A Comparative Study of Cranial Growth in *Homo* and *Macaca*[1]

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ABSTRACT This study deals with the postnatal growth and remodeling changes that take place in the cranial bones of *Macaca mulatta*. Multiple ground sections were prepared throughout each component bone from the calvaria and cranial floor of young, rapidly growing specimens having primary or mixed dentition. These sections were then analyzed for (1) the different types of inward-growing and outward-growing bone tissues present, and (2) the distribution of resorptive and depository periosteal and endosteal surfaces. Using this information, the remodeling history of each bone was reconstructed and the overall growth pattern of the cranium as a whole was determined. The growth changes that characterize the brain case of the monkey were then compared and contrasted with those in *Homo*. While a number of distinct similarities were observed in their respective growth and remodeling processes, several marked differences were also found. These occurred largely in certain parts of the cranial floor and they appeared to be associated with corresponding differences in the size, configuration, and disposition of the brain in the two species and also with factors related to body posture and facial prognathism.

The purposes of this study are (1) to describe and illustrate the postnatal remodeling processes that take place in the cranium of *Macaca mulatta*, (2) to interpret these processes according to the morphological and functional factors that are related to them, and (3) to compare growth changes in the cranium of the Rhesus monkey with those that characterize the human skull. This study is a sequel to previous reports dealing with the growth of the human facial skeleton (Enlow and Harris, '64; Enlow and Bang, '65) and comparative studies of facial growth between the human and the monkey (Enlow, '66, '68b).

MATERIALS AND METHODS

Multiple ground sections were prepared from each of the component bones in the cranial roof and floor. Dried skulls from 15 well preserved specimens having either primary or mixed dentition were used. The sections were analyzed for the detailed arrangement of both resorptive and depository surfaces on all endosteal and periosteal sides of the cortex in each of the individual bones. Using this information, the inward and outward directions of cortical growth movements were determined and mapped for each bone as a whole (fig. 1). Overall growth and remodeling patterns for all of the bones in relation to each other were then analyzed. These interpretations are based largely on three basic principles of bone growth that have been utilized in preceding reports (Enlow, '68a). They are briefly summarized below.

Surfaces facing toward and away from the direction of growth. Those surfaces of a bone, both endosteal and periosteal, which are oriented so that they face toward the growth direction receive new bone deposition. Conversely, those particular surfaces that face away from this direction are resorptive. A cortical plate undergoes direct *growth movement* (a process termed "drift") by the combination of new bone addition on one side and removal from the contralateral side. An analysis of the distribution of resorptive and depository surface types provides a basis for interpreting the behavior of all the regional parts of a bone during continued enlargement. Any given bone has a characteristic pattern in the arrangement of these two types of surfaces, and the composite of all the cortical changes that correspondingly take place represent the process of *remodeling* which

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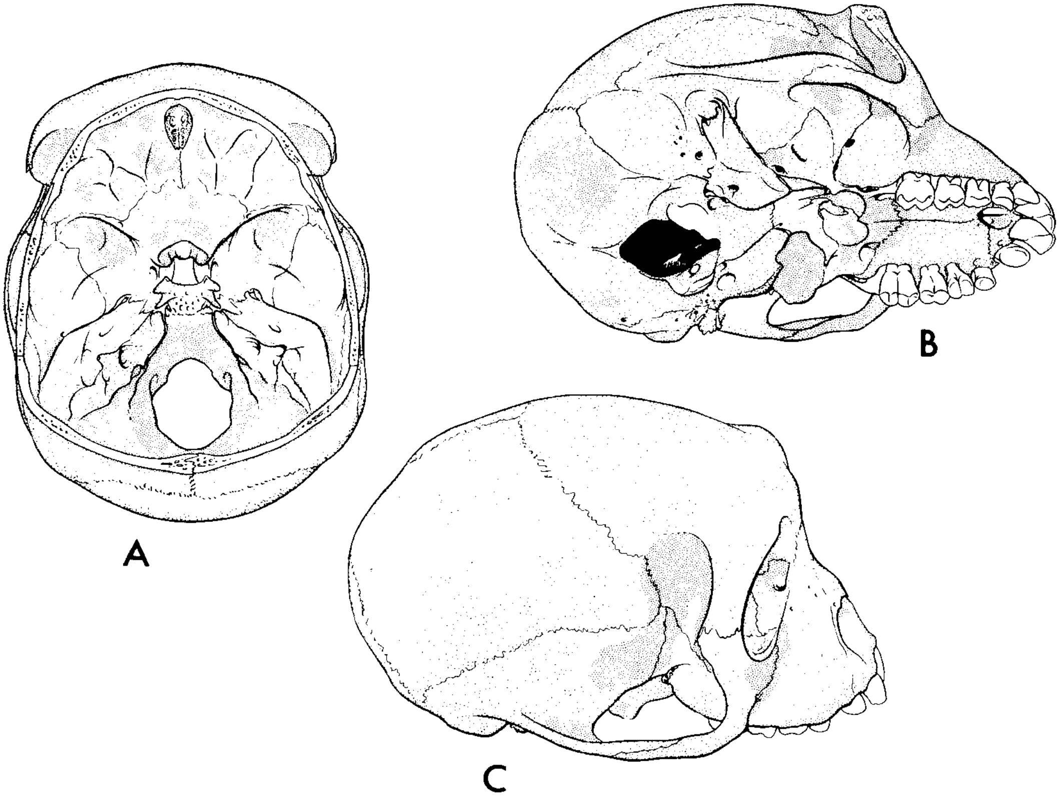


Fig. 1 The detailed distribution of resorptive and depository surfaces in the monkey skull are mapped in this diagram. Ectocranial and endocranial periosteal surfaces that undergo progressive resorption during growth are indicated by *dark stippling*. Depository surfaces are indicated by *light stippling*. A. inner aspect of the cranial floor; B. ventrolateral aspect; C. lateral aspect. Note the widespread occurrence of surface-resorptive growth fields in the occipital and temporal areas, within the orbit, on the cranial floor, on the posterior oral side of the hard palate, and within the pterygoid fossa.

produces the proportionate expansion of the bone as a whole.

Relocation. As a new bone continues to be deposited on a given surface, the other regional parts of that bone necessarily become altered in their relative locations. In order to maintain proportionate positions, these parts simultaneously undergo actual growth movements that serve to place them in a succession of new locations as the whole bone continues to enlarge. This factor of relocation is a major feature of bone growth, and it underlies the process of remodeling itself. Thus, a bone does not grow simply by continued apposition at one or two major "centers" of growth. Rather, *all parts of the whole bone* are involved in regional cortical changes that provide proportionate increases or decreases which function locally to sustain the overall configuration of the entire bone.

Displacement. Two basic types of growth movement are involved in skeletal enlargement. As described above, actual cortical movement occurs as a result of drift; i.e., deposition and resorption on opposite sides of the same cortical plate. In addition, whole bones become passively moved or carried ("displaced") as a consequence of the enlargement of a group of bones in relation to each other. Thus, the floor of the cranium *grows* downward (toward its articulation with the atlas), but becomes correspondingly *displaced* in an opposite, superior direction. The progressive increase in the mass of soft tissues that house the bones is believed to contribute directly to these complex movements by displacement (Moss, '62).

OBSERVATIONS

Growth patterns in the cranium of macaca

The calvaria. The greater part of the external (cutaneous) side of the frontal and parietal bones, and also a portion of the squamous portion of the temporal, is characterized by a uniformly depository type of periosteal surface (fig. 1b). The inner periosteal (meningeal) surface adjacent to the brain is similarly of a depository nature. The cortex is usually composed of a single layer of lamellar bone tissue. Where large diploic spaces occur, the cortex is arranged into two tables, and the resulting endosteal surfaces are resorptive.

The outward growth movement of the calvaria is believed to be produced largely by passive displacement in conjunction with sutural bone growth rather than direct cortical drift (Massler and Schour, '41; Vilmann, '68). The process of new bone deposition on the external and internal periosteal surfaces of these bones is not concerned primarily with the direct enlargement of the brain case, but rather with proportionate increases in the thickness of the bony wall itself and with adjustments in its curvature as the whole cranium enlarges. A variable distribution of external surface resorption has been observed near the lambdoidal and sagittal sutures. The walls in the suture areas are much thicker than the remainder of the bones, and these scattered patches of external resorptive remodeling reduce cortical thickness as the regions involved become successively relocated away from the thicker suture areas during continued growth. On the meningeal side of the cortex, variable and scattered resorption patches were also found immediately adjacent to the various sutures and expand the concave contour of the internal cortical surface. These transient resorptive spots apparently undergo constant change in location and extent according to the configuration and the growth activity of the underlying brain. Frequent reversals are observed in their structure, and former localized areas of resorption have become covered by thin layers of more recently deposited periosteal bone.

The growth pattern of the occipital bone differs from that of the other calvarial elements. The flattened portion which forms the floor and a part of the wall in the posterior cranial fossa is typically thin. It is composed of a single layer of lamellar bone containing a few small diploic spaces. In figure 1b, note that a large zone of external resorption is present in the nuchal region, and that the remainder of the cutaneous side is depository. This remodeling pattern provides a means of calvarial adjustment adapted to the differential extent of expansion by the various parts of the underlying brain. Because the cerebral hemispheres enlarge to a greater degree than the more inferiorly located cerebellum, the superior part of the occipital bone necessarily becomes displaced in an ectocranial direction to a proportionately greater extent than does the more basal region adjacent to the cerebellum. The combination of external resorption and endocranial deposition in the latter area functions to move its cortex in an endocranial manner as the superior (squamous) part of the bone is carried outward with the expanding cerebrum (fig. 2). The effective result is a "rotation" of the bone, so that as the whole bone becomes displaced ectocranially, the basal part simultaneously pivots inward to sustain its contact with the slower-growing cerebellum (fig. 3). Although a small range of variation was found in the placement of the reversal line that separates the resorptive from the depository growth fields involved, only one specimen showed a total absence of a resorptive area. One other individual had several scattered patches of surface resorption rather than a single, large resorptive field.

