A Comparative Study of Facial Growth in *Homo* and *Macaca*

DONALD H. ENLOW
Department of Anatomy and Center for Human Growth and Development, The University of Michigan, Ann Arbor, Michigan

ABSTRACT Sections were prepared throughout all areas of the various facial bones in young, growing Rhesus monkeys. The detailed distribution of resorptive and depository surfaces and the distribution of endosteal and periosteal bone tissue types were determined. From this information, the sequence of remodeling changes associated with the growth of the facial skeleton was then interpreted. This study is a sequal to previous reports in which growth and remodeling processes in the human face were described using similar procedures. In the present report, growth changes in the monkey and human facial skeleton are compared and contrasted. The general plan of facial growth is similar in both species, but major differences exist in the area of the muzzle. The maxillary arch in the monkey is entirely depository in nature, and it grows in a forward and downward direction as the maxillary tuberosity simultaneously grows backward. In the human, the forward part of the maxillary arch is resorptive in character. This contrasting growth factor results in a downward but not forward movement of this area. The result is decreased prognathism. Other differences in growth pattern exist in the forehead, malar, chin, and orbit. The developmental and phylogenetic basis for the upright human face is discussed and evaluated.

The purpose of this study is to compare and contrast the detailed sequence of remodeling changes that take place during the growth of the human and monkey facial skeleton. In previous studies, the variety of growth processes occurring in the bones of the human face, including the frontal bone, the maxilla, nasal, zygomatic, and the mandible have been described (Enlow and Harris, '64; Enlow and Bang, '65; Enlow, '66). A history and a survey of the literature dealing with facial growth was also presented. In the present report, growth changes taking place in corresponding facial bones of *Macaca mulatta* are described and illustrated. Differences and similarities in the sequence of growth and remodeling processes between these two primates are then discussed and evaluated.

MATERIALS AND METHODS

Complete, well preserved, dried skulls from 11 normal Rhesus monkeys having mixed deciduous and permanent dentition were selected for study. Only young, rapidly growing individuals were used since sequential growth changes were determined by an interpretation of remodeling processes associated directly with skeletal growth (see below). Multiple ground sections were prepared from the right side of each skull throughout all areas of the frontal bone, the maxilla, premaxilla, the nasal, and the zygoma. Serial stained sections prepared by decalcification and microtome sectioning were made throughout the entire right half of each mandible. In all preparations, the whole thickness of the cortex was sectioned and studied in order to analyze internal as well as external surface remodeling changes.

During bone growth, a companion process of structural remodeling takes place that functions to continuously maintain the configuration of the bone as a whole (Enlow, '63). As the bone increases in overall size, its various parts and areas become successively repositioned into new locations. This continuous process of relocation requires constant remodeling adjustments in the regional shape and dimensions of all the local parts of the bone. A bone does not increase in size simply by new bone deposition on all outer surfaces. Rather, processes of bone removal and deposition on different periosteal and endosteal surfaces throughout the entire growing bone bring about generalized in-

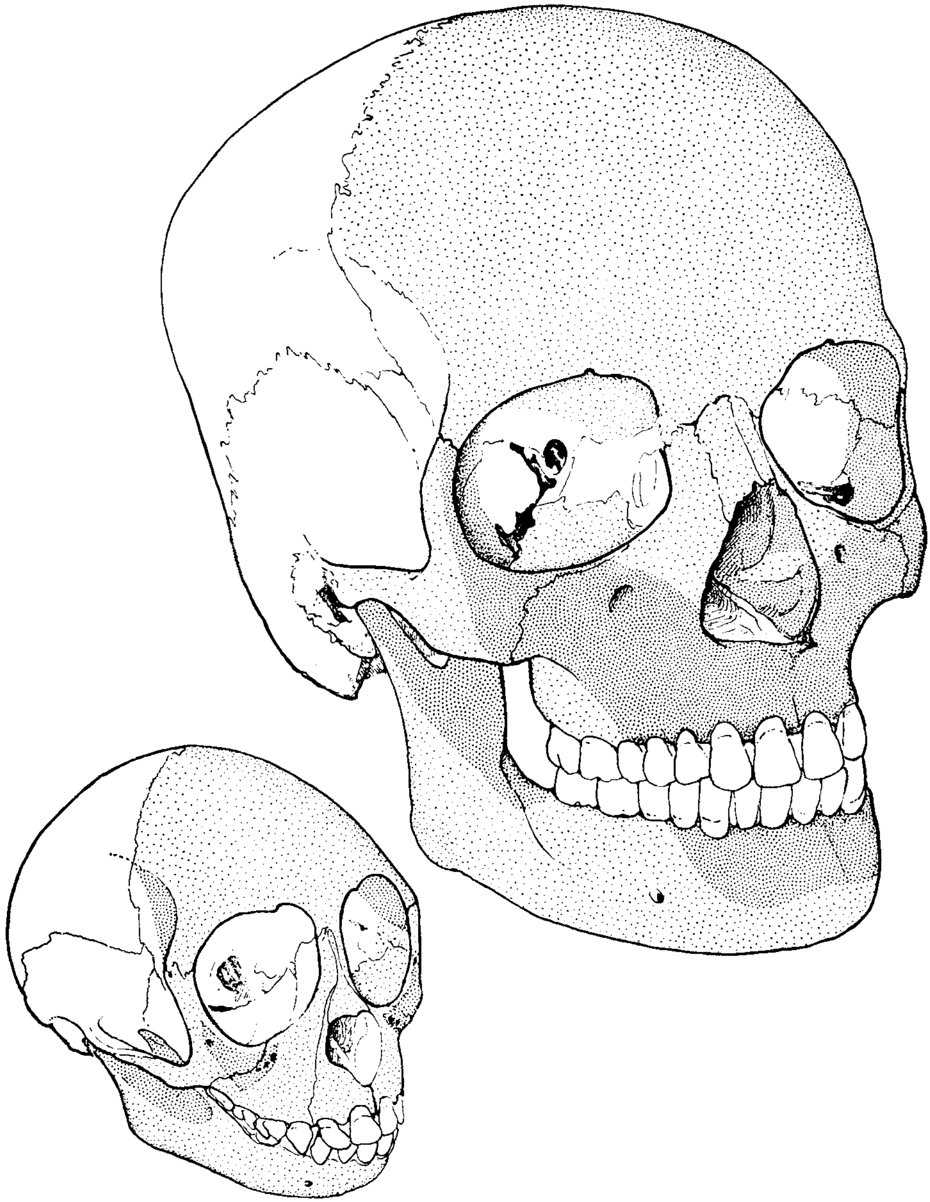

Fig. 1 The distribution of resorptive and depository surfaces in the human and monkey skulls are mapped in this diagram. Periosteal surfaces that undergo progressive resorption during growth are indicated by *dark stippling*. Outer surfaces that are depository in nature are indicated by *light stippling*. See text for further descriptions.

creases in size in such a manner that new parts constantly become remodeled from older areas. The calcified matrix of bone tissue provides a record of these remodeling changes and movements, and interpretations of the growth history of an entire bone or any part of a bone can be made by a detailed analysis of such growth stages preserved in the cortex.

In the present study as in previous reports, interpretations of growth history in each of the various facial bones are based upon (a) the distribution of resorptive and depository surfaces on all periosteal and endosteal exposures of the bone and (b) the pattern and arrangement of the various kinds of bone tissues involved in these remodeling movements. Each section was analyzed for the distribution of endosteal and periosteal bone tissue types. Patterns of these various tissue types observed in the facial bones of the monkey were mapped, and a composite picture representing a summary of the most commonly observed patterns was then prepared (fig. 1). Endosteal bone is a result of inward cortical growth and is produced by the combination of endosteal deposition of bone with, typically, corresponding resorption from the opposite periosteal side of the cortex. Periosteal bone tissue is produced by the converse process of periosteal deposition in conjunction with contralateral endosteal resorption. Various layered combinations of both periosteal and endosteal zones result from growth reversals as local dimensional changes and shifts in position become involved during growth and remodeling.

Mapping the detailed distribution of endosteal and periosteal deposits of bone with corresponding patterns of resorption and deposition in all areas of the face makes possible an accurate interpretation of *localized directions of growth movement* during remodeling adjustments in each part of the facial skeleton. The application of several basic principles of bone remodeling permits a reconstruction of the overall sequence of growth. These principles are reviewed briefly in pertinent areas of the text and are described in greater detail in previous reports (Enlow, *loc. cit.*). They include the principle of "area relocation" and the basic principle stating that those particular surfaces of a cortex facing the actual direction of growth movement are depository in nature. Those surfaces that face away from the direction of growth, in contrast, are generally resorptive. Descriptions of the variety and the identification of endosteal and periosteal bone tissue types are also described in previous studies.

Growth sequence in the facial skeleton of *Macaca*

The maxillary complex. The muzzle of the face, including the separate premaxillary and maxillary bones, grows in a generally anterior and inferior course. The entire periosteal surface of the lamina externa is depository in nature. The contralateral endosteal surface of this external cortical plate is resorptive. The bone is, therefore, of a periosteal type (figs. 5, 8). The cortex is characteristically thin in regions covering teeth and is usually composed of a single plate of relatively non-vascular, lamellar bone tissue. In thicker areas of the cortex, the bone may be made of fine cancellous, non-lamellar bone tissue in the young growing skull. The presence of this type of bone indicates relatively rapid deposition during the period of active facial growth. Together with simultaneous resorptive re-

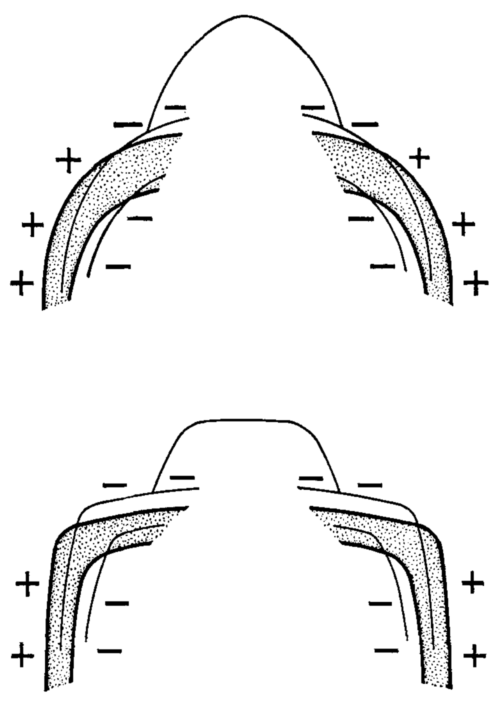

Fig. 2 This schematic diagram illustrates remodeling differences in the malar area of the monkey (top) and the human (bottom) face. Note that the anterior surfaces of both are resorptive (−) but that the squared configuration of the human zygomatic complex involves more extensive surface resorption which extends around onto the lateral side of the zygoma. The rounded contour of the monkey zygomatic region, in contrast, involves a lateral depository (+) surface that extends farther onto the anterior face of the malar.

moval of bone from the nasal side of the palate, the entire maxillary arch is carried in a downward (inferior) direction as well as anteriorly (fig. 3). Maxillary teeth are shifted in corresponding directions during remodeling by a process of "drifting" (Enlow and Bang, '65). During these various remodeling movements, new bone deposition along the entire free alveolar margin brings about an increase in the depth of the maxillary arch. This growth process also contributes to the progressively increasing prognathism of the muzzle as a whole.

