bite table while their interdigitation did not restrict the growth patterns of the upper and lower jaws. For this to occur, and the bony processes in which they are embedded needed sufficient plasticity to be able to maintain the supportof the bite table at the teeth while allowing each tooth to shift in any way necessary to accommodate the forces imposed on it while maintaining support in a vertical plane.

During childhood, some locking in of the occlusion was important to coordinate the maxillary and mandibular growth processes. In both primary and permanent dentitions the anterior teeth erupted into an overbite relationship so that the relatively rapid anterior translation of the corpus tended to carry the maxillary anterior teeth out with the mandibular anterior teeth and keep the upper and lower incisors coupled. The steep cusps and fossae of the posterior teeth, interdigitating much like the jagged edges of bone in cranial sutures, also kept maxillary and mandibular dental arches in close proximity in spite of the diversity of growth patterns of their basal bones. Keeping the opposing teeth close enough for efficient mastication was vital to survival.

Eruption paths of the teeth cannot be controlled very precisely by intrinsic mechanisms, so they were assisted by the light steady background tensions directed inward from the lips and cheeks and outward from the tongue. Then, as upper and lower teeth came into contact, their interdigitation refined their alignment. Since each upper tooth interdigitated with two lower teeth and each lower tooth with two upper teeth, the precise alignment of opposing teeth spread up and down the arch. A little later, as the primary teeth were replaced by the permanent teeth, the stability of the occlusal table was maintained by a tripod of the earliest erupting permanent teeth. The permanent incisors and the six year molars produced a three legged platform which maintained the stability of the bite table while the primary teeth between them were replaced one or two at a time by their permanent successors.

During adulthood, the bite table continued to maintain its stable position and orientation in the face. Teeth usually wore down at the rate of about .4 mm per year and also erupted at about the same rate, driven by a light steady eruption force that has been estimated at 6 to 8 grams.(134-136) The resulting stability of clinical crown heights allowed alveolar crest height to remain constant (137), so that the periodontal structures maintained constant pocket depths and a shape that prevented the trapping of food while allowing uninterrupted passage of the gingival and transseptal fibers.

Continual eruption was so common in our ancestors that it may have become necessary to maintain the health of the periodontal structures by allowing the old cementum which had accumulated bacterial toxins at the bottom of the sulcus to be continually replaced by new sterile cementum on the erupting root surfaces. DuBrul explains, "Cementum, like bone, ages and finally degenerates. In bone this process leads to resorption of the old and its replacement by new bone. In the cementum such turnover is impossible. Instead, the aging cementum is covered by the formation of an additional young layer of cementum. This continuous apposition of new cementum occurs, in all probability, in waves separated by periods of rest. Growth of cementum is evidently indispensable for the integrity of the dentition. Continued growth of the cementum, however, needs space, and space is provided by the continued active eruption of the teeth. The latter in turn depends on continued occlusal and incisal wear. Thus attrition as the prerequisite of compensatory active eruption is itself a necessary factor for the health of the teeth."(138)

One source of dento-alveolar adaptability was occlusal wear. By shortening the cusps, occlusal wear made the interdigitation progressively less steep and thus more easily able to accomodate changes in relative positions between opposing teeth. In many people, the wear was so rapid that the cusps were completely eliminated by adulthood and provided no obstacle to the diverse growth patterns continuing in the basal bones above and below them.

The other source of dento-alveolar adaptability was periodontal remodeling. The alveolar bone surrounding the roots of the teeth remains plastic throughout life. Each root is surrounded by a metabolically active periosteal layer on one side and a proliferating layer of cementoblasts with embedded Sharpey's fibers on the other side. This delicate and dynamic network of fibers and connective tissues was able to alter the location of the root in the alveolar bone to accomodate changes in the positions of the teeth whenever they occurred. The effectiveness of this adaptive tooth positioning mechanism can be seen in the way it enables us to perform orthodontics at any age.

After maturity, once the permanent occlusal table was well established, locking together of the upper and lower dental arches to coordinate their growth was no longer necessary to ensure masticatory ability. As masticatory forces continued to move the mandibular and maxillary bony bases differentially in adulthood, the teeth could not be too tightly locked together, because they had to be able to adapt to these differential movement patterns above and below them without sacrificing occlusal stability. The teeth had to adapt by moving within the jaw bases rather than restraining the movement of the jaw bases. As the mandibular corpus translated forward and brought a wider part of the V-shaped lower dental arch under any portion of the upper dental arch, the palate and upper dental arch was widening directly due to expansion of the midface. The anterior forward translation of the corpus relative to the maxillae brought the lower buccal cusp tips up the lingual-facing and distal-facing inclines of the upper buccal cusps, even as a slight continued widening of the maxillary dental arch moved these upper buccal cusp inclines further buccally. Thus the mandibular molars moved anteriorly relative to the maxillary molars while the maxillary molars moved buccally relative to the mandibular molars. The net effect was to keep the upper and lower dental arches in close proximity while they moved in slightly different directions.

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CHAPTER 3) MODERN HUMAN CRANIOFACIAL GROWTH

Then, in a development which was extremely sudden by evolutionary standards, modern civilization altered the craniofacial growth process by changing the functional environment in which the masticatory system grows and develops.

The human diet had been softening slowly but steadily accompanying civilization ever since the use of fire for cooking. However, with the rapid spread of industrialization in the nineteenth and twentieth centuries, foods became so soft that they came to require only a fraction of the jaw muscle strength which had been used universally among humans for tens of thousands of years.

Without tough resistant foods to stimulate the ideal type of exercise the jaw muscles get from functional mastication, our jaw muscles no longer develop as fully as they did in our ancestors. In modern children, bite forces no longer increase rapidly with age after the primary dentition(1), and in modern adults average bite force is now less than half of what it used to be.(2) Similar losses of jaw muscle strength also affect animals raised experimentally on soft-food diets.

At the same time jaw muscle strength has decreased, other changes have also occurred in the environment of the craniofacial system. Head posture has shifted forward, and the verticalization of jaw movements has made the dental occlusion more vertically oriented, steeply interdigitated, and less stable. Generally these changes occur together with the weakening of the jaw muscles in about the same degree all over the world when people change from traditional life styles to modern ones, making it difficult to separate the effects of each change in population studies.

These changes in the environment of the masticatory system have altered the craniofacial growth process and thereby also the dimensions of the average human craniofacial structure. Each one of these changes in the environment of the masticatory system has been shown capable of altering craniofacial growth experimentally, and they seem to alter it synergistically – they each influence growth in approximately the same direction. This fact also makes it difficult to discern which change in the environment of the masticatory system is responsible for which alterations of craniofacial growth.

To quantify these average changes in recent human craniofacial form, they must be seen against a background of increased variability of all craniofacial dimensions due to the loss of resting tonus of the craniofacial muscles which help regulate craniofacial growth. As the craniofacial muscles have become weaker, irregularity and asymmetry in the craniofacial skeleton have increased. As a result, there are now extreme variants in craniofacial structures, even among populations relatively sheltered from the genetic mixing which has generally accompanied civilization. Certain craniofacial skeletal structures that have become fairly common today are rarely or never found in skeletal material from previous societies. Studies have shown that animals raised on soft diets develop less symmetrical craniofacial structures than normals, and that asymmetry of the craniofacial skeleton and the range of variation of several facial angles and dimensions have risen markedly in recent centuries. Weston Price noted that, in tribes still eating traditional diets, the people all looked like brothers and sisters, but when they switched to modern diets they lost their resemblance.

These average changes in recent human craniofacial form must also be seen against a background of secular changes which have made nearly all skeletal dimensions significantly larger within even within one generation after industrialization.(56-72) The cause of this increase in skeletal dimensions is thought to be likely related to nutrition, such as the effects of increased sugar intake on growth hormone production. Whatever the cause, the effect is a uniform increase in all post-cranial dimensions, which is probably at least partly due to an increased elongation of cartilage. In the craniofacial area, this increased elongation of cartilage is probably responsible for an increased lengthening the cranial base and at least some of the height increases in the face due to increased body height.

Yet, in spite of the complexity of craniofacial growth and the large number of variables involved, there have clearly been some profound changes in the average human craniofacial growth pattern due to modern civilization. These craniofacial growth changes have not affected everyone the same way, and they are not easy to quantify against a background of genetic mixing and normal variation which often dwarf them. However, when large samples are compared and genetic mixing is minimized, the same pattern of altered craniofacial growth and altered craniofacial structures can be seen to have occurred in the faces of all racial groups in all parts of the industrialized world.

THE LOSS OF OCCLUSAL STABILITY

One change which has accompanied civilization is that the occlusal table has become more irregular. The shape of the occlusal table is determined less by genetics than other aspects of the craniofacial area. Without sufficient elevator forces to align the teeth and keep them aligned, the mechanism by which the bite table accomodates the normal pattern of functional jaw movements and thereby becomes smooth no longer operates effectively. One result has been an increase in the irregularity of the bite table. (4) The prevalence of malocclusion has risen far beyond the 10 percent level found in earlier humans and in primates.(5-12) Corruccini collected a great deal of cross-cultural occlusal data using a variety of native populations before and after adopting a modern diet and concluded that the increases in malocclusion occur directly in proportion to the change of diet. He noted, "Cross cultural data dispel the notion that considerable occlusal variation is inevitable or normal. Rather it is an aberrancy of modern urbanized populations. Furthermore, the transition from predominantly good to predominantly bad occlusion repeatedly occurs within one or two generations' time in these (and other) populations, weakening arguments that explain high malocclusion prevalence genetically. Cumulatively, over these study samples, there is no chance for consistent inbreeding, racial mixing, or genetic change accounting for the transition."(13)

The most common occlusal irregularity which has accompanied modern civilization is a loss of occlusal stability. While our ancestors had occlusal tables that were stable along a large portion of the superior surface of their mandibular range of movement and maintained by large areas of perfectly fitting opposing facets, modern humans generally have only a small area of occlusal stability maintained by ten to twenty pinpoint contacts or very small facets. In some people the loss of occlusal stability can be seen progressing with age as an increase in the number of occlusal interferences.(15-16)

One contributer to modern occlusal instability is the prevalence of tooth decay, which has closely followed the spread of sweetened refined foods around the world.(17) Tooth decay can bring about sudden losses of areas of tooth contact and cause rapid shifting of teeth. Fillings may restore the lost tooth structure, but they can’t reverse any misalignment which may have occurred and, even if the decay did not cause misalignment of teeth, fillings rarely recreate the exact same tooth height that was present before the decay occurred.

Another contributer to modern occlusal instability is the prevalence of periodontal disease which has also followed the spread of sweetened refined foods around the world. Periodontal disease can destabilize the occlusion by making individual teeth susceptible to drifting.

A sudden increase in periodontal disease can be seen within a matter of years after the switch from a tough traditional diet to a softer modern one. After studying Australian aborigines who had recently moved into a settlement and abandoned their native diets, Henry Beyron noted, "Chronic marginal gingivitis was present in most of the children and young adults examined; gingival hemmorage was a common occurrence during examination. Presence of food debris at the gum margins of the anterior teeth was also observed in most of the subjects. Lack of the friction which occurs during the vigorous use of anterior teeth in chewing hard foods (such as would be provided, for example, by stripping half cooked flesh and tendons from a kangaroo cooked in native fashion) has resulted in soft hyperaemic gum margins which contrast markedly with hyperkeratinized gum margins seen in natives living under natural conditions. Lack of the natural detergence effected by tough fibrous foods permits retention and stagnation of farinaceous material and oral debris which has a continued toxic irritant effect on the gum margins... The gingival condition of children improved whenever they spent some time away from the settlement, living with their family groups on hunting excursions." (18) Taylor compared two groups of Polynesian natives; one eating native foods that were tough and fibrous, and the other eating native foods that were softer and sweeter. The tough food group showed no evidence of generalized chronic gingivitis or periodontal disease and little alveolar bone resorption; while the soft food group showed widespread chronic periodontal disease, extensive deposits of calculus, and some localized alveolar bone resorption.(19)

JAW MUSCLE FORCES AND OCCLUSAL STABILITY

While tooth decay and periodontal disease probably play some role, the most important cause of the loss of occlusal stability in modern populations is the weakening of the jaw muscles. Occlusal stability is highly correlated with jaw muscle strength (21), and intra-individual studies show that the jaw closing muscles are larger on the side of the arch which has the largest number of tooth contacts.(22) In fact, recently the strength of the jaw muscles has become more highly correlated to occlusal stability than to general body strength.(26-27) The ultimate size of the jaw muscles is now determined more by the way the neuromuscular system reacts to the lack of functional stimuli than its ability to grow muscle tissue where it is needed. This situation stands in contrast to our ancestors whose jaw muscle strength was proportional to their overall musculoskeletal proportions.

The loss of jaw muscle strength has been shown able to cause loss of occlusal stability. Studies of baboons raised on soft food have verified the role of dietary consistency in decreasing occlusal stability and producing other occlusal variations.(14)

Conversely loss of occlusal stability can also causes a loss of jaw muscle strength. When the teeth don't form a regular evenly sloped uniform bite table, reflex mechanisms designed to prevent traumatic contacts between teeth inhibit jaw muscle closing forces.(20) Jaw closing muscle function becomes more delicate and careful, like your leg muscles might behave when you walk barefoot on gravel. One study showed that elimination of occlusal interferences can lead to increased bite forces.(23) Other studies have shown that restrictive lateral and anterior guidance or balancing side interferences can inhibit jaw closing forces and restrict the mandibular range of movement. (24) The loss of occlusal stability even compromises the jaw closing forces used for bracing the mandible during swallowing. Although mandibular bracing is part of a well coordinated set of neuromuscular reflexes triggered by initiation of the swallowing process, the jaw closing forces used for mandibular bracing may be diminished or even sufficiently counteracted by the bracing of the jaw opening muscles to create a myogenous means to stabilize the mandible in the presence of pain. Such recruitment often results in swallowing without occluding the teeth. One study showed that postorthodontic patients who had teeth-apart swallowing converted to teeth-together swallowing after occlusal equilibration.(25)

With weak jaw muscles able to cause a loss of occlusal stability and loss of occlusal stability able to cause a loss of jaw muscle forces, occlusal instability and jaw muscle weakness are co-dependent variables.

NARROWING OF JAW MOVEMENT PATHWAYS

A second change which has accompanied civilization is the narrowing (verticalization) of jaw movements and consequently also of the structures which adapt their form to jaw function. These include the TMJs and the dental occlusion.

Chewing pathways automatically widen in response to tough foods, while they stay close to the midline for simple mashing of softer foods. (28-29) Today much of our food is so soft that it doesn't even provide a coherent resistant bolus on which the mandible can pivot during power-crushing. As a result, in many people, instead of power-crush strokes following-through to the balancing side, the mandible comes to a full stop in the intercuspal position (30), and the lower teeth are simply squeezed against the upper teeth, mashing the food in between while making tooth contact right through the bolus. The tooth contact shuts down the jaw closing muscle activity and elicits a jaw opening reflex, minimizing any gliding contact. Thus the shape of the average modern functional jaw movement is much narrower than it was in our ancestors.

In the TMJs, this verticalization of functional jaw movements has caused the glenoid fossa to become deeper and the articular eminence to become more steeply inclined. Studies of rabbits have shown that raising them on soft food causes very similar changes in the contours of the TMJs.(96)

In the dental occlusion, the verticalization of jaw movements has changed the shape of the dental arches and particularly the interdigitation of the teeth. Because the pterygomasseteric slings no longer drag the mandible across the maxillary bite table in long gliding strokes with follow-through to the balancing side, the bite table no longer acquires a contour shaped to accommodate such long strokes. Thus, while the steep interdigitation and overbite of the teeth in our ancestors rarely even lasted until adulthood, most modern dentitions retain these features throughout life.

MAXILLO-MANDIBULAR SYNOSTOSIS

The verticalization of the dentition may have negative impacts on facial growth. Researchers have long likened the dental occlusion to a cranial suture functioning to retain a physical connection between the upper and lower jaws. When steep dental interdigitation and overbite are retained past the time during which they are useful in the growth process, the resultant locking together of the upper and lower teeth may act much like a prematurely closed cranial suture (synostosis). This partial synostosis may be able to restrict the forward translation of the mandibular corpus by connecting it to a maxillary bite table which cannot translate easily, and it may be able to restrict the expansion of the maxillary bite table by connecting it to a mandibular corpus which cannot expand at all. Experimental studies have shown that premature synostosis of craniofacial sutures in animals impairs the growth of the involved bones and causes increased variability of craniofacial growth patterns.(31)

FORWARD HEAD POSTURE

A third change which has accompanied civilization is that head posture has shifted forward. On average, the center of mass of the head in normal standing posture has shifted forward relative to the long axis of the spine.

Forward head posture can be caused by airway blockage in the pharynx. Airway blockage causes extension of the head in order to pull the mandibular corpus further forward and away from the cervical column and thereby increase the space available for airway antero-posteriorly. At the same time the head is extended, forward repositioning of the head occurs to keep the head level. Thus the head simultaneously shifts forward and into extension. The connection between airway blockage and this change in head posture has been demonstrated in clinical and cross-sectional studies.(32-36) Oral breathing and other effects of partial airway blockage seem to have become more common with recent civilization, probably because of the rise of allergens and pollutants in the air and/or asthma and other autoimmune diseases affecting respiration.