The meningeal side of the squamous part of the occipital is characterized by a predominantly depository type of surface (fig. 1a). Small, isolated spots of resorption occur in relation to the sutures, however, and function in adjustments of internal surface contour during active sutural bone growth. A broad, distinctive zone of resorption is characteristically present on

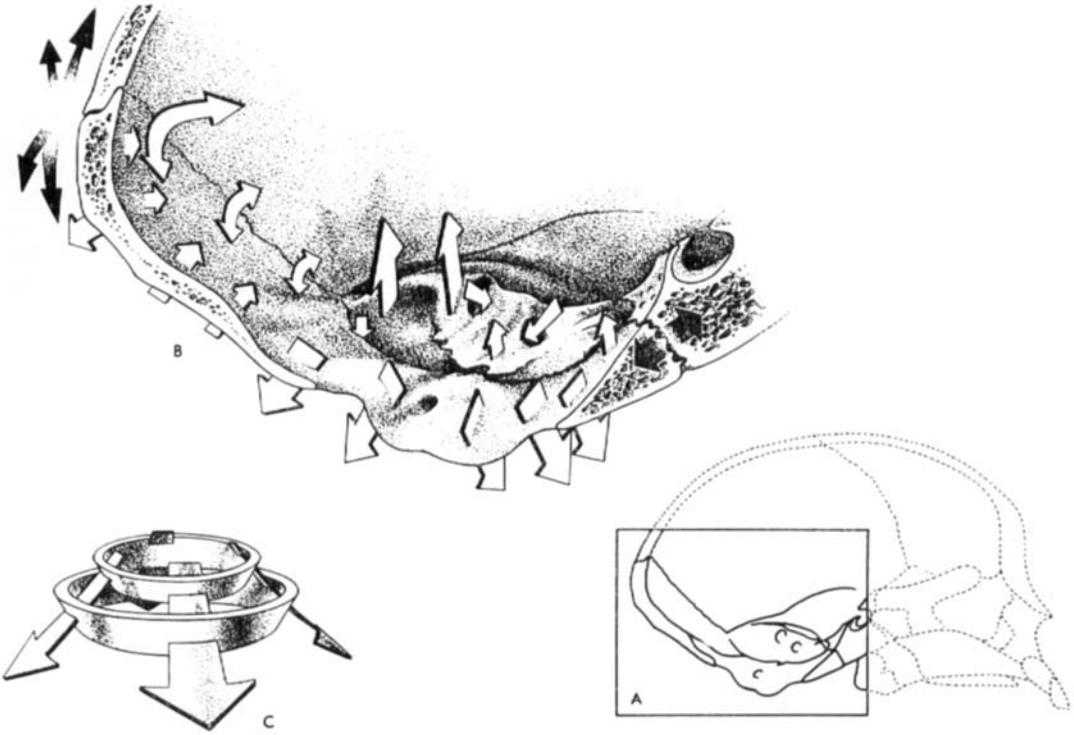


Fig. 2 This composite diagram illustrates the various regional remodeling changes that take place in the occipital area of the Rhesus monkey skull. Diagram A shows the area analyzed in B. Diagram B is an interpretation of regional growth directions occurring in the occipital fossa. The endocranial zone around the foramen magnum is resorptive; the contralateral ectocranial (ventral) surfaces are depository. Ventrally-moving cortical drift produces coordinated downward-directed growth. Simultaneously, the foramen itself becomes enlarged by this same process. A schematized illustration of this growth movement is shown in diagram C.

the meningeal surface surrounding the perimeter of the foramen magnum (fig. 6). The cortical linings of the sigmoid sulcus and the vermian sulcus are similarly surface resorptive in nature, and the greater part of the occipital segment of the clivus is also marked by endocranial surface resorption during its period of active growth. The placement of the reversal line that separates the depository from the resorptive parts of the clivus is variable but most frequently occurs slightly below the spheno-occipital synchondrosis. The ectocranial surfaces of the cortex encircling the foramen magnum and that part of the occipital bone adjacent to the pharynx are uniformly surface-depository in type. A circumspinal reversal line, quite constant in occurrence and placement, is present on the crest of the foraminal rim and thereby separates the external depository from the endocranial resorptive growth fields. In three of the older specimens studied, a thin layer of surface bone had been deposited over the resorptive growth fields lining the meningeal side of the occipital bone. This addition increased the thickness of the cortex itself following the earlier period of active cranial growth.