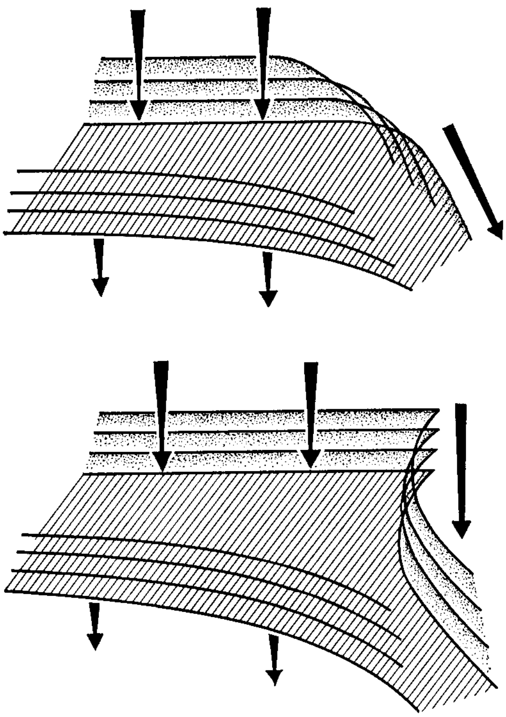

Fig. 3 The premaxillary area and the hard palate in both the monkey (top) and the human (bottom) grow in a downward direction. In the monkey, the forward part of the maxillary arch also grows in an anterior course by new bone deposition on outer premaxillary surfaces. The vertical depth of the maxillary arch simultaneously undergoes elongation by continued bone deposition along alveolar margins. The forward part of the human maxilla, by comparison, grows essentially in a straight downward course. The outer (labial) surface of the human muzzle is resorptive in character, since this side of the bone faces away from the actual direction of growth. The opposite (lingual) surface of the cortex is depository. The vertical depth of the maxillary arch becomes lengthend by alveolar bone deposition on its free margin, which can result in a slight protrusion of the premaxillary region during growth. Remodeling differences between the human and monkey maxillary bones provide the morphogenetic basis for the decreased prognathism which is characteristic of the human skull.

The external surface of the maxillary tuberosity (posterior side of the maxillary body) is composed of periosteal bone. This area moves in a progressively posterior direction as the maxillary dental arch becomes lengthened, a growth process contributing to the marked "forward displacement" of the entire naso-maxillary complex. Although the maxillary arch is also increased in length by periosteal bone deposition on the forward-facing surfaces of the premaxillary area and by suture growth between the maxilla and the premaxilla (in contrast to the human), the overall increase in the anterior-posterior dimensions of the maxilla is largely brought about by the posterior mode of growth of the posterior-facing maxillary tuberosity. With simultaneous displacement in an opposite (anterior) manner, the face thereby enlarges essentially in an anterior course even though the predominant direction of actual growth proceeds posteriorly (see also under "Discussion").

The nasal area. The external bony walls of the nasal chambers, including the paired nasal bones and the frontal processes of the maxilla, grow essentially in a combined forward and lateral direction. This growth movement proceeds in combination with the vertical elongation of the entire nasal chamber as the floor of the nasal cavity grows in a downward course (fig. 3). Since the outer surface of the bony wall of the nasal cavity faces both anteriorly and laterally, surface deposits of new bone serve to carry this area in corresponding anterior and lateral directions. The periosteal surface is entirely depository in character (fig. 1). Contralateral surfaces on the inner side of the lateral nasal walls are resorptive. The floor of the nasal chamber, in general, is also resorptive, although several reversals were found as a result of complex topography with corresponding shifts during growth due to area relocation. In conjunction with progressive subperiosteal deposition of bone on the oral side of the palatal shelf, the hard palate shifts in an inferior direction as the nose and muzzle simultaneously grow and move in a forward course.

The malar area. The outer (periosteal) surface of the malar region of the maxilla is resorptive (fig. 1). The corresponding inner side of the cortex receives deposits of bone during growth so that this area of the maxilla is composed entirely of endosteal bone tissue. This growth circumstance is related to the posterior mode of growth at the distal ends of the maxillary dental arch and the entire posterior surface of the maxillary tuberosities. In order to maintain constant positional relationships between all of these areas, the anterior face of the malar must receive a corresponding shift in a posterior (as well as lateral) direction (Enlow and Bang, '65). As the overall length of the maxillary arch increases in a predominantly posterior direction, the resorptive and regressive nature of the malar surface serves to move the entire cheekbone in this posterior course. A range of variation was found in the actual placement of the reversal lines on the maxilla and zygomatic.

Of the 11 specimens studied, one showed a layer of periosteal bone superimposed over the endosteal cortex in the anterior malar area. This suggests that the period of active posterior elongation of the dental arch, with accompanying remodeling adjustments in the malar region, had already ceased. A subsequent but slight increase on the surface of the maxilla resulted in the formation of a thin outer zone of periosteal bone.

The zygomatic arch and lateral orbital rim. This laterally-facing area moves in a corresponding lateral direction during growth by a process of bone deposition on the outer side together with resorption from the medial surface of the arch (fig. 2). The lateral rim of the orbit faces essentially anteriorly and laterally. Deposition of bone on this face of the orbital rim carries it in a lateral direction in conjunction with the lateral shift of the zygomatic arch and the entire orbital cavity. The contralateral posterior surface of the orbital rim, like the inner side of the zygomatic arch, is resorptive and the cortices in these areas are composed of typical endosteal bone tissue.

The forehead. The outer periosteal (cutaneous) surface of the entire frontal bone receives deposits of bone during its active period of growth (fig. 1). The meningeal surface on the inner side of the frontal bone is also largely depository in nature. These observations agree with the interpretation that outward expansion of the calvarium is produced primarily by sutural growth and that additions of bone on both inner and outer surfaces of the calvarium function essentially to adjust surface curvature during growth and to increase the proportionate thickness of the cortical plates (Massler and Schour, '41). Isolated, restricted patches of resorption on inner surfaces, however, were observed in scattered areas. Also, surfaces on the inner table in this prefrontal region were seen in which some older layers produced by such resorptive endosteal growth activity had subsequently been covered by inner periosteal (meningeal) bone. These observations indicate that some outward growth by direct external surface deposition with corresponding inner resorption had taken place as well as growth by sutural activity. This growth process would serve to move the prefrontal area in an anterior as well as a generally superior direction. Whether such outward growth by direct periosteal deposition and meningeal resorption occurred during the active period of sutural growth or subsequent to it cannot be determined from the evidence at hand.

The mandible. Detailed descriptions of growth processes in this bone have been presented in a previous report (Enlow, '63). Differences and similarities in growth pattern compared with the human mandible are evaluated in a later section of the present study.

DISCUSSION

General plan of facial growth. In both man and the monkey, the overall growth of the face is a cumulative, composite result of three basic but closely interrelated processes. First, the paired maxillary tuberosities (and the associated posterior free ends of the dental arch) grow in a posterior course, thereby increasing the anterior-posterior dimensions of the entire maxilla and elongating the arch as teeth are added. Second, as the growth of the maxillary tuberosity proceeds in a posterior direction, the entire naso-maxillary complex is simultaneously displaced in an opposite, anterior course. This produces the essential result of a forward (anterior) increase in overall facial size (Scott, '53; Enlow and Bang, '65). The complex pattern of maxillary growth is directly comparable to the posterior mode of condylar and ramus growth in the mandible. As the mandible grows in an actual posterior course, it is simultaneously displaced in a forward direction. Third, all regional areas and parts of the entire facial complex each undergo their own independent, localized progression of growth and remodeling changes. These changes proceed in a complex variety of directions and at variable rates of growth, as determined by the particular growth circumstances in each area. Thus, the whole maxilla becomes elongated by new bone deposition on its posterior surfaces. At the same time, the nasal walls, premaxilla, chin, zygoma, bones of the orbit, and all other parts of the various facial bones undergo a succession of independent remodeling movements that serve to enlarge each area and to maintain localized shape and relative position.

It has been generally assumed that the forward translocation of the face during development is primarily a result of new bone growth at the sutures separating facial bones from the various other cranial bones lying behind them (Weinmann and Sicher, '55). Studies using metallic implant markers clearly demonstrate such a process of facial expansion occurring at sutures (Gans and Sarnat, '51). The zygomaticotemporal and zygomaticomaxillary sutures show particularly active bone growth. It has been suggested, also, that the enlargement of the growing cartilaginous nasal septum functions to carry the facial complex in a forward and downward course resulting in continual separation at the various craniofacial sutures, thereby stimulating progressive osteogenesis on their contact surfaces (Scott, '53). A suture can function, thus, as a "growth center" in a manner somewhat comparable to the cartilaginous epiphyseal plate in a typical long bone. Factors that are presumed to exert an influence on such sutural growth centers in the craniofacial skeleton include the growing and expanding brain, tongue, eyeballs, and the nasal septum. When the growth of each of these structures begins to cease at a succession of age levels, continued growth is said to proceed by overall surface accretion of new bone rather than by sutural bone growth (Scott, *loc. cit.*). A factor of basic importance must be considered, however, when evaluating the role of any growth center in the development of the face as a whole. While a primary center of growth can be responsible for the generalized enlargement of a given bone in a particular direction, the remainder of the same bone must necessarily undergo at the same time a complex series of additional growth and remodeling changes. These changes, described in previous paragraphs, are essentially independent of the primary growth center itself, although any such center in any bone can function as a pacemaker for the overall growth of the entire bone (Enlow and Bang, *loc. cit.*). In a typical long bone, the entire bone experiences a succession of extensive remodeling changes throughout all of its regions as the whole bone elongates. The lengthening of the bone at its ends, of course, is paced by epiphyseal plate activity. Similarly, the facial skeleton is displaced in a generally forward and downward course essentially as a result of the expanding nasal septum, bone deposition within sutures, and the formation of endochondral bone within the condylar growth center of the mandible. However, all of the various local regions in the different facial bones must simultaneously undergo (1) remodeling adjustments as a consequence of the progressive relocation of each component region and (2) separate growth increases at each local level. These growth increases follow a complex variety of different directions as each part moves in its own particular course independent of growth directions occurring at primary growth centers.

Comparison of facial growth in man and the Rhesus monkey. The general plan of facial growth, as outlined in the preceding two paragraphs, is basically

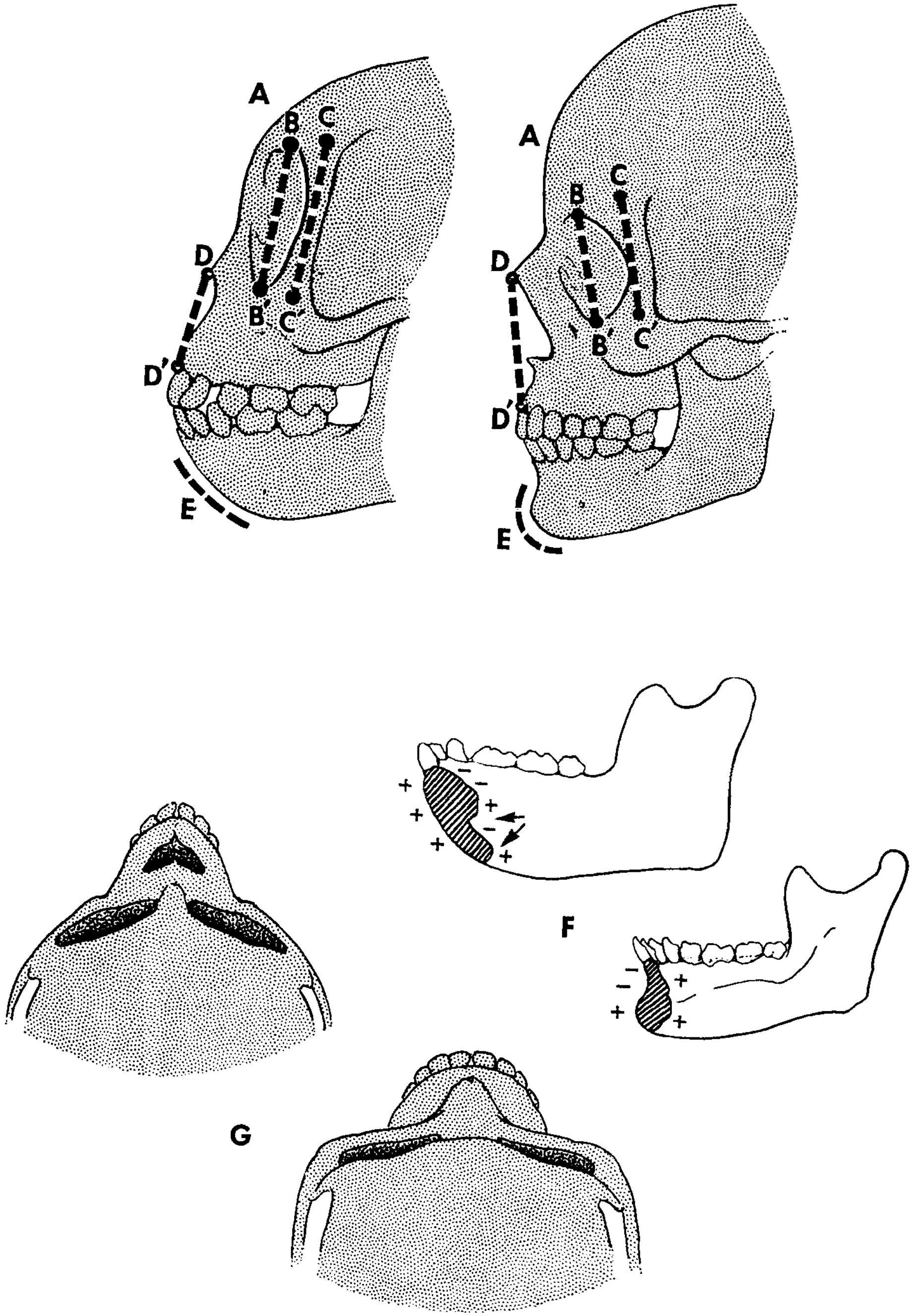

Fig. 4 Because of remodeling differences involved in the growth of the monkey and human facial bones, corresponding anatomical differences are produced in several major areas. Compare the slope of the frontal bone (*A*), the relative positioning of the upper and lower orbital rims (*B*), the angle of the lateral orbital rim (*C*), the relationships between the tip of the nasal bone and the premaxilla (*D*), the structure of the mental region of the mandible (*E*), the presence of a simian shelf in the monkey mandible (*F*), and the differences in contour seen in the malar area (*G*). See text for more complete descriptions and discussion.

similar in both *Homo* and *Macaca*. Several marked differences exist, however, in the sequence of remodeling changes that take place in certain major areas of the face. These are outlined below.

Differing remodeling patterns in the muzzle region of man and the monkey result in a basically dissimilar mode of growth (figs. 1, 4). In the Rhesus monkey, note that the entire maxillary arch anterior to the malar region is depository in nature, in contrast to a *resorptive* periosteal surface in the anterior part of the human maxilla (fig. 7). This surface is convex in the monkey but concave in the human maxilla. In both species, the maxillary complex grows in a downward direction. In the monkey, however, the forward part of the convex maxillary arch (including the premaxilla) simultaneously grows in a forward course by additional subperiosteal deposits of bone on these anterior-facing surfaces (figs. 3, 4). In the human skull, the resorptive nature of corresponding periosteal surfaces and the production of endosteal cortical bone functions to carry the anterior part of the maxillary arch downward in an essentially vertical plane, in contrast to a combined downward and forward movement in the monkey. Note that these differing remodeling combinations result in a premaxillary region in the monkey that protrudes forward of the nose. In the human, however, reduction of forward growth in the premaxillary region combined with the anterior mode of bony and cartilaginous growth in the nasal area result in the formation of the characteristic human nose which extends well beyond the maxillary arch. The forward projecting nasal spine in the human skull is also related to this regressive process of downward premaxillary growth.

Similarly, the anterior part of the mandible demonstrates comparable differences between man and the Rhesus monkey (fig. 4). In *Macaca,* the entire labial side of the point of the mandible is depository in nature. Conversely, the alveolar portion of the human mandible in the arch located forward of the bilateral mental foramina is resorptive in character. This growth movement brings about a distinct recession of the area above the mental protuberance. Periosteal bone deposition on this projecting protuberance together with recession (endosteal bone formation) in the alveolar region are responsible for the formation of the distinctive chin, a unique characteristic of man. It would appear that the presence of resorptive labial surfaces in the anterior parts of the human maxilla and mandible serve to complement each other during development and are functionally interrelated in order to accommodate occlusion.

On the opposite (lingual) side in the forward part of the mandible, further differences exist between man and *Macaca* (fig. 4). This surface in the human mandible is entirely depository. In the monkey, however, the combination of resorption on the periosteal surface of most of the lingual cortex but with progressive new bone deposition along the crest below the genial fossa produces the characteristic "simian shelf," a feature not present in man. It has been suggested that the simian shelf in anthropoids and its counterpart on the opposite side in man (the chin) both function to brace the fused right and left sides of the mandible (Hooton, '46; DuBrul and Sicher, '54).

In the monkey as in man, the marked downward rather than primarily forward growth of the entire nasal area is associated with decreased prognathism. As a related factor, reduced dentition contributes to a facial profile in the monkey approaching that of the human skull. In man, however, the unique resorptive nature of periosteal bone surfaces on the anterior part of the maxillary and mandibular arches is responsible for the extreme lack of prognathism found in the human face.

Although the malar area in both man and the monkey is resorptive in nature and regressive in growth pattern, a difference in extent is involved between the two species. In the human maxilla, note that the cheekbone is squared in contrast to the more rounded malar bone of the monkey (fig. 2). Because of this, the lateral (as well as posterior) movement of the zygomatic arch in the monkey requires a depository surface that extends farther around onto the anterior-facing surface, as schematized in the accompanying diagrams.

The entire endocranial surface in the prefrontal area of the human forehead is resorptive and shows a massive distribution of typical endosteal bone (fig. 6). This is in contrast to the prefrontal area in the monkey, which demonstrates only a limited and irregular distribution of meningeal resorptive surfaces. This observation may be correlated with the less bulbous forehead of the monkey skull and the relative enlargement of the prefrontal cerebral cortex. The roof of the skull in both species is entirely depository on both the meningeal and cutaneous sides.

Differences in basic growth pattern also exist in the lateral orbital rim of the human and simian skulls. In man, this region is much more vertically oriented (fig. 4). Its anterior face is entirely resorptive and the postorbital surface is depository. This combination functions to move the rim in a progressively backward direction. Regressive malar growth in the human together with the marked forward movement of the forehead results in a vertically aligned lateral orbital rim. In the monkey, however, the anterior surface of this forward-facing lateral orbital rim is entirely depository and its postorbital side is largely resorptive. This growth pattern, in conjunction with the lesser extent of anterior growth at the forehead, produces a lateral orbital rim in the monkey that is correspondingly sloping and which grows essentially forward and laterally rather than posteriorly and laterally as in the human skull. In the more upright face of man, note that the supraorbital rim is positioned well forward of the infraorbital margin (fig. 4). In the monkey, however, the lower orbital rim remains anterior to the upper. These distinct differences are a result of the greater degree of forward frontal growth and backward malar movement in the human skull as compared with the monkey.

The upright human face. The unique, vertically oriented face of man is a composite result of several growth and remodeling circumstances. First, the human muzzle grows essentially downward rather than in the usual forward direction characteristic of other vertebrate groups. This is a result of the resorptive nature of the concave, alveolar portion of the maxillary arch. Further, the nasal chambers in the human skull, as well as in the monkey, grow and move in a course that is predominantly downward (Enlow, '66). As they do so, the maxillary arch is necessarily carried in a corresponding inferior direction, thereby adding significantly to its total downward movement. The ramus of the mandible has become correspondingly elongated to accommodate this combined inferior rather than primarily anterior enlargement of the nasal chambers and the maxillary arch. These growth patterns, together with a regressive alveolar region in the mental part of the mandible, result in a vertically aligned face. The bulbous forehead and the development of the frontal sinuses further extend this upright orientation. The regressive and upright lateral orbital rims and the wide-set, forward-facing orbits complete the vertical disposition of the human facial complex.

The human face is also noticeably flattened in appearance. This feature is produced by the regressive growth of the flattened incisor region in the much shorter premaxilla and mandible, in comparison to the angular and pointed jaws of most other forms. The squared malar areas, the parallel zygomatic arches, the massive development of the lateral mandibular trihedral eminances, the expanded temporal region, and the wide-set, forward-facing orbits all contribute to the flattened character of the human face. In figure 1, note also that the solid lateral orbital wall (a primate characteristic) faces forward in the human skull but laterally in the monkey.

The large maxillary sinus of the primate skull, which is particularly massive in the human face, is a developmental product of several interrelated morphogenic factors. First, the orbital cavities each have a complete floor, in contrast to some other non-primate mammals in which the bottom of the orbit is directly continuous with the infratemporal fossa. This orbital floor is a horizontal expansion of the maxillary bone, and it greatly extends the suborbital region occupied by the maxilla. The floor of the orbit also serves as a roof for the underlying maxillary sinus. The partitioning of the primate orbit from the temporal fossa is completed by the development of latero-posterior walls representing extensions of the zygomatic, temporal, and frontal bones. The large area occupied by the sinus itself is produced by the unique downward rather than primarily forward growth of the maxillary arch. In addition, the distinctive forward-facing nature of the orbit is associated with a squared malar region that is oriented in a pronounced forward manner, thereby significantly increasing the volume of the maxilla below each orbital cavity. These various factors, in combination, bring about the development of a suborbital maxillary region that is quite extensive as compared with other mammals. This general area is first occupied by cancellous trabeculae, but it becomes progressively hollowed by a process of internal resorption to form the maxillary sinus.

The vertical alignment of the skull on the vertebral column and the forward positioning of the occipital condyles on the cranial base are apparently related to the upright posture of man (DuBrul and Sicher, '54). This arrangement, in conjunction with the expanded prefrontal cerebral cortex (producing the forehead) and decreased prognathism, provides the morphogenic basic for the upright human face. It has been suggested that bipedal posture may also be correlated with the development of the human hand which, in turn, is functionally dependent upon the enlarged cerebral cortex. Related to these circumstances, the shorter snout and jaws of man reflect, phylogenetically, their subordinate utility. Effective stereoscopic vision and the increased use of hands in manipulation have become dominant primate features (review by Howells, '49).

It has long been realized that the upper and lower jaws of man and other primates are reduced (Hooton, '46). Associated with reduction in dentition, the decreased forward extent of anterior facial growth is characteristic of the higher anthropoids in general. In the monkey, this is the result of the lesser degree of forward alveolar growth in conjunction with a decreased forward displacement of the entire maxillary and mandibular complex. It is noted, however, that alveolar surfaces of both jaws nevertheless grow in a forward direction by progressive periosteal bone deposition. In man, the growth process appears unique in that forward-facing surfaces of the jaws are actually resorptive in character. Thus, the "regressive" character of the lower face in man is actually recessive in its growth pattern, a fact not previously realized. It is emphasized, however, that the regressive nature of the outer (periosteal) surface in the anterior part of the maxilla is concerned primarily with marked downward naso-maxillary growth rather than a direct posterior regression (fig. 3).

Detailed studies of remodeling patterns in the facial skeleton of extinct members of the genus *Homo* as well as other related genera and species, both living and fossil, are now needed. It should be determined if the distinctive resorptive nature of the forward part of the maxillary and mandibular arch is a specific characteristic of *H. sapiens*. Possible variations in growth patterns among different ethnic groups have yet to be determined.

CONCLUSIONS

The growth and remodeling sequence of the facial skeleton in the young Rhesus monkey is described and illustrated. The growth of the human face, discussed in previous studies, is compared with that of the monkey.

Major differences in several regional growth patterns occur between these two primate forms. In the monkey, the entire maxillary arch anterior to the malar region is depository in character. As it is carried downward during the inferior enlargement of the nasal chambers, it simultaneously grows in a forward course by continued subperiosteal bone deposition on all of its outer surfaces. In contrast, the concave periosteal surface on the forward part of the human maxilla is *resorptive*. This growth factor serves to move the entire maxillary arch in an inferior direction since the outer side of this entire region faces away from the downward course of growth. Although a degree of maxillary recession is involved, the free margin of the human maxillary arch becomes elongated as a result of bone deposition along its alveolar crests. These additions bring about a slight protrusion of the anterior maxillary margin even though the outer surface of the muzzle itself is resorptive and regressive. The forward growth of the nasal area in the human face combined with endosteal bone growth (cortical regression) of the premaxillary region results in protruding nasal walls and a nasal spine. A similar growth combination in the mental region of the mandible brings about the formation of the distinctive human chin. In the monkey, a converse growth process in the mandible produces the characteristic simian shelf on the opposite, lingual side of the lower jaw. Reduced dentition in both the human and monkey skull are correlated with a decreased muzzle. The regressive nature of the anterior part of the upper and lower dental arches in the human greatly augment this primate characteristic.

Massive endocranial resorption in the prefrontal area of the skull brings about an outward and forward expansion of the frontal bone, thereby contributing to the bulbous human forehead. The expansion of the frontal sinuses further extends the forehead.

The paired, enlarged maxillary sinuses in the primate skull are a product of several morphogenic factors. First, the formation of the unique orbital floor by an extension of the maxillary bone provides a roof for each underlying maxillary sinus. Second, the pronounced downward growth of the maxillary arch greatly increases the mass of the maxilla located beneath each orbit. Third, the forward-facing orbital cavities are associated with squared and prominent cheekbones, particularly in the human skull, which further increase the volume of the suborbital maxillary regions. The progressive hollowing of these areas on each side brings about the formation of the massive maxillary sinuses.

The upright human face is a composite result of (1) the expanded prefrontal area, (2) the essentially downward growth of the nasal cavities, (3) a regressive and downward growing muzzle, (4) an upright and regressive lateral orbital rim, (5) more vertically positioned superior and inferior orbital margins, and (6) a regressive and flattened anterior-facing malar region.

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LITERATURE CITED

DuBrul, E. Lloyd, and Harry Sicher 1954 The Adaptive Chin. Charles C Thomas, Publisher, Springfield, Illinois.

Enlow, D. H. 1963 Principles of Bone Remodeling. Charles C Thomas, Publisher, Springfield, Illinois.

——— 1966 A morphogenetic analysis of facial growth. Am. J. Orthodontics, *52:* 283–299.

Enlow, D. H., and D. B. Harris 1964 A study of the postnatal growth of the human mandible. Am. J. Orthodontics, *50:* 25–50.

Enlow, D. H., and S. Bang 1965 Postnatal growth and remodeling of the human maxilla. Am. J. Orthodontics, *51:* 446–464.

Gans, B. J., and B. G. Sarnat 1951 Sutural facial growth of the Macaca rhesus monkey. A gross and serial study by means of metallic implants. Am. J. Orthodontics, *37:* 827–841.

Hooton, E. A. 1946 Up From the Ape. The MacMillan Co., New York.

Howells, William 1949 Mankind So Far. Doubleday and Co., Garden City, New York.

Massler, M., and I. Schour 1941 The growth pattern of the cranial vault in the albino rat as measured by vital staining with alizarine red S. Anat. Rec., *110:* 83–101.

Moore, A. W. 1949 Head growth of the Macaque monkey. Am. J. Orthodontics, *35:* 654–671.

Sarnat, B. G. 1963 Postnatal growth of the upper face; some experimental considerations. Angle Orthodont., *33:* 139–161.

Scott, J. H. 1953 The growth of the human face. Proc. Roy. Soc. Med., *47:* 91–100.

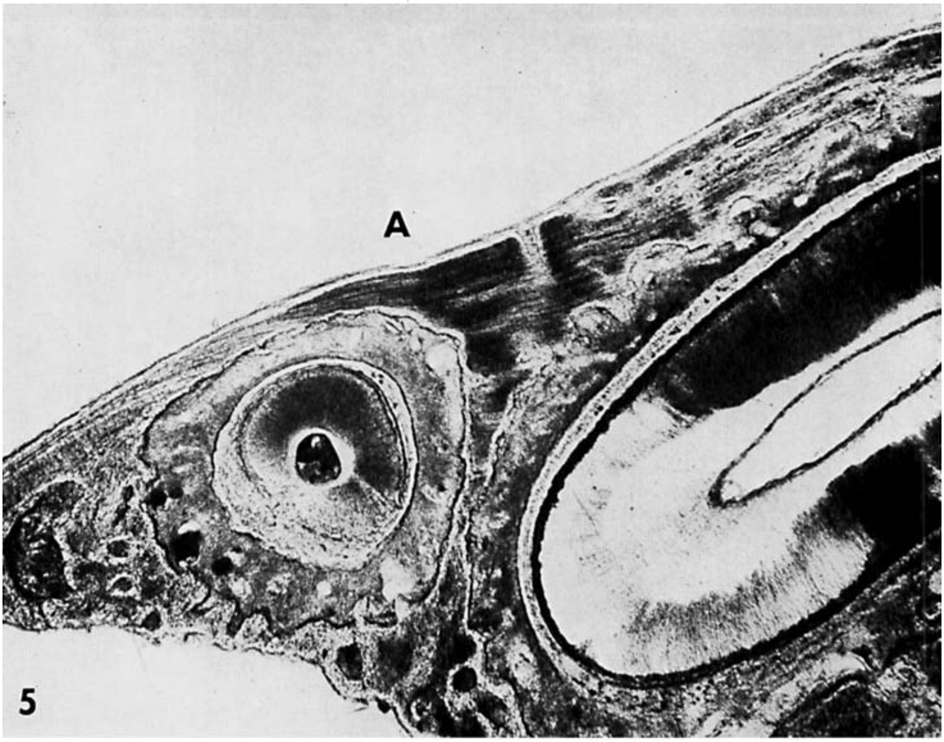
Weinmann, J. P., and H. Sicher 1955 Bone and Bones. Second edition, C. V. Mosby Co., St. Louis, Missouri.

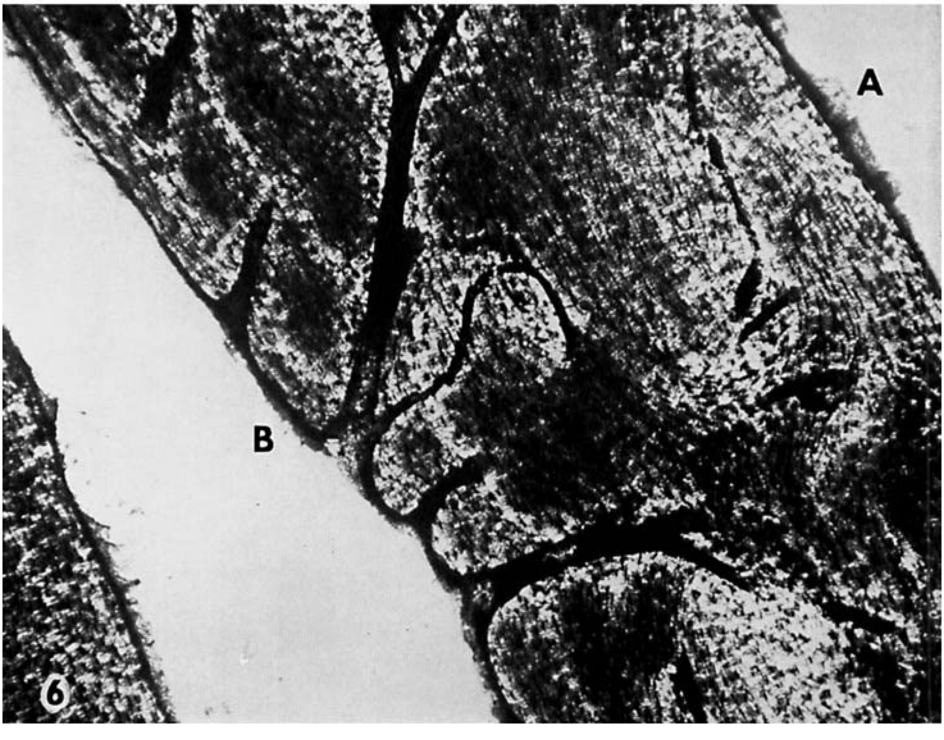
PLATE 1

EXPLANATION OF FIGURES

5 The periosteal surface (*A*) on the labial side of the premaxillary cortex in the monkey skull is entirely depository. Compare with figure 7, which shows the resorptive nature of a comparable area in the human maxilla. × 30.