Forward shifting and extension of head posture can cause a relative clockwise rotation of the mandible and face, because, as the midface rotates up and away from the sternum, the mandible is still attached by muscles and fascia to the sternum. One longitudinal study suggested that the head posture changes lead the way; because the morphology of the first cervical vertebra, which is a function of head posture, can be used as an indicator of the subsequent pattern of mandibular growth.(37)

Conversely, clockwise rotation and retrusion of the mandibular corpus may be able to cause extension and forward translation of head posture. Clockwise rotation or retrusion of the mandibular corpus can impinge directly on the pharyngeal airway and thereby cause the head to go into extension to maintain the patency of its airway.

Thus the extension of the head and the clockwise rotation (and retrusion) of the mandibular corpus are also co-dependent variables. (38)

EFFECT OF LOSS OF SKELETAL MUSCLE ON THE CRANIUM

The average weakening of the skeletal muscles, as well as the jaw closing muscles, has affected the growth of the cranial vault. On average, the cranial vault has become rounder as a result of a growth pattern that is influenced less by elevator muscle forces and more by the circumferential expansion of the brain. Long skulls have become shorter and wide skulls have become narrower, with both dolichocephalics and brachycephalics normalizing to become more mesocephalic (73-78) much like infant skulls which have not yet been influenced by the pulls of the musculoskeletal system.

EFFECT OF LOSS OF MASTICATORY FUNCTION ON THE FACE

The face is the portion of the cranium which has been most affected by civilization. The cranial base angle has become more acute(79), and the facial growth processes extending from the cranial base have been redirected vertically and posteriorly. The resulting growth pattern is, on average, more retrusive at the mandibular corpus and the midface, narrower in the midface, and longer vertically at the front of the face (causing a relative clockwise rotation of the mandibular corpus and midface).

With the face becoming longer, narrower and more retrognathic even in those with strong skeletal muscles and short wide cranial vaults, mismatches may be produced between the shapes of the vault and the face. In our ancestors, those with strong overall musculature had shorter and wider vaults (brachycephalic) with shorter and wider faces, and those with weaker overall musculature had longer vaults (dolichocephalic) with longer faces (leptoprosopic). Some researchers even refer to short wide faces as brachyfacial and to long narrow faces as dolichofacial. However, today some people with strong musculature may have relatively long narrow faces, because they failed to develop the jaw muscles as much as their other muscles.

Thus, unlike in skeletal remains, relatively leptoprosopic faces may be found on brachycephalic crania.

LOSS OF FUNCTIONALLY STIMULATED FACIAL GROWTH

The fourth change which has accompanied modern civilization, and the change which has had the most impact on human craniofacial growth, has been the loss of functionally stimulated facial growth. The weakening of the jaw muscles has diminished the amounts of forward translation, counterclockwise rotation, and midfacial expansion experienced in facial growth. Decreasing facial growth in these directions has been demonstrated experimentally in rats, monkeys, rabbits, hyraxes, and minipigs by raising them on soft diets (51, 39 96) and in humans with muscle disease (40).

RETRUSION

One result of the loss of functionally stimulated facial growth is that, in modern humans, the mandible is shorter and more retrusive, because the corpus no longer translates as far forward and therefore as far from the condyles.(81-87) Today there is so little forward facial translation produced by functionally stimulated facial growth that total facial prognathism is determined more by cranial base shape than by functional forces or jaw muscle strength.(41) Prognathism is only positively correlated with jaw muscle strength when jaw muscle strength is high enough to exert a significant effect on growth.(42) Decrease in size of the mandibular corpus and retrusion of the mandibular corpus also occur commonly in patients with muscle diseases that weaken the craniofacial muscles.(40)

One result of the retrusion of the mandibular corpus is that class two malocclusions (in which the lower first molar fits behind its normal contact with the upper first molar) have become common today, while they are relatively rare in museum skulls. In fact, until recently, class two malocclusions comprised only about the same small percentage of the population in all different genetic groups. Suddenly, in the last century, they have come to comprise nearly half the population in industrialized countries.

A second result of retrusion of the mandibular corpus is a pattern of remodeling in the TMJs. The necks of the condyles frequently display a forward bend due to a pattern of adaptive remodeling which maintains contact between the mandible and the temporomandibular joints in spite of mandibular retrusion. Such forwardly bent condyles are never seen in the skeletal remains of our ancestors. Histologic studies have shown that remodeling is most often regressive on the posterior aspect of the condyle and progressive on the anterior aspect of the condyle.(88-89) Similar progressive remodeling on the anterior aspects of the condyles in combination with regressive remodeling on the posterior aspects of the condyles has been produced in animals using inclined planes(90-91), or chin cups to retrude the mandible (132). While condylar remodeling was proportional to age in our ancestors, it is now dependent on mechanical factors and independent of age.(92) Because of the increased variability in modern craniofacial growth, condylar remodeling has also become more variable. One researcher found that the range of variation in condylar growth among untreated normal subjects may be as much as 42 degrees.(93)

A third result of retrusion of the mandibular corpus is a pattern of tissue damage and degenerative changes which commonly occurs at the backs of the condyles. Autopsy studies have shown that the lesions of osteoarthritis appear first on the upper posterior surface of the condyle(94), and a scanning electron microscope study found osteoclastic resorption on the posterior condylar slope in 19 of 20 joints examined.(95) A study using a catheter to measure intrajoint pressure found that pressure only became high and therefore pathological only when the condyle was moved in a backward direction. An experimental study of autopsy specimens found that anterior displacement of an articular disc can be produced by incision of the tissues of the posterior disc attachment, implying that damage to the posterior tissues precedes anterior displacement of the disc.(94)

Retrusion of the mandibular corpus also affects the midface. In class 2 malocclusions, it is more common for both maxillae and mandible to be retrusive relative to the rest of the cranium than for the maxilla to be located too far protrusively. Studies comparing modern and ancient crania have found that the modern crania have more retrusion of the midface and the lower face in Japanese(72, 131), Egyptians(48), and Americans.(80)

RELATIVE CLOCKWISE ROTATION

A second result of the loss of functionally stimulated facial growth is that the mandibular corpus (and to a lesser extent the midface) exhibit less counter-clockwise rotation during growth than they did in our ancestors.(53-54) The back of the face no longer grows as far vertically, and the front of the face grows farther vertically.(44-45) Orthodontists have long recognized that many of the problems in their patients are due to excess height at the front of the face.(46-47) Loss of elevator forces has been shown to lead to dramatic increases in the vertical dimensions at the front of the face - whether the loss is caused by disease which impairs muscle development (48), cutting or removing muscles or motor nerves, or natural trauma.(130) When experimental impairment of the elevator muscles is carried out unilaterally in animals, increased dental height occurs on the side of impairment. Furthermore, in cross-sectional studies of normal children, anterior facial height is inversely proportional to elevator muscle strength.(49-50)

The trend toward a more clockwise rotating facial growth pattern in modern humans can be seen in studies where researchers have compared mean facial diagrams of traditional Australian aborigines with those of modern Swedes and those of modern with prehistoric Nubian populations.

Some modern faces even rotate backward (clockwise). There is no evidence of this type of growth pattern in the skeletal remains of our ancestors. In one study of children with clockwise (backwardly) rotating faces, using an exercise gum to strengthen the jaw muscles temporarily changed their facial rotation into a more counter-clockwise growth pattern.(43)

One result of this average change in the direction of growth of the mandibular corpus is that the gonial angle, where the corpus meets the very stable mandibular ramus, has become more open.(57- 62) In addition, it's common to find an antegonial notch where the ramus meets a steeply inclined corpus.

The front of the midface has descended following the corpus, increasing the distance from the incisal edges of the maxillary central incisors to the nasal floor.(98) In fact, generally all the facial shelves, in proportion to their distance from the cranial base, have followed the clockwise rotation of the mandibular corpus and diverged at the front of the face. The intermaxillary angles and the angles between mandibular base and nasal floor have increased (99-103) as the facial shelves have fanned out anteriorly. One result is that gummy smiles, never seen in pictures of tribal peoples, have become common. In some modern faces, the framework of bones and teeth has become so long that the lips show visible strain when trying to maintain a seal during swallowing, and maxillary impaction surgery is the only way to remedy the situation and restore normal resting lengths in the jaw closing muscles.

The relatively clockwise rotation of the face has exerted its strongest effects laterally over the buccal segments of the dental arch where the bulk of the masticatory forces are transmitted. With the cheekbones sinking down and back while the cartilaginous elongation in the midline has only increased, the face has become more convex. Thus the nose has become more protrusive on both a sagittal and frontal plane.(80)

The relatively clockwise rotation of the face has also changed the orientation of the teeth. With the roots of the mandibular incisors carried down and back by their basal bone, they don't upright as readily as they did previously.(104) The long axes of upper and lower incisors form a smaller angle than in skeletal remains.(105)

CONSTRICTION OF THE MIDFACE

A third result of the loss of functionally stimulated facial growth is that the modern human midface expands less. Some of midfacial expansion of our ancestors appears to have been redirected vertically, resulting in a marked narrowing of the palate and its supporting structures during the last several centuries.(106-110) Similar maxillary narrowing has also been produced in animals raised on soft diets.(51-53), and in humans without masseter and pterygoid muscles.(54) Monkeys raised on soft diets often develop crowding of the upper teeth much like that frequently seen in modern children.(55)

Sir Arthur Keith studying the secular change in facial shape of Englishmen commented, "Misplacements of the teeth, long narrow dental arches, high vaulted palates, and carious teeth, which are so common among Englishmen of today, were almost unknown amongst the British people of the Neolithic and Early Bronze periods; these conditions make a sporadic appearance as the Roman period is approached, becoming more frequent in this period. They are conditions which are rarely seen amongst the remains from Saxon graveyards. Indeed they do not assume anything approaching their present frequency until the eighteenth century is reached and England entered upon her life of industrialism."(111)

The narrowing of the maxillary bite table has affected the width of the facial structures which buttress it. Thus while most overall craniofacial dimensions (except mandibular size) have increased with civilization, facial width has either stayed the same or diminished slightly.(112)

ADULT FACIAL GROWTH

As it did in our ancestors, facial growth still continues throughout adulthood at about a tenth of its previous rate, even though there is no longer any need for continued functionally stimulated facial growth to compensate for continual tooth wear. Increases in craniofacial dimensions have been documented in the third and fourth decades (113),the fifth decade (114), the sixth decade, and even the eighth decade. Recently Behrents recalled a large number of subjects from an extensive growth study and found that, in the subsequent thirty years, extensive growth had taken place.(115)

In addition to growing continuing to grow according to each individual’s unique facial growth pattern, many faces grow significantly in height at the front of the face during adulthood. (116-118) Studies have shown that, during adolescence and young adulthood, modern humans tend to maintain a facial growth pattern that is consistent with their earlier facial growth pattern. Horizontal growers tend to keep growing horizontally, and vertical growers tend to keep growing vertically. However in later adulthood vertical dimensional changes appear to be common to all adults.(119) Morphologic face height in individuals possessing an intact or relatively intact natural dentition increases with age up to the fifth or sixth decades.(120)

One contributor to the increase in height at the front of the face may be the eruption force of the teeth and their surrounding bones. If the eruptive force inherent in the opposing teeth is greater than the jaw closing muscle forces which naturally limit tooth eruption, the teeth can erupt too far – elongating the framework of bones and teeth at the front of the face. It's interesting that the rate at which teeth wore down and erupted in some pre-industrial cultures is very similar to the rate at which faces lengthen in modern post-industrial cultures where teeth no longer wear down significantly.(121)

RESPONSES TO GROWTH RESTRICTIONS

The way an individual craniofacial structure is affected by inhibition of normal growth depends largely on the response of that individual's neuromuscular system. Studies have shown that individuals have relatively consistent, unique, physiological response patterns to a variety of stressors. For example, a "muscle responder" will respond repeatedly with tension in the same set of muscles to a wide range of emotional stimuli. Similarly each type of person has a relatively consistent individual response to an occlusal change. Some people avoid an experimentally placed occlusal interference while others ignore it. Because of the influence of resting muscle forces on growth and the control of those forces by the central nervous system, a different modification of the growth process occurs in each different personality type. The two most distinct personality responses are the aggressive and the passive ones.

AGGRESSIVE RESPONDERS

Aggressive responders seem to react to a growth restriction by fighting against it. They develop strong parafunctional habits (clenching or grinding). Once these reactions become habitual, they can significantly alter the pattern of late craniofacial growth depending on their frequency and direction. Often they are able to limit verticalization of the craniofacial skeleton and keep the corpus located up high in the face so the gonial angle remains small and anterior face height is not permitted to increase excessively.

Sustained clenching, especially during nocturnal bruxism, frequently causes intrusion of the posterior teeth more than the anterior teeth. In the presence of a retained overbite, it is very difficult to use clenching to apply forces axially to the front teeth. With axial forces limited to the back teeth, the front teeth only receive clenching forces after they have superupted far enough to contact at the same time as the back teeth. This stands in contrast to the dentitions of our ancestors in which the front teeth did not touch when the back teeth were in solid contact. When the front teeth receive clenching force, it is directed forward on the upper front teeth and backward on the lower front teeth. In addition, clenching is a non-physiologic exercise in that it produces sustained isometric muscular contractions and continuous pressure on bones and other connective tissues that may inhibit blood flow, unlike the intermittent functional pressures which enhance blood flow.

Grinding the teeth is not isometric like clenching, and may even be rhythmic like functional masticatory system stimulation. The increased resting tension in the elevators is combined with lateral forces that alternate somewhat the way functional forces do. Grinding is a healthier form of exercise than clenching, and the jaw muscles retain more strength than they do under the influence of isometric exercise. In addition, grinding may occur with sufficient force to wear down the cusps and thereby eliminate at least some aspects of the maxillo-mandibular synostosis. However, in many people with relatively deep overbites, grinding is still confined to the back teeth, and, even when grinding does include the front teeth, it doesn't produce an occlusal table which supports the mandibular articulation like an occlusal table formed in response to functional forces. The pattern of wear from chewing on a resistant bolus which the mandible pivots around eliminates balancing side interferences and overbite of the front teeth, maintaining a central bracing position but gradually broadening it in all directions. In contrast, the pattern of wear from bruxism generally lacks the variability produced by healthy chewing function. In some people, the dentition may be worn flat and left without a central bracing location.(122)

In some cases aggressive responders establish what is known as a dual bite. This uniquely modern type of occlusal table is remarkable for having two bracing positions. In the posterior bracing position the condyles tend to be positioned retrusively in the glenoid fossae.(123) In the anterior bracing position the teeth form a platform against which the mandible can be braced for clenching, swallowing, and some chewing without driving the condyles back against the posterior limits of the joints. The presence of this anterior platform appears to allow the system to operate with relatively little pathology and few symptoms compared to groups with otherwise similar occlusions.(124)

PASSIVE RESPONDERS

Passive responders seem to react to a growth restriction by avoiding it as much as possible. A strained bite is usually avoided by minimizing the use of the bite. Without bite forces sufficient to counteract eruption forces, there may be increases in the resting lengths of the elevator muscles and the facial muscles. Supereruption of the posterior teeth may leave an anterior open bite. Supereruption of the entire dentition may leave the facial framework so long that the lips are unable to maintain a seal during swallowing without visible signs of strain.

THE LOSS OF ADAPTIVE MECHANISMS

A fifth change which has accompanied modern civilization has been a loss of adaptability in the craniofacial area. The decrease of strong rhythmic masticatory forces has diminished the pumping of the craniofacial area and thereby also the accessory circulation to several of the craniofacial tissues.

In the dentition, the cessation of occlusal wear and the diminished health of the periodontal tissues limit the ability of opposing teeth to shift positions relative to each other. Opposing molars, each with four deeply interdigitating cusps, can certainly not shift relative to each other as easily as opposing molars with low and rounded or completely flattened cusps. In addition, teeth with less functional stimulation have less periodontal health, which probably limits their ability to shift positions. Supererupting teeth with inflamed periodontal tissues causes loss of gingival height.

In the temporomandibular joints, a decrease in weeping circulation limits the potential for remodeling activity. There is evidence that the loss of long rhythmic masticatory movements which has accompanied soft diets can result in a decrease of circulation at the articular surfaces. Monkeys raised on soft diets appear to have less dense fibrous tissue in the articular zone of the temporomandibular joints.(125) One researcher points out, "Experimental studies in mice, rats, rabbits, and non-human primates have shown that mechanical loads are vital for maintaining normal growth, morphology, and function of the secondary cartilage of the temporomandibular joint... In vitro studies confirm that normal mechanical loading stimulates cell division, matrix synthesis, and enzyme activity in the tissues of the TMJ."(126) There is also evidence that periosteal remodeling on the surface of the mandible is diminished when functional loads are made smaller.(127) It's interesting that the changes observed in the condylar cartilage of monkeys raised on soft diets is very similar to the changes in the condylar cartilage of rabbits whose mandibles were surgically (128) Animals raised on soft foods demonstrated less evidence of remodeling activity than normal animals. (129)

In the facial sutures, a loss of the rhythmic compressive loading from the maxillary bite table across the membrane bones of the face decreases suture widths and increases suture ossification. Similar effects of function have already been demonstrated in animals experiments which inhibit movement across cranial sutures by glueing them together, pinning them together with plates, or softening the diet.

Of course, adaptive capacities in all these areas are still relatively strong in youth, when circulation is profuse and versatile. It was primarily in adulthood when the accessory circulation from functional activity was needed to enhance adaptive capacities, and it is primarily in adulthood when loss of that accessory circulation limits adaptive capacities.

FOOTNOTES

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