The sizeable endocranial resorptive zone surrounding the foramen magnum and which extends superiorly onto the occipital portion of the clivus functions to lower this entire area and to move it anteriorly during continued growth. A process of direct cortical growth (drift) is necessarily required here since the placement of sutures is such that these changes could not be produced by sutural growth. Thus, the combination of resorption on the endocra-

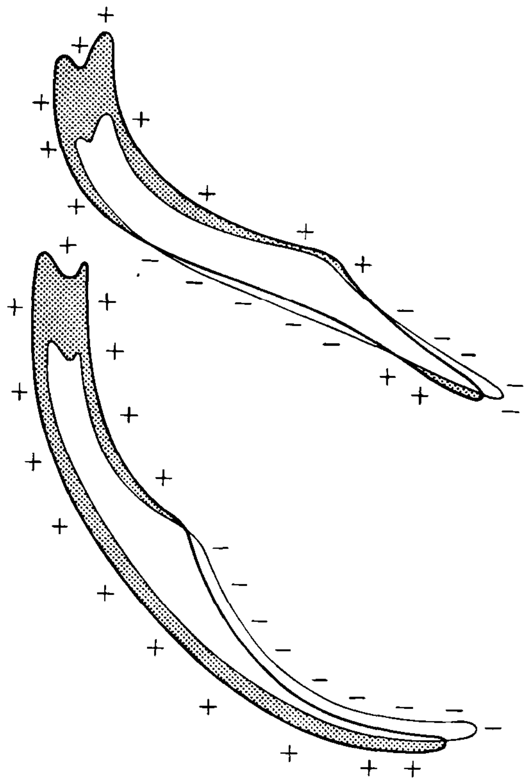


Fig. 3 This schematic diagram illustrates remodeling differences in the nuchal region of the occipital bone of *Macaca* (top) and *Homo* (bottom). Note the extensive resorptive area (—) on the external (cutaneous) surface of the flattened monkey occipital squama. In man, this comparable surface is entirely depository. Resorption on the internal (meningeal) surface of this bone in the monkey is limited to a distinctive zone surrounding the foramen magnum. In man, resorption on meningeal surfaces is much more extensive and includes the entire cortical lining of the occipital fossa. See text for further description and discussion.

nial surface and deposition on the ectocranial side (1) moves the entire area inferiorly; (2) enlarges the basal portion of the posterior cranial fossa in a posterior direction; (3) moves the clivus anteriorly; and (4) proportionately enlarges the lumen of the foramen magnum itself (fig. 2).

In contrast to the smooth, even-contoured endocranial surface of the skull roof, the internal topography of the cranial floor is complex and irregular. A number of partially isolated compartments are present that house the various ventral parts of the brain, including the hypophysis, olfactory bulbs, temporal lobes, cerebellum, and the auditory apparatus. In addition, major vessels and nerves pass through the floor, a situation that does not exist in the roof. The placement and the orientation of sutures in the cranial floor is such that the process of sutural bone growth cannot in itself entirely accommodate the extent of expansion required since many divergent growth directions are involved. Further, a decreasing gradient of growth is involved as the midventral axis of the cranial base is approached. These multiple factors represent the functional basis for the marked differences in growth processes that characterize the cranial floor and roof, respectively (Enlow, '68a).

In figure 1a, note that a number of small, scattered resorptive areas characterize the meningeal surfaces of the anterior cranial floor, the prefrontal region of the forehead, and the anteroinferior depression of the middle cranial fossa. All of these regions are isolated, confined "cul de sacs" that require an ectocranial mode of direct cortical drift. Sutures do not occur in most parts of these separate fossae, and growth therefore cannot take place in a manner comparable to that in the skull roof. Transient spots of endocranial resorption function to enlarge each fossa and to move the floor in an ectocranial direction as the ventral parts of the brain simultaneously increase in size. The variable resorptive patches also provide localized cortical remodeling adjustments required to accommodate the differential gradient of growth between the midventral part of the floor and its more lateral regions associated with the hemispheres. This pattern, further, makes possible the adjustments required in sustaining the positions of vessels and nerves passing through the cortex, a function that could not be carried out if the sutural growth process represented the sole mechanism of growth expansion.

The cortical lining of the pituitary fossa is depository, although zones of surface resorption occur on the clinoid processes and within the nearby optic foramina (fig. 1a). As previously mentioned, the sphenoidal part of the clivus is depository. Thus, the prominent, medial elevation that comprises this general region, and which separates the left and right middle cranial fossae, grows in a superior direction as the entire area itself becomes displaced inferiorly by the expanding brain. This upward mode of growth not only functions to enlarge the median elevation but also to sustain its position in relation to the slower-growing midventral part of the brain as the lateral bony areas associated with the hemispheres descend to a proportionately greater extent. The longitudinal growth of this region is provided, in part, by the spheno-occipital synchondrosis, the sphenoidal synchondrosis, and the sphenoethmoidal juncture. The prominent petrous elevation within the cranial cavity, like the midline sphenoidal elevation, also has a depository type of surface. This serves to proportionately enlarge the convex partition that separates the concave middle and posterior cranial fossae as all continue to expand simultaneously.

The surface of the cortex lining of each auditory canal is resorptive, and a reversal line occurs at the rim of the meatus. The external side of the petrous portion of the temporal bone, like the outer surfaces of the adjacent squamous part, is depository in nature. Similarly, the contiguous pharyngeal side of the occipital and the sphenoid bones are of a depository surface type.

The orbit, zygomatic arch, and the temporal fossa. Growth of these topographically complex, contiguous regions of the skull involves a correspondingly complex pattern of remodeling in order to produce the proportionate enlargement of each in relation to the others. In figures 1a and 1b, note that large fields of periosteal resorption occur on the posterior side of the massive lateral orbital rim, on the medial side of the zygomatic arch, and on the surface lining the temporal fossa. Although these resorptive areas are all directly continuous with each other, their regional remodeling functions during growth are quite different. Note that the reversal lines that separate these various resorptive fields from adjacent depository surfaces *cross* those sutures present rather than follow them. Each individual bone thus does not behave as an isolated growth unit that is essentially independent of the rest. Rather, these regional fields participate in a coordinated, composite pattern of growth that utilizes different parts of several different bones.

The sizeable, irregular region of surface resorption that occurs on the greater part of the external cortex lining the temporal fossa involves portions of the temporal, parietal, frontal and sphenoid bones (figs. 1a,b,c). This variable resorptive area serves as a growth *pivot* that adjusts the changing contour bridging the bulging lateral cranial wall with the medially tapering depression just behind the orbital rim. As the protruding, convex lateral wall is carried ectocranially by displacement associated with expansion of the brain, sutural bone growth simultaneously enlarges the coverage of the bones involved. A differential extent of growth occurs, however, so that the concave anteroinferior region, located within the temporal fossa, necessarily rotates inward to adjust its relative position in response to the outward carry of the whole bones. Thus, as these bones all become displaced ectocranially in company with the cerebrum, that portion located within the fossa maintains contact with its own slower-growing, smaller, anterior part of the brain by means of a growth movement in a medial (inward) direction. This remodeling adjustment requires a resorptive cortical surface on the external side of the bone, a feature that differs from the remodeling pattern found in the human skull (see later discussion).

Cortical remodeling changes on the posterior side of the lateral orbital rim and on both sides of the zygomatic arch are essentially identical to those found in the human facial skeleton. The entire medial surface of the arch as well as the posterior side of the orbital rim are characteristically resorptive. This contributes to a movement of the rim in a progressively anterolateral course, and a movement of the arch in a direct lateral direction. The cortex in both regions is composed of typical endosteal bone tissue of a compacted cancellous type (fig. 7). Note that the contralateral surfaces in both regions (the anterolateral side of the rim and the lateral surface of the arch) are depository in nature. This remodeling combination, like the others described above, follows the principle dealing with "surfaces facing toward and away from the direction of growth," as previously defined.

The lengthening of the zygomatic arch is produced largely by bone additions within the zygomaticotemporal suture (Gans and Sarnat, '51). As the horizontal dimension of the cranial cavity expands, concurrent deposition of bone in the suture proportionately lengthens this zygomatic bridge between the temporal and the malar bones. The point of union between the arch and the cranium is characterized by a reversal line that separates the resorptive field on the medial side of the arch from the depository field on the lateral surface of the temporal squama.

The lining of the orbital cavity is marked by a sizeable resorptive region that occupies the lateral half of the thin, single-layered roof and the superior half of the lateral wall. The contralateral endocranial side, which forms the lateral part of the floor in the anterior cranial fossa, is depository. This remodeling combination moves the entire superolateral portion of the orbit, which lacks sutures in this region, in a lateral direction as the cranial fossa, the zygomatic arch, and the zygomatic process of the frontal bone all grow simultaneously in a corresponding direction. With the exception of the diminutive lacrimal bone, the remainder of the bony orbital lining is depository. The lacrimal itself functions as an adjustment linkage between the differentially growing bones that surround it (Enlow, '68a). A converse arrangement of resorption and deposition occurs in the medial portions of the orbit and the anterior cranial fossa, in contrast to the lateral parts just described. The orbital side is depository and the opposite endocranial surface is irregularly resorptive. Thus, the various cortical surfaces that form both sides of the orbit follow the rule in which surfaces facing away from the growth direction are resorptive. The entire orbit grows and moves in a combined anterior and lateral course as the frontal lobe of the cerebrum expands in a corresponding direction. Except for its superolateral surface, which is resorptive, the cortical lining of the orbit faces these directions.

The pterygoid processes. The two plates that form the walls of each pterygoid fossa are oriented so that their outer sides face anteriorly, which is the direction of progressive growth. These external surfaces are depository, while the cortical lining within the fossa itself is resorptive. As the cranial floor elongates, the relative positions of the adjacent forward-facing pterygoid plates are thereby maintained by a proportionate anterior growth movement. It is noted that the directly contiguous maxillary tuberosity (posterior surface of the maxillary corpus) grows in a posterior direction. The maxilla and the pterygoid plates, separated only by the narrow pterygomaxillary fissure, thus grow toward each other. However, the entire maxilla becomes displaced (carried) in an anterior course as it grows posteriorly, thereby sustaining a constant positional relationship with the pterygoid processes.

DISCUSSION

Three basic modes of growth are operative during the postnatal enlargement of the neurocranium in both man and the Rhesus monkey. First, increases in some linear dimensions of individual bones in the skull roof and cranial floor are produced by continued additions of new bone at either *sutures* or *synchondroses*. Second, surface *remodeling*, involving differential deposition and resorption of bone according to local directions of growth, occurs on virtually all endosteal and periosteal surfaces, both on the internal and external sides of the cranium. This functions to adjust the regional shape of each growing bone and to produce proportionate changes (decreases as well as increases) in regional size. Third, all of the bones become *displaced* as they enlarge, thereby expanding their spatial relationships to one another. Because of different morphological factors in the cranial floor as compared with the calvaria, the combinations of these three basic growth processes are correspondingly different in the two regions. The predominant mode of calvarial enlargement involves sutural growth with only relatively minor surface remodeling changes, primarily in regions just adjacent to sutures. In the more complex cranial floor, however, a decreasing gradient of sutural growth takes place. This is accompanied by a much more widespread occurrence of regional remodeling which serves to expand the various endocranial fossae, stabilize the passage of vessels and nerves during skeletal growth, and to provide differential degrees of enlargement among the different parts of the braincase on its ventral side. Because of differences in the proportions and rates of growth in the cranial floor of *Macaca* as compared with *Homo*, corresponding differences in respective remodeling patterns also occur.

The endocranial side of the human neurocranium is characterized by a distinctive *circumcranial reversal line* that separates the growth fields of the skull roof from those in the floor (Enlow, '68a). This long line completely encircles the cranium at a level approximately midway across the inner aspect of the forehead and continues around the lateral and posterior internal walls of the skull. The meningeal surface of the bony cortex above this line is depository, while the surface below it is largely resorptive in nature. This arrangement is associated with differences in mode of growth in the two general areas, as outlined above. In the monkey, a continuous circumcranial reversal line does not occur as such. Rather, a number of smaller but discontinuous resorptive regions are present. Scattered patches of endocranial surface resorption are found in the frontal and prefrontal regions, the anteroventral part of the middle cranial fossa, variable portions of the floor in the occipital area, and a prominent region surround the foramen magnum. Thus, smaller and separate zones of resorption characterize the cranial floor of the monkey while a continuous resorption-deposition interface occurs in the human cranium. It is noted, however, that these are differences in relative extent rather than basic pattern, since the underlying sequence of remodeling changes and the anatomical factors that predispose them are comparable. Because of differences in the proportions of the various parts of the brain in these two species, related differences in the extent of coverage by resorptive and depository endocranial surfaces exist, even though the plan of remodeling itself is essentially similar. In the human cranial floor, the cerebral lobes markedly overhang the midventral cranial base, both anteroposteriorly and laterally. The floor of the anterior cranial fossa (and the orbital roof) is thereby situated much lower in relation to the sphenoid than the more elevated and convex frontal floor in *Macaca*. The human forehead is proportionately larger, much higher, and it is more vertically disposed. The floor of the middle cranial fossa of man is depressed in configuration, and the ectocranial petrous pyramid is largely incorporated within its bony

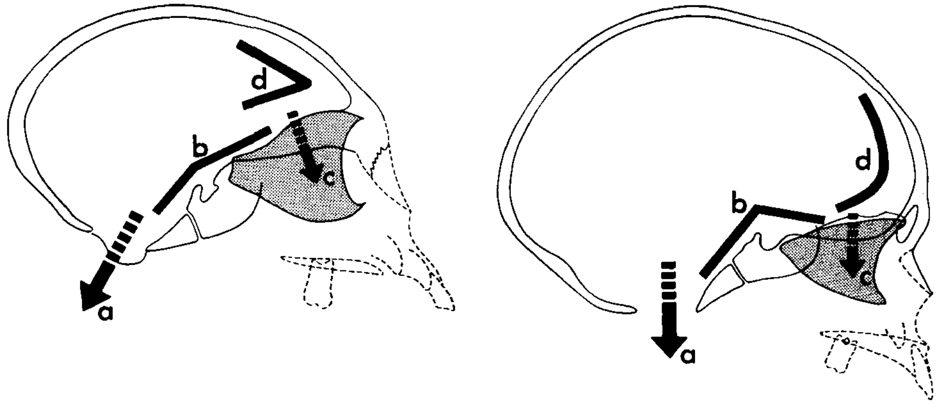


Fig. 4 In these diagrams, key differences between man (right) and monkey (left) in the orientation of the cranial floor (b) and forehead (d) are schematized. The relative size and placement of the orbital region (c, shaded area) in relation to the size of the cranium is shown. Note the differences in the inclination of the foramen magnum (a) and the anterior cranial fossa (arrows), and the degree of flexure of the cranial base (b).

cortex. This arrangement is in contrast to that found in the monkey. The human posterior cranial fossa is also much deeper as compared with the relatively flat occipital fossa of the monkey. It is suggested that the combination of these morphological factors is directly related to a much more extensive distribution of surface resorption on the meningeal side of the bony cortex lining the human cranial floor as a whole. This results in a differentially greater extent of outward cortical drift (direct growth movement) of the bony plates involved, a process that accompanies the limited extent of growth expansion by sutures and synchondroses. These same remodeling differences, also, are apparently associated with the greater downward angulation of the cranial base flexure in man as compared with the monkey (fig. 4). This in turn is related to the more upright posture of the human skeletal frame and the vertical disposition of the facial complex.

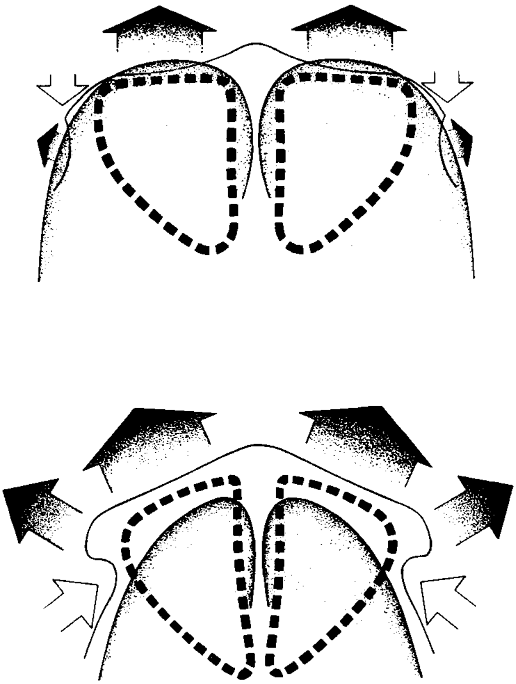
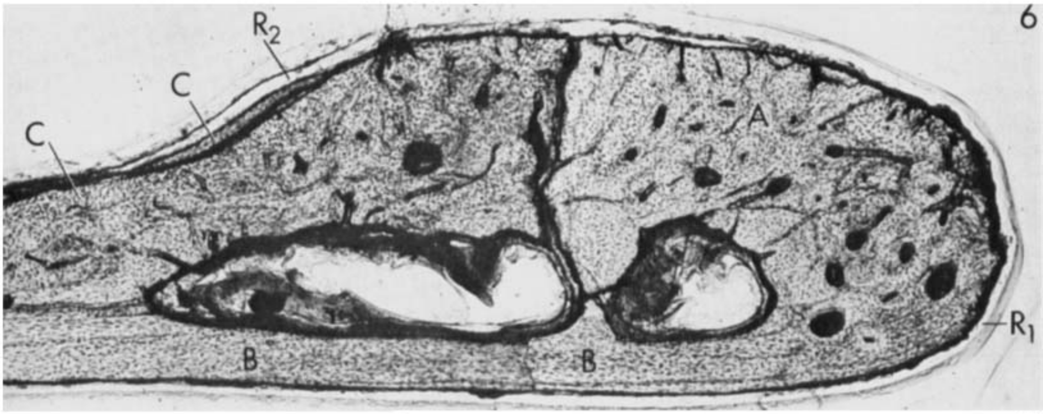


Fig. 5 In the top diagram, the frontal cerebral lobes (shaded area) of man extend over the orbits (heavy dashed line). The orbits are oriented in a parallel fashion, and a diminished supraorbital ridge grows slightly forward (dark stippled arrows). The anterior surface of the lateral orbital rim, however, is resorptive and grows backward (white arrows). The lateral post-orbital surfaces are depository and grow laterally. These multiple growth directions result in a flat, squared appearance of the whole region in the human face. The growth of the comparable area in the monkey differs (bottom diagram). The frontal lobes of the cerebral hemispheres are much less bulbous, and the orbits have a laterally oblique orientation. In contrast to the human skull, note that the anterior part of the monkey orbit is not covered by the frontal lobe. The supraorbital ridge grows forward and laterally. The lateral orbital ridges are depository on their anterior facing surfaces and resorptive (white arrows) on their posterior facing side. The lateral orbital rim of the monkey drifts laterally and anteriorly. The adjacent temporal region is resorptive. See text for a correlative discussion of relationships between these anatomical factors and the growth processes associated with them.

A number of close similarities as well as differences exist in the complex remodeling patterns of the orbit in these two primates (fig. 5). These patterns are associated with the comparative anatomical placement of the orbits and their enclosing rims in relation to the anterior cranial fossa above and behind each orbit as well as the protruding muzzle below and in front of them. As in most other regions of the craniofacial skeleton, the basic plan of remodeling is more or less comparable in both species. The medial (nasal) wall and the floor of the orbital cavity are depository in both species, and the lateral half of the inferior-anterior surface of the rim and the lacrimal area are resorptive. The lateral half of the cortical lining of the domed roof is also resorptive, but the extent is proportionately much larger in the monkey and occupies the entire length of the cavity. In man, this resorptive field is restricted to the anterior part located deep to the overhanging supraorbital ridges. However, the essential similarity in overall remodeling patterns produces growth movements that carry the human and monkey orbits in a predominantly anterior and slightly lateral course. The overlying floor of the anterior cranial fossa moves in a corresponding direction, although the more restricted, upward-sloping floor of the monkey does not descend to the level that occurs in man. As a result, the orbits in the monkey lie anterior to an obliquely oriented frontal region, while in the human skull they are situated almost directly beneath the frontal area (see pre-



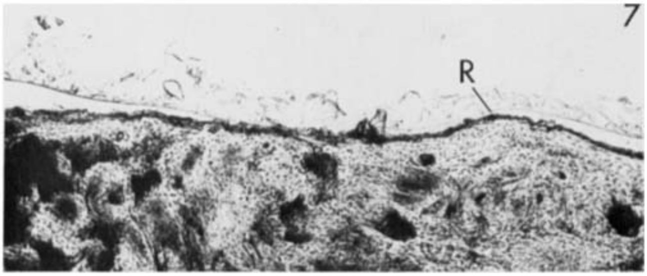


Fig. 6 Section through the occipital bone of *Macaca mulatta*, × 30. The meningeal surface (top) is resorptive from reversal R_1 to R_2. R_1 is the circumspinal reversal line on the rim of the foramen magnum. R_2 is the internal (meningeal) occipital reversal line. Area A is composed of endosteally formed bone. Note the many replacement osteons and resorption spaces. Area B is lamellar bone deposited by the periosteum on the ventral (ectocranial) surface. In area C, periosteally formed bone has been laid down over a previously formed layer of endosteal bone. In man, the reversal line R_2 is not present, but reversal line R_1 characteristically occurs.

Fig. 7 This section is a part of the posterior-facing cortex of the lateral orbital rim from a young growing monkey (× 30). The surface is resorptive from the left border of the picture to the reversal line (R). The comparable surface in man is depository. This difference contributes to the morphogenetic basis for the anatomical differences in this area between the human and monkey skulls. See the text for descriptions.

vious descriptions concerning corresponding differences in growth changes). This situation, together with the circumstances in the following paragraph, appear to be directly related to the more prognathic facial profile of *Macaca* in comparison with that of man.

A distinct difference in the growth pattern of the external part of the protruding lateral orbital rim occurs between these two species. In the monkey, the anterolateral surface is entirely depository, while a resorptive periosteal surface is characteristic in the human skull. The posterior-facing surface of the lateral orbital rim (within the temporal fossa) is resorptive in *Macaca* but is depository in man. These differing growth patterns are adapted to the greater extent of upward and forward rotation of the upper human face in conjunction with the marked anterior positioning of the forehead. As a result, the human lateral orbital rim is distinctively upright as compared with the sloping nature of this region in the monkey.

The large resorptive region on the lateral side of the monkey skull, within the large temporal fossa and posterior to the lateral orbital rim, is entirely absent in man. This is related to the much less massive development of the temporal lobe of the monkey cerebrum, a feature which requires a medial direction of bone growth to adjust the position of the bony wall in response to the generalized ectocranial direction of calvarial displacement. The temporal fossa in the monkey is, correspondingly, relatively large. Because of the more prognathic facial contour in *Macaca,* the zygomatic arch is relatively long as compared with the arch in the proportionately shorter and more upright face of man. A much wider temporal fossa, also, is a feature of the monkey skull related to his more massive jaw musculature.

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