6 The meningeal surface of the human frontal bone in the prefrontal region (forehead) is characterized by widespread resorption. The resulting cortex of the lamina interna is composed entirely of endosteal bone, as shown in this photomicrograph. The meningeal surface (*A*) had undergone progressive resorptive removal during growth, and the endosteal side (*B*) received bone deposits. The convoluted, whorled pattern of the compact bone is a result of endosteal bone deposition within the cancellous spaces of the irregular diploë. The lamina externa (not seen) is characterized by an outer (cutaneous) surface that is depository and an inner endosteal surface which is resorptive. × 75.


A
5


A
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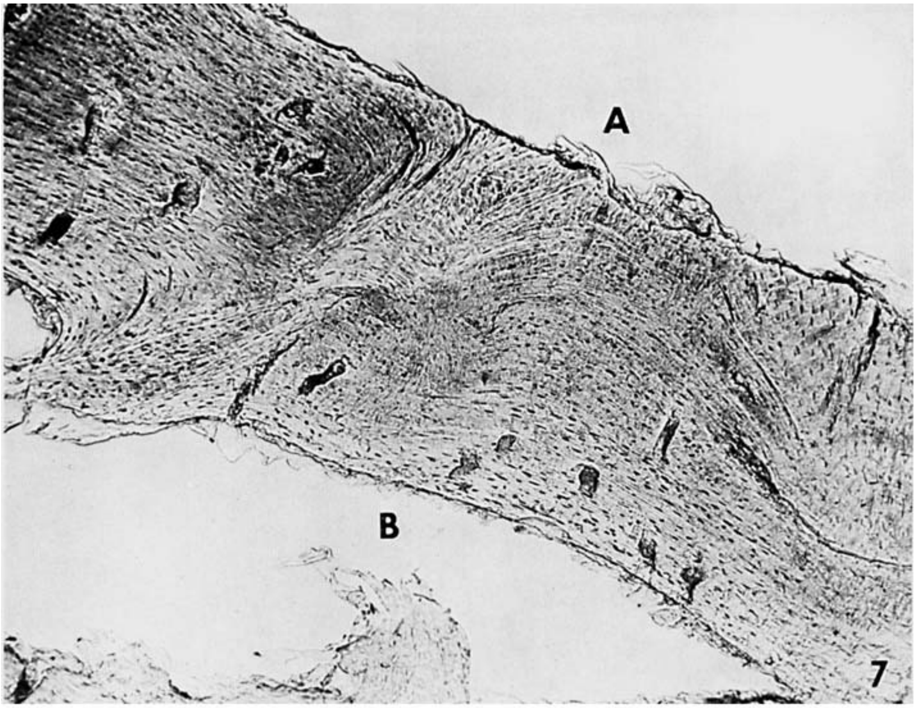
6

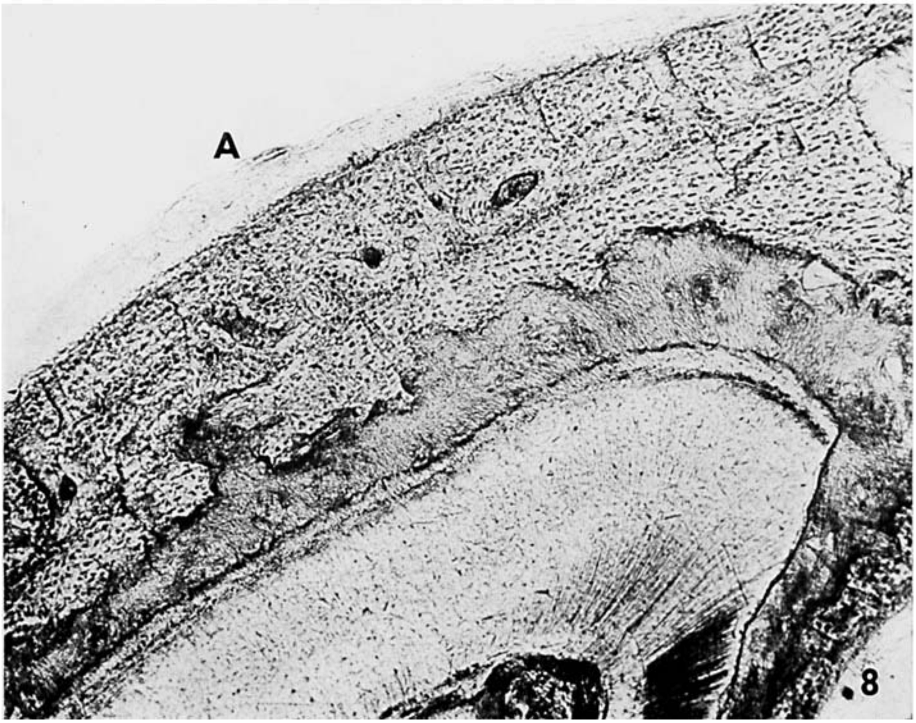
PLATE 2

EXPLANATION OF FIGURES

7 This photomicrograph shows the cortex in the area of the human skull where the malar grades into the premaxilla. Both regions are characteristically composed of endosteal bone, and they have outer (labial) surfaces which are resorptive (*A*). The compact bone seen here was produced by a combined process of external resorption and internal deposition. The irregular, convoluted pattern of structure is typical and was produced by a process cancellous compaction as the cortex moved in an endosteal direction (toward side *B*). × 70.

8 The outer cortex (side *A*) in the forward part of the maxillary arch in the monkey is depository, in contrast to characteristic resorptive surfaces in comparable areas of the human skull (compare with fig. 7). It is composed entirely of periosteal bone. The cortical bone may be vascular, as seen here, or it may be almost entirely non-vascular, as in figure 5. × 30.


A
B
7


A
8