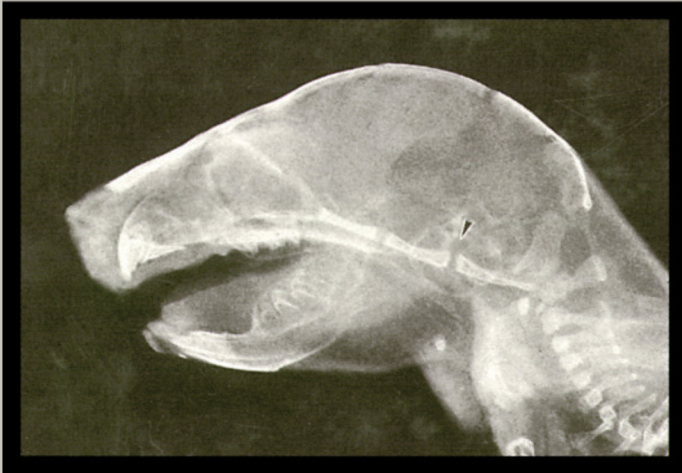
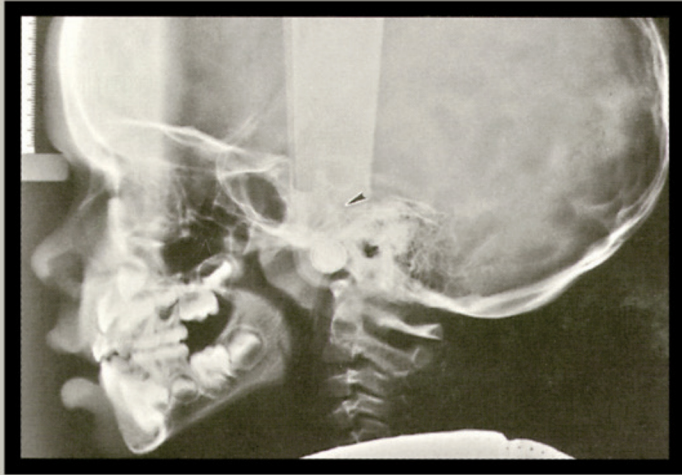


*Fundamentals of*  
**Craniofacial  
Growth**



*Edited by*  
Andrew D. Dixon  
David A.N. Hoyte  
Olli Rönning

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# Preface



This new book had a simple genesis. It was an outcome of graduate level courses on craniofacial development and growth that one of us (A.D.D.) chaired for a number of years at UCLA. The content of the courses derives great benefit, in terms of both depth and breadth of interest, from the participation of select faculty drawn from the Schools of Medicine and Dentistry. The courses are taken by postdoctoral students in several clinical specialties, including orthodontics, pediatric dentistry, and periodontics. Many of them complete additional work for graduate degrees in Oral Biology. This postdoctoral education pattern has its counterparts at many other institutions, not only in the United States but internationally as well.

It is inevitable in our teaching that we place great reliance for our knowledge base on a spectrum of scientific works drawn from many sources, including scientific journal publications, symposia, and conference proceedings. While this has unquestionable advantages and should continue to be a vital part of the student's experience, the present comprehensive text is written in a review format that attempts to bring together selected important topics in craniofacial growth into a single volume for students and their instructors. Additionally, the book is intended to go beyond the classroom experience by providing graduate students, experienced researchers, and clinicians alike with current analyses of issues, concepts, and perspectives fundamental to a variety of bone growth studies.

The book, which is multi-authored to ensure the appropriate depth of expertise, is intended as a core text for the study of craniofacial growth. Beyond that, it is not our objective that the readership be confined solely to those studying or researching within the field of Dentistry but that it will also have value for a much wider audience in any of the biologic and biomedical fields, where an in-depth knowledge of craniofacial bone growth is both germane and applicable.

To meet these goals, our contributors come from a number of different backgrounds in addition to the practice of medicine and dentistry, including anatomy, biology, biomathematics, embryology, orthodontics, physical anthropology, and plastic and reconstructive surgery. They have brought to their individual contributions a wealth of experience in directly related scientific research that permeates their writings. In the selection of the contributors we had the advantage of personal knowledge of a wide range of colleagues who had participated at three international conferences on bone growth held at UCLA between 1982 and 1991, the last one dealing with methodology and applications of bone growth research and also published by CRC Press. This was a stimulus to give this book a distinct international flavor also.

There are seventeen chapters, liberally illustrated with relevant explanatory figures and extensive reference lists. Each topic is treated comprehensively, giving it a place in the larger story of craniofacial growth, both in animals and humans. Balanced basic science and clinical viewpoints are presented, including the consideration of abnormalities of development and growth. These are in fact exercises, sometimes defiant ones, in our understanding of the complexities of the craniofacial growth process.

While each chapter is written as an individual topic for study or discussion, the overall design of the book follows a logical sequence, beginning with three foundation chapters. The first considers principles of general skeletal growth, including the influence of genetic, epigenetic, and environmental factors; the second presents a comparative phylogenetic approach to an understanding of form in the craniofacial complex; and the third is a review of osteogenesis and its control by a variety of endocrine substances and growth factors. The two subsequent chapters examine the early development of the human jaws, cranial base, and craniofacial joints. Then, as a prelude to an emphasis on fundamentals of postnatal growth throughout the remainder of the book, two chapters review a spectrum of some of the more

classical experimental methods for assessing postnatal craniofacial bone growth, including direct and indirect measurement; and morphometric techniques that give us the ability to closely model in numeric terms what is readily seen visually.

Next, a series of six chapters deals with regional growth of the skull, considering in turn postnatal growth of the mandible, the nasomaxillary complex, the orbit, cranial base, ear capsule, and cranial vault. With this extensive background, it is then appropriate to devote two chapters to the central significance of cartilage and bone remodeling in craniofacial morphogenesis and growth. In the last two chapters, the influence of muscles and other soft tissues on growth of the craniofacial complex and the outcomes of changes in muscle function on bone growth and skull form are discussed.

We wish to thank our colleagues for their willingness to contribute to this volume, their attention to detail, and their timely efforts. We are most grateful to Ralph Hoyte for his indispensable translation work, from the German, of Professor Schumacher's contributions and to Graeme Churchard for his computer skills in the preparation of Dr. Hoyte's chapters. As has been the case on many previous occasions, we are deeply appreciative to Mary and Vera, who once again had to tolerate their spouses intense work ethic. Finally, books are enormously enhanced by one's publisher and, accordingly, it is a great pleasure to thank Marsha Baker, Senior Editor; Debbie Didier, Project Editor; and the staff at CRC Press for their careful attention to every phase of the publication process.

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**David A.N. Hoyte**  
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# Principles of Skeletal Growth

*Gert-Horst Schumacher*

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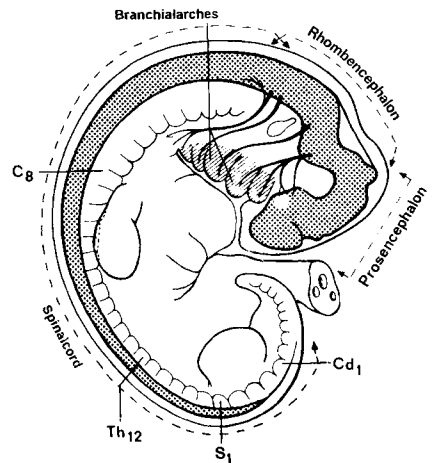
## I. STRUCTURE OF THE HEAD

Humans and vertebrates both share in common a regional division of the body into head, trunk, and extremities. Both also exhibit branchomery, that is, the arrangement of branchial arches, as well as metamerism, that is, segmental organization of the trunk wall.

The structure of the head differs from that of the trunk in that there is an absence of segmental organization. The development of the organs of the head has resulted in the disappearance of the cranial somites and their being taken up into the structure of the cranial base. The dorso-caudal part of the cranium is thus the only part still of metameric origin. The occipital vertebra (proatlas) anterior to the atlas forms the posterior main condyle and the superior joint facets of the first cervical vertebra. These differentiations become evident in cases of developmental disorders, as, for example, manifestations of the occipital vertebra or atlas assimilation.

The rostro-dorsal segment of the skull, on the other hand, consists of unsegmented head mesectoderm and prechordal mesoderm. The structural material of the rostroventral cranium stems from the first two branchial arches.

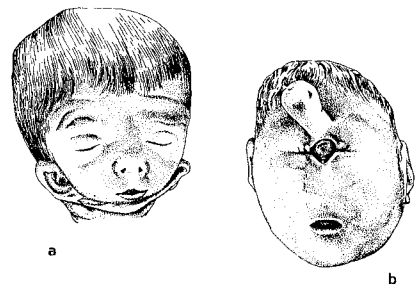
The structural arrangement originates in regionally specific inductors under the influence of the central nervous system. It is presumed that the head possesses two induction centers and the trunk one (Figure 1.1).



**Figure 1.1** Organization of the head and trunk in the human embryo. (After Starck, D: *Embryologie*, 3rd ed., G. Thieme, Stuttgart, 1975. With permission of Georg Thieme Verlag, Stuttgart.)

The induction center of the anterior head region for the nose, the eyes, and anterior skull base is subject to the influence of the frontal brain, the prosencephalon. The posterior head region where the labyrinth, ultimobranchial bodies, and posterior skull base develop are influenced by the rhombic brain, the rhombencephalon, and the trunk by the caudal section of the neural tube.

The existence of two skull formation centers is substantiated by cyclopic and otocephalic malformation patterns (Figure 1.2).



**Figure 1.2** Craniofacial dysplasias: a, cyclopia; b, otocephaly. (After Schumacher, G-H: *Anatomie, Lehrbuch und Atlas*, Edition Zahnheilkunde. J.A. Barth, Leipzig, 1991, Vol.1. With permission.)

## II. SKELETAL MORPHOGENESIS

Bone formation can ensue in two ways, either through desmal ossification, that is, directly from the mesenchyme, or indirectly through a hyaline cartilage stage, that is, through chondral ossification. Both cases first result in woven bone. The activities of osteoblasts and osteoclasts are crucial to the formation of bone as well as to its constant remodeling and regenerative capabilities.

### A. OSTEOBLASTS AND OSTEOCLASTS

**Osteoblasts** differentiate from mesenchymal cells. Their ultrastructure exhibits the properties of cells with high synthetic capabilities. Their initial task is to produce noncalcified osteoid, consisting of basic material (proteoglycans, glycoproteins) and collagen fibres. Osteoid production is omnidirectional, walling in the osteoblasts which then turn into osteocytes.

**Osteoclasts** are 30 to 100  $\mu\text{m}$  multinucleate giant cells which use enzymes (primarily proteases and phosphatases) to break down bone. They are equipped with microvilli on the side facing the bone. Their emission of lactic acid increases the pH and thus dissolves the minerals. Osteoclasts are usually found in small pockets of the broken down bone, the Howship's lacunae. They can move in amebic fashion.

## B. DESMAL AND CHONDRAL OSSIFICATION

**Desmal ossification** begins in centers of mesenchyme cell concentration, where they become differentiated into osteoblasts. The osteoblasts synthesize the osteoid in which hydroxylapatite crystals are formed by calcium and phosphate ion enrichment. Bone trabeculae are initially laid down and converge to eventually form a network. The osteoblasts and osteoclasts mold the bone trabeculae, resulting in lamellar bone arising from the woven bone. Growth of the desmal bone follows by apposition.

The bones of the skull vault and of the facial skull as well as the lower jaw and the diaphysis of the clavicle arise through desmal ossification (Table 1.1).

**Table 1.1** The Mode of Ossification of the Bones of the Skull

In cartilage	In membrane
Os ethmoidale	Maxilla
Concha nasalis inferior	Os zygomaticus
Os sphenoidale	Os palatinum
Os temporale:	Vomer
- Pars petrosa	Os nasale
Os occipitale:	Os lacrimale
- Pars basilaris	Os frontale
Malleus	Os parietale
Incus	Os temporale:
Stapes	- Pars squamosa
	- Pars tympanica
	Os sphenoidale:
	- Lamina medialis
	(processus pterygoidei)
	- apex of Ala major
	Squama occipitalis
	Mandibula

**Chondral ossification** is the mode of ossification of the base of the skull, the vertebrae, the ribs, as well as of all the tubular bones (Figure 1.3). Cartilage here represents the first stage in bone development. Initially, a process of perichondral ossification results in the formation of a bone collar around the cartilage. Then the cartilage cells in the interior of the cartilage change into hypertrophic cartilage. Some of the cells are destroyed and the basic substance takes up calcium salts. Through endochondral ossification, mesenchyme cells from outside invade the cartilage and commence the formation of bone from the inside out. Concurrently, white blood cells (monocytes) become differentiated into chondroclasts which break down the cartilage, and mesenchyme cells become differentiated into osteoblasts which deposit bone matrix on the remaining cartilage.

Growth in diameter starts with the periosteum and is thus appositional. Longitudinal growth ensues endochondrally on a base of remaining cartilage and is thus interstitial. When there is no more cartilage remaining, bone formation and longitudinal growth ceases.

## III. SKULL MORPHOGENESIS

As described above, the anlage of the skull consists of cranial somites, nonsegmented head mesectoderm, prechordal mesoderm, and the first two branchial arches.

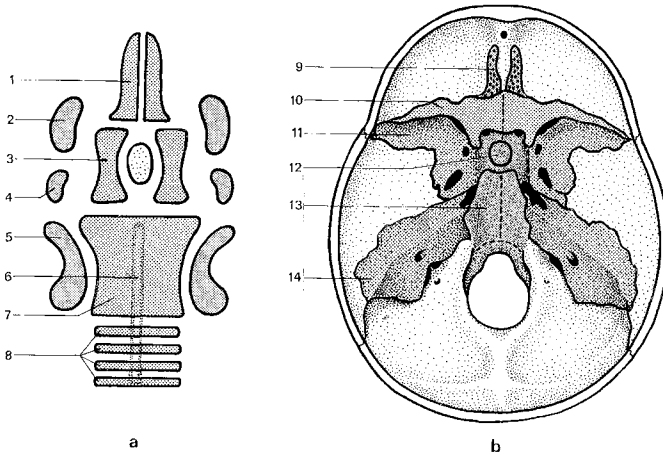
The mesenchyme becomes concentrated into an envelope around the brain vesicles from which the skull bones arise partly through chondral and partly through desmal ossification. The cartilaginous anlage of the skull is called the chondrocranium and that arising from connective tissue, the desmocranium.

### A. CHONDROCRANIUM

The chondrocranium arises from the fusion of several cartilage elements. In the second embryonic month, the first cartilage deposits begin to form in the basal part of the mesenchymal envelope at the anterior end of the notochord (Figure 1.4). The cartilaginous ear capsules surrounding the labyrinth arise independently of this, as do the nose capsules surrounding the olfactory organs.



**Figure 1.3** Ossification centers in a 5 cm embryo. (After Schumacher G-H and Christ, B: *Embryonale Entwicklung und Fehlbildungen des Menschen, Anatomie und Klinik*, 10th ed., Ullstein Mosby, Berlin, 1993. With permission.)



**Figure 1.4** The anlage of the chondrocranium. a, The cartilaginous laminae; b, Their derivatives; 1, trabecular cartilage; 2, ala orbitalis; 3, hypophyseal cartilage; 4, ala temporalis; 5, labyrinthine capsule; 6, notochord; 7, parachordal cartilage; 8, occipital cartilage; 9 ethmoid bone, 10, lesser wing of sphenoid; 11, greater wing of sphenoid; 12, body of sphenoid; 13, basilar part of occipital bone; 14, petrous temporal bone. (Modified from Clara, M: *Entwicklungsgeschichte des Menschen*, 6 Aufl., Georg Thieme, Leipzig, 1966. With permission of Georg Thieme Verlag, Stuttgart.)

The mesenchyme situated at the cranial end of the notochord differentiates into the parachordal cartilage which then connects with the cartilage formed from the cranial somites. The trabecular and hypophyseal cartilages form anterior to the cranial chordal extremity, i.e., prechordally. The above-mentioned cartilage deposits fuse to form a long plate reaching from the nose region as far as the back of the head. The center of this cartilaginous plate contains the hypophyseal pouch (Rathke's pouch) from whose epithelium the anterior lobe of the hypophysis arises. On both sides two further cartilaginous plates, the ala orbitalis and the ala temporalis arise. In the third month the notochord extends further caudally.

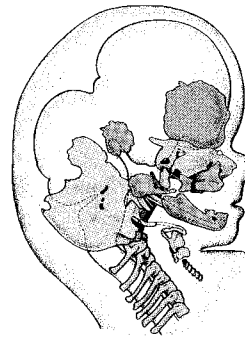
The bones of the base of the skull originate essentially in the chondrocranium (Table 1.1). The chondrocranium persists as the nasal capsule.

The auditory cartilage apparatus of the malleus, the incus, and the stapes as well as the processus styloideus of the temporal bone originate in the cartilaginous bar of the first and second branchial arches (Meckel's and Reichert's cartilages).

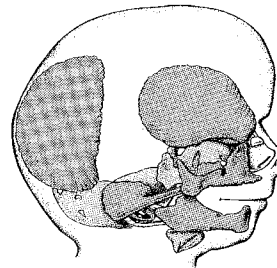
The ossification of the chondrocranium emanates from several ossification centers which differentiate in all directions. Any cartilage remaining between the bones in the form of synchondroses acts as a growth center in a similar way to the epiphysial plates of hollow bones. By about the age of 20 years, the synchondroses of the base of the skull have completely ossified and longitudinal growth is complete. Premature or delayed ossification of the synchondroses can result in a shortening or lengthening of the base of the skull.

## B. DESMOCRANIUM

The desmocranium is that part of the skull which ossifies directly out of the connective tissue. The bones of the roof of the skull, the majority of the nasal skeleton, and the jaw apparatus, among others, arise from it (Figures 1.5, 1.6).



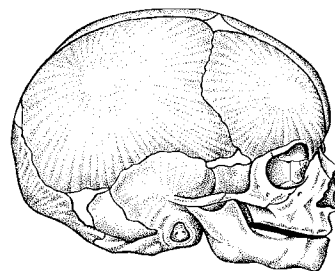
**Figure 1.5** Development of the skull. The form in a 40 mm embryo. The chondrocranium is stippled. (After Macklin from Hamilton, WJ, Boyd, JD, and Mossman, HW: *Human Embryology*, 4th ed., Macmillan, London, 1976. With permission.)



**Figure 1.6** Development of the skull. The form in an 80 mm fetus. (After Heitig from Hamilton, WJ, Boyd, JD, and Mossman, HW: *Human Embryology*, 4th ed., Macmillan, London, 1976. With permission.)

The skull vault ossifies at various places corresponding to the future eminences. The bony nuclei arise at the beginning of the third month and proliferate in lamellar fashion, thereby reducing the amount of connective tissue remaining to small gaps, the sutures. Further bone growth can occur in the sutures up to young adulthood, as occurs similarly in the synchondroses of the cranial base. Growth in thickness of the skull vault is from the periosteum outwards.

The fontanelles persist initially at the midline junction of the coronal sutures (Figure 1.7). The large anterior fontanelle ossifies by the end of the second year of life whereas the small posterior fontanelle ossifies by the end of the first year. Both lateral fontanelles, the sphenoidal and mastoid, close within the first few months after birth.



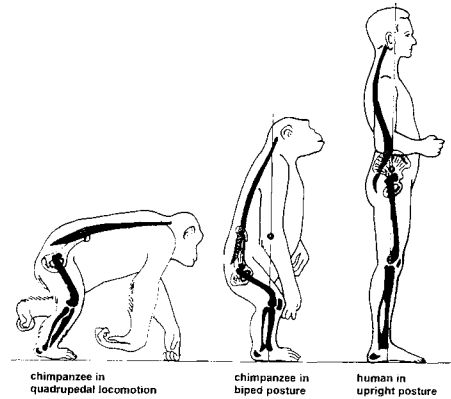
**Figure 1.7** The human skull at birth. (From Schumacher, G-H: *Anatomie, Lehrbuch und Atlas*, Edition Zahnheilkunde. J.A. Barth, Leipzig, 1991, Vol. 1. With permission.)



The masticatory apparatus develops from the mesenchyme of the mandibular arch, giving rise to an upper and a lower jaw anlage. The mesenchyme cells of the upper jaw anlagen give rise to the maxilla, zygoma, palate, and nasal bones. Meckel's cartilage is laid down in the lower jaw swelling, the lower jaw ossifying in membrane on both sides of this. At the same time the ventral part of Meckel's cartilage recedes, its dorsal end differentiating into two auditory bones, the malleus and incus.

### C. PHYLOGENETIC FACTORS

A bony skull roof, a secondary jaw joint, the bony auditory apparatus, a secondary palate, as well as heterodonty and diphyodonty are characteristic of mammals. The most significant differences between humans and other mammals are, however, verticalization and cerebralization (Figure 1.8).



**Figure 1.8** Verticalization of the trunk. (After Kummer, B from Schumacher, G-H: *Kompendium und Atlas der Allgemeinen Anatomie mit Zytologie und Histologie*, 2 Aufl., VEB G. Thieme, Leipzig, 1987. With permission of Georg Thieme Verlag, Stuttgart.)

The verticalization of the trunk has resulted in the legs being responsible for forward motion and the arms for grasping. The effect of this is a change in static relationships. The skull, which is hung on the vertebrae at the posterior head region in quadrupeds, is balanced on the vertebrae in the case of humans. This gives rise to several peculiarities: the nuchal musculature of humans is relatively weak; the bony ridges of the human skull are flattened. The foramen magnum as well as the occipital condyles have extended anteriorly, so that the centre of gravity of an adult skull lies some 3 cm in front of the posterior main condyle (Figure 1.9). The angle of inclination of the base of the skull is also found to be reduced.

Cerebralization concomitantly resulted in an increase in consciousness in humans. It allowed the development of learning ability, the storing of knowledge, the gathering of experience, and the development of creativity. The resulting change in the way of life has left its mark in morphological changes to the skull, the chief signs being an increase in the size of the neurocranium and a reduction of the jaw apparatus. Numerous functions of the jaw apparatus such as the use of the teeth as a weapon or tool have in the course of human phylogeny been taken over by the hands. The foreshortening of the jaws has meant that the dental arches in humans have taken on a parabolic shape, whereas in apes they are U-shaped. Other characteristic human features are a reduction in the size of the teeth and that the tooth rows no longer have gaps (diastemas).

Fanghänel (1974) has correlated further formative factors (Figure 1.10) which were significant in our humanization.

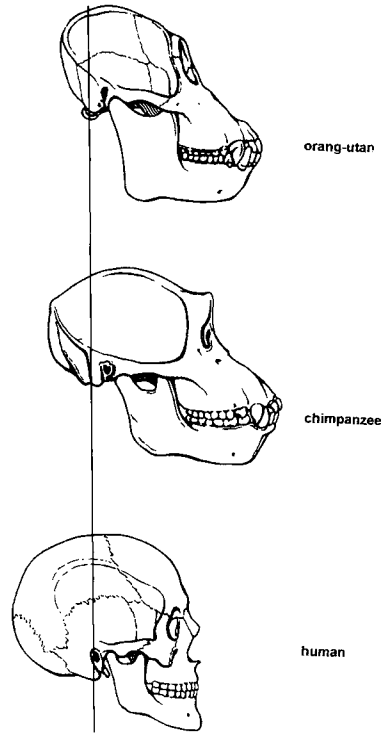
Speech as a result of cerebralization has led to specific differentiation of muscle groups. Through increased curvature of the palate, the tongue has gained more freedom for articulation. The lips and the cheeks have increased their muscularity, resulting in increased freedom and expressiveness of mimicry and gesture.

Work is a characteristic feature of humans and affects both manipulative ability and speech, the skull responding both in form and function.

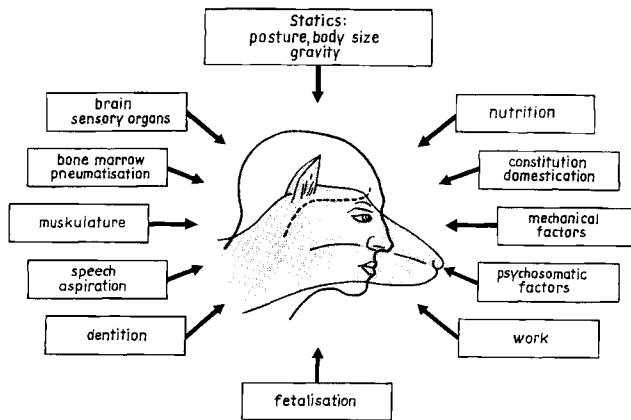
The type of nutrition also affects skull morphology as is recognizable in the various masticatory patterns in carnivores, herbivores, and rodents.

Fetalization is a hypothesis according to which the shape of the human skull is the result of arrested development. The cause is said to be a constellation of endocranial factors.

Domestication led as a rule to a foreshortening and widening of the skull. An appropriate example is a comparison of the skull of the wild boar with that of the domestic pig.



**Figure 1.9** The displacement of the occipital condyles in man compared with the orangutan and chimpanzee. (From Schumacher, G-H: *Kompendium und Atlas der Allgemeinen Anatomie mit Zytologie und Histologie*, 2 Aufl., VEB G. Thieme, Leipzig, 1987. With permission of Georg Thieme Verlag, Stuttgart.)

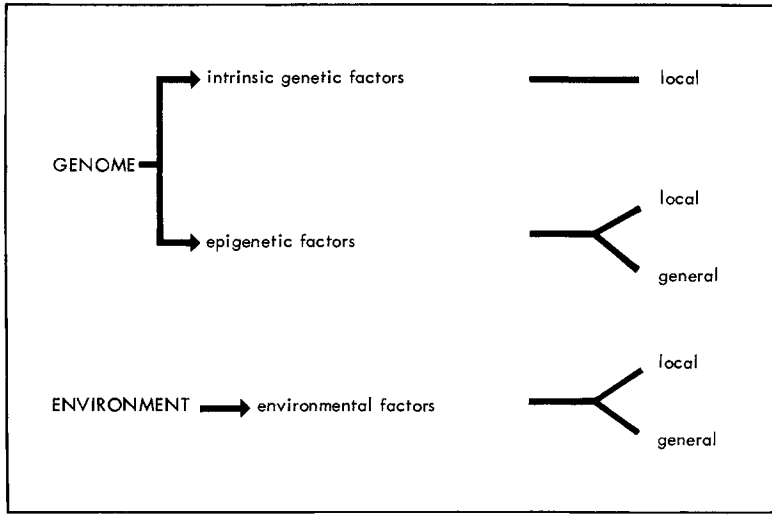


**Figure 1.10** Structural factors in the phylogeny of the human skull. (After Fanghänel, J, from Schumacher, G-H: *Regulationen und Adaptionen im Kraniofazialen Wachstum. Symposium der Deutschen Gesellschaft für Kieferorthopädie*, Bad Homburg, 1989, Urban & Vogel, München, 1991. With permission.)

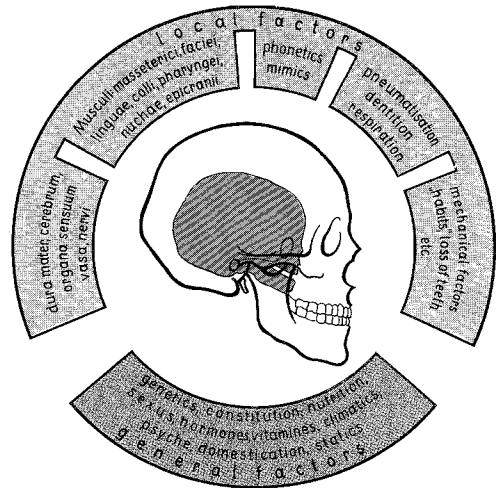
**D. ONTOGENIC FACTORS**

Skull morphogenesis is controlled by a genetic program modifiable by environmental factors (Figure 1.11). In the embryonic period, the expansion of the brain and the sense organs determine morphogenesis. In the postnatal period the determining factor is the development of the jaw apparatus. During this process genetic factors and environmental factors overlies one another so that the causes of morphological changes are often disguised. The extent and effect of environmental influences are, in any case, difficult to estimate.

Figure 1.12 shows a sample of morphologically influencing factors, drawn up on the basis of a detailed search of existing sources (Schumacher, 1968). General factors are those which affect the whole organism or the whole skeletal system. Local factors directly influence the skull. Both sets of factors operate in prenatal and postnatal development.



**Figure 1.11** The regulation of skull morphogenesis by genetics and the environment. (After Limborgh, J van: The role of genetic and local environmental factors in the control of postnatal craniofacial morphogenesis. *Craniofacial Conference, Nijmegen, The Netherlands, 1972, 47-58. With permission.*)



**Figure 1.12** Structural factors in the ontogenetic development of the human skull. (From Schumacher, G-H: Der maxillo-mandibuläre Apparat unter dem Einfluß formgestaltender Faktoren. *Nova Acta Leopoldina*, J.A. Barth, Leipzig, 1968, Vol. 33. With permission.)

**IV. GENERAL FACTORS**

The formation of characteristics is generally polygenetic, i.e., influenced by multiple genes.

Genes which attack cartilage or bone can lead to morphogenic skull changes. Chondrodystrophy, in which the formation of vertebral cartilage is partially or even totally disrupted is an example of this. This condition is characterized by dwarfism with short extremities yet nearly normal axial skeletal growth. The skull is disproportionate, as only the growth of the base of the skull is affected. The bones of desmal origin as well as periosteal growth, however, are unaffected.

The constitution and skull shape have significant characteristic correlations. Leptosomes have a long and narrow face whereas pygmies have a wide head and short neck.

Gender affects growth in different ways. The onset of hormone controlled sexual maturity initiates cartilage growth over varying time periods. Cessation of longitudinal growth is generally accepted as taking place in girls at the age of 20 and at 23 years in the case of boys. Rhythmic variations have also been observed during the growth period. The sexual dimorphism of the skeleton manifests itself especially

clearly in the bony pelvis but can also be seen in the skull. The skulls of animals can exhibit considerable sexual differences.

Hormones affecting cartilage bone growth can activate or deactivate the synchondroses. Somatotrophic hypophyseal hormone stimulates the proliferation of cartilage cells. Overproduction during cartilage growth leads to lengthening of the base of the skull with consequent acromegaly. Underproduction during the growth phase leads to foreshortening of the base of the skull and thus to underdevelopment of the middle face. Sexual hormones are also believed to stimulate chondral growth. Corticosteroids inhibit cell proliferation and the formation of the extracellular matrix.

The vitamins (A,C,D) can influence osteogenesis in cases of hyper- and hypovitaminosis and thus influence skull growth as in, for example, cases of rickets caused by a lack of vitamin D.

Nutrition as an ontogenic factor plays an important role. It is well known to animal breeders, for example, that adequate nutrition leads to round heads whereas inadequate nutrition leads to narrow skulls. Inadequate nutrition results in a longer growth period with concomitant disproportionalities in the size relationships of the head and the extremities to the trunk. A protein rich diet can delay the onset of sexual maturity and as this directly affects cartilage growth, open epiphyses, synchondroses, nose cartilage, etc., can initiate a longer lasting growth period or the opposite. Insufficient nutrition leads to osteopathic presentations consisting of calcium disturbances and vascular damage.

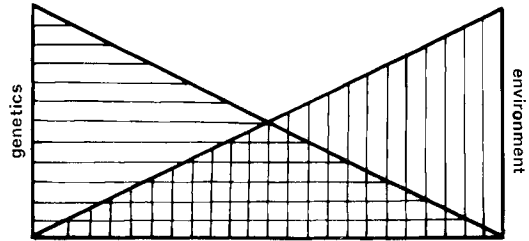
The climate affects growth processes and thus skull formation. The growth factor of a cell is, for example, also affected by temperature variations. Early maturity can, for example, be observed in southerly countries. It can further be observed that animals born in the autumn grow more slowly than those born in the spring. The influencing factors are here also complex, consisting of a melange of functions such as diet, vitamins, hormones, temperature, light, and so on.

The psyche can influence skull growth through lack of activity of the facial, tongue, jaw, and floor of the mouth muscles.

Statics is illustrated through the example of verticalization. Skull shape can be influenced by posture. The impressions of the cerebral gyri on the basal fossae of the skull are an example of the effects of gravity.

**Local factors** are numerous, influence each other reciprocally, and are overlaid by more general factors, each through its local effect necessarily affecting the functioning of the whole physiological system (Figure 1.13). Thus the local function of the maxillomandibular apparatus consists in taking in and grinding up food and thereby providing the preconditions for metabolism, growth, hormonal effects, and so on.

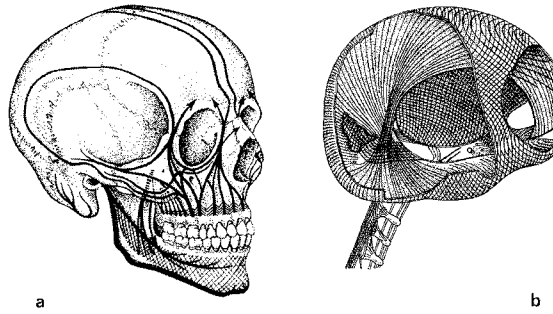
**Figure 1.13** Gene–environment interaction. The overlapping area is where both groups of factors are interacting. (From Schumacher, G-H: Factors influencing craniofacial growth, in *Normal and Abnormal Bone Growth: Basic and Clinical Research*, Dixon, AD and Sarnat, BG, Eds., Alan R. Liss, Inc., New York, 1985, 3–22. Reprinted by permission of John Wiley & Sons, New York.)



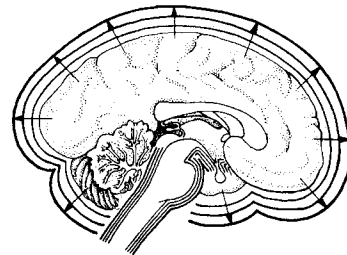
The dura mater belongs to the osteofibrous connective tissue system of the skull. It stimulates the formation of trajectories and plays a part in the spatial construction of the skull by extremely small scale excitations (Figure 1.14). After birth, the dura is strengthened considerably. The sagittal and transverse arches form a symmetrical construction on the base of the skull which is influenced by the actions of chewing, motion, variations in brain pressure, weight and posture, teeth, etc. (Popa, 1936). In old age its attachment to the sagittal arch and the transverse arch is much looser, this leading to the effective ending of the role of the dura as an excitatory mechanism.

The brain as well as the organs of vision, hearing, and balance have through their expansive growth (pressure effect) a considerable influence on skull shape. This is documented by measurements on the human brain as well as by examples of anencephaly, hydrocephaly or experimental excision of the hemispheres (Moss, 1958) as well as cerebral hemiatrophy. The arch construction of the skull and especially that of the hemispheres is the result of brain growth (Figure 1.15).

The organs of sense are closely connected to brain development. They and their immediate relationships in the skull have a decisive influence on the shape of the cranium, for example, the nose, orbits, and tympanic bulla. As the organs of sense develop in the prenatal period as quickly as the brain, in



**Figure 1.14** Functional structures: a, framework of construction of skulls; b, mechanical structure of the dura mater.



**Figure 1.15** Expansion of the telencephalon.

order to be fully functional at birth and thus to be able to relate to the outer world, the newly born exhibit a relatively mature differentiation.

Vessels and nerves influence cranial growth through their effect on metabolism. Unilateral ligation of the A. carotis communis in young rats and rabbits leads to skull deformities in the adult animals (Koester and Mierzwa, 1985; Beleites and Brehmer, 1986; see Chapter 17). The nerves have a similar trophic function towards the tissues with disruptions or paralyses having been shown to result in atrophies, growth defects of the jaw or positional abnormalities of the teeth. The dentition is intimately connected with the development of the alveolar process and of the jaw. The maturing tooth buds push the jaw out during growth. The growth impetus is at its greatest during the pre-eruptive phase. The alveolar process forms on eruption of the teeth.

An increase or decrease in the number of teeth as well as loss of teeth during growth results in changes to the alveolar process, influencing the configuration of the facial skull to a greater or lesser extent.

Breathing affects the shape of the palate, oral respiration having been observed to lead to an increased curvature of the palate. In oral respiration the tongue rests at the bottom of the mouth or sinks back into the pharynx. The upper jaw is unable to extend itself through lack of tongue pressure, with consequent compression and increased curvature of the palate vault, as well as growth disturbances of the nasal cavity and possibly decreased pneumatization in the maxilla.

The muscles occupy a special place in the enumeration of morphogenetic factors as their activities are used therapeutically, foremost among these being the perioral musculature.

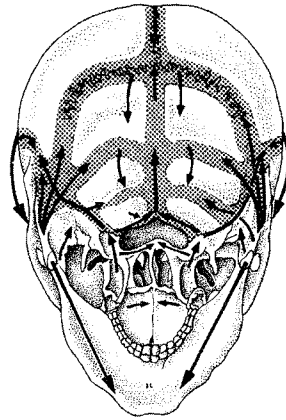
The strongest muscle group in the skull, however, is undoubtedly the masticatory muscles. They deploy the energy of chewing and thus have a considerable influence on cranial shape.

The tongue and muscles of the floor of the mouth have a close relationship to the growth of the lower jaw. The morphogenetic influence of the floor muscles is traceable in toothless lower jaws of old people, the mylohyoid line forming a more pronounced ridge and the mental spine being drawn out to a long spike.

The throat and neck muscles have a considerable involvement in the formation of the external base of the skull (Figure 1.16).

Pneumatization in the viscerocranium develops from the nasal cavity. The paranasal sinuses thus develop closely in association with the development of the nose and work together with this to shape the facial skull.

Habits such as finger sucking, sucking the lower lip, as well as deeply-placed tooth braces can also lead to abnormalities of tooth position and to deformities of the jaw skeleton.

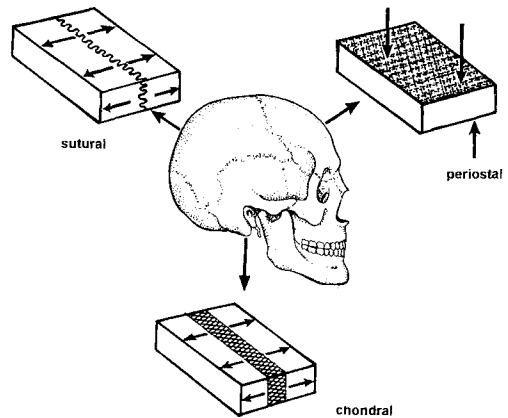


**Figure 1.16** The reinforcement of the skull capsule by the attachment of the dura mater, the masticatory, and nuchal muscles. (From Popa, GT: *Mechanostruktur und Mechanofunktion der Dura mater des Menschen. Gegenbaurs morphol. Jahrb.*, Leipzig, 1936, 78:85.)

## V. MECHANISMS OF BONE GROWTH

The postnatal changes in skull shape are ascribable to chondral and desmal growth. These are effected in three ways.

1. Chondral growth is achieved by interstitial growth of cartilage, originating in cartilage, for example, the synchondroses.
2. Sutural growth is appositional growth, taking place in the skull sutures on the edges of the skull bones, and
3. Periosteal growth, which is also appositional growth, originates in the periosteum (Figure 1.17). In contrast to chondral and sutural growth, periosteal growth continues into advanced age.



**Figure 1.17** The methods of craniofacial growth. (From Schumacher, G-H: *Regulationen und Adaptionen im Kraniofazialen Wachstum. Symposium der Deutschen Gesellschaft für Kieferorthopädie*, Bad Homburg, 1989, Urban & Vogel, München, 1991. With permission.)

### A. CHONDRAL GROWTH

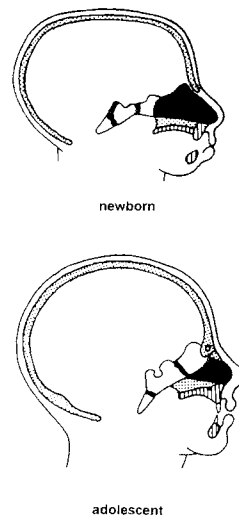
Cartilage occurs at the base of the skull in the form of synchondroses, as the cartilaginous nasal septum as well as symphyseal and temporomandibular joint cartilage.

The significance of synchondroses for bone growth is comparable to that of the epiphyseal cartilage in the tubular bones. Synchondrosal growth continues until the bone is ossified.

The sphenoccipital synchondrosis unites by the age of 20 years, or somewhat earlier in the case of females, thus ending longitudinal growth of the base of the skull. Growth in thickness, on the other hand, originating from the periosteum, continues throughout life and thus allows deposition and resorption of bone to continue in response to functional needs.

The anterior and posterior intraoccipital synchondroses have already fused between the fifth and sixth years of life, the other synchondroses ossifying shortly before or after birth (Figure 1.18).

The growth activity of the synchondroses is controlled by the growth hormone (STH). This somatotrophic hypophyseal hormone stimulates the proliferation of cartilage cells. Overproduction of STH results in a lengthening of the base of the skull and after cessation to acromegaly, characterized by undue prominence of the nose and chin as well as oversized fingers and toes. An underproduction during the



**Figure 1.18** Cartilage growth centers of the skull.

growth phase leads to foreshortening of the base of the skull and thus to underdevelopment of the middle face. The sexual hormones are also believed to stimulate chondral growth.

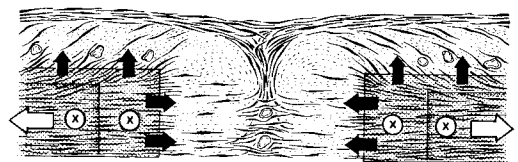
The significance of the cartilaginous nasal septum for craniofacial growth is disputed. The presumption that its growth continues throughout life is certainly erroneous. The nasal cartilage has a functional significance in reinforcing the nose, its growth activity ceasing by the age of maturity.

The cartilage in the symphysis menti retains its growth potential up to the first year of life. Of greater significance, however, is the joint cartilage of the head of the mandible. Its growth activity is traceable up to maturity.

## B. SUTURAL GROWTH

Sutural growth emanates from the osteoblasts of the connective tissue and is in this respect comparable with periosteal growth, the difference being that bone apposition takes place at the bone edges.

Active skull sutures can histologically be classified into differing zones, a cellular osteoblastic layer bordering the bone, a fibrous layer, and a middle zone (Figure 1.19). The last-mentioned zone contains numerous blood vessels and connects both the fibrous layers to one another. The active growth zone of a suture is thus to be found at the bone edges.



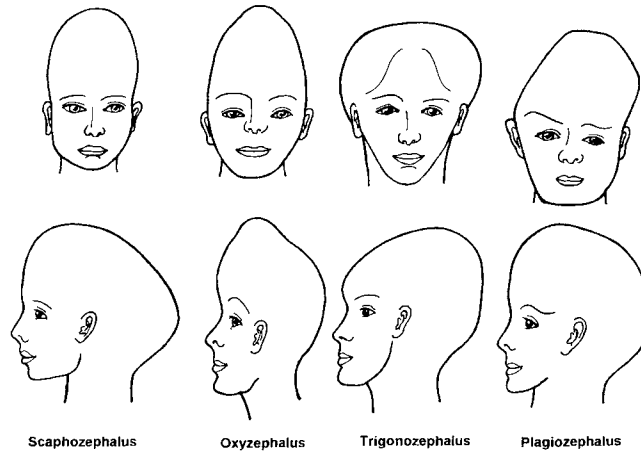
**Figure 1.19** The suture as a growth center. (After Enlow, DH: *The Human Face*, Harper and Row, New York, 1968. With permission of Harper Collins, Publishers, New York.)

By the onset of maturity the osteoblastic layer has for the most part disappeared, with a concomitant decrease in growth. The formation of ossified bridges over the sutures ends sutural growth, the lambdoid suture being the last to close sometimes between the ages of 40 and 50 years. In the sutures of the skull vault, independent ossification centers can also form and give rise to sutural bones.

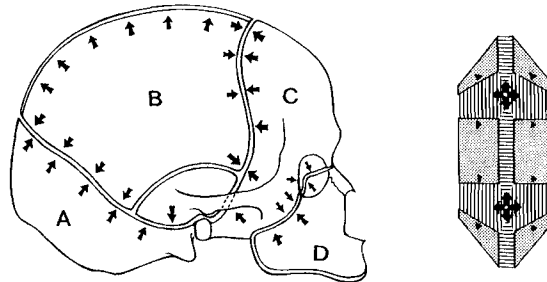
Premature fusion of the sutures (premature synostosis) leads to skull deformities (Figure 1.20). Premature sagittal suture synostosis manifests as scaphocephaly; premature symmetrical fusion of the coronal suture as oxycephaly (tower skull), asymmetric synostosis of the coronal suture as plagiocephaly, and premature fusion of the metopic suture as trigonicephaly (wedge skull).

According to Scott and Dixon (1978), the craniofacial sutures can be summarized as follows (Figure 1.21).

1. The lambdoid suture system divides the occipital squama from the parietal and temporal bones. The active growth impulse emanating from here affects mainly the back of the skull.



**Figure 1.20** Skull deformities following premature synostosis of sutures. (From Schumacher, G-H and Aumüller, G: *Topographische Anatomie des Menschen*, 6th ed., G. Fischer, Stuttgart Jena, 1994. With permission.)



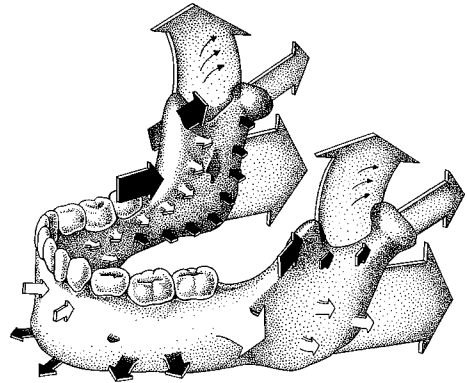
**Figure 1.21** Skull segments and an exploded schema of sutural growth in the cranial vault. (After Scott, JH and Dixon, AD: *Anatomy for Students of Dentistry*, 4th ed., Livingstone, Edinburgh, 1978. With permission.)

2. The coronal suture system runs between the frontal bone and the parietal bone by way of the skull vault and then down the lateral slopes to the cranial base. Here it divides and ends at the foramen lacerum. It promotes longitudinal growth of the skull.
3. The craniofacial and maxillary suture system divides the anterior section of the cerebral skull from the facial bones and possibly the upper jaw. The active growth potential emanating from here contributes to forcing the middle face down and forwards. Some sutures can remain open to an advanced age, which has a practical application in cases of upper jaw protrusion in adults.
4. The sagittal suture system follows the midline of the skull vault from posterior to anterior, and in the case of the neonate continues on between the frontal bones, nasal bones, and maxillae, right down to the mandibular symphysis. In the case of fetuses this sutural system connects to the synchondroses of the base of the skull. The sagittal suture system is mainly responsible for the growth in width of the cerebral and facial skull. Skulls in which the separate frontal bones persist tend towards broadheadedness and brachycephaly.

### C. PERIOSTEAL GROWTH

All resorption and deposition of bone during maturity is under the control of the periosteum and, to a lesser extent, the sutures. Periosteal growth depends on the laying down of bone by osteoblasts. On the cranial vault, deposition on the convex surface ensues in concert with bone resorption by osteoclasts on the concave surface. This process of balanced apposition and resorption facilitates skull vault growth. Should apposition and resorption occur with differing intensities, deformities or remodeling of the skull follows (Figure 1.22). This process is also of great significance for proportional growth as well as for the structuring of the nasal and nasal sinus cavities, as well as the orbits.



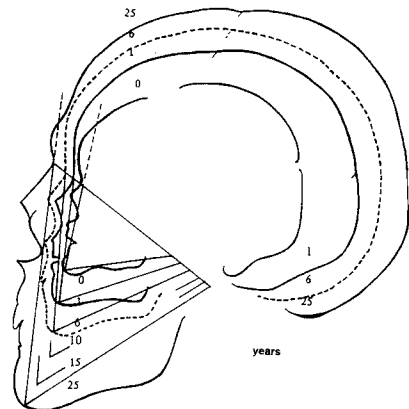


**Figure 1.22** Periosteal growth on the lateral and medial aspects of the lower jaw. (After Enlow, DH: *The Human Face*, Harper and Row, New York, 1968. With permission of Harper Collins, Publishers, New York.)

The bones of the skull vault of the newborn consist of only one layer. The typical triple layering of lamina externa, diploe, and lamina interna arises only in childhood.

## VI. DIMENSIONAL GROWTH

The cranial and facial skulls grow at different speeds (Figure 1.23). In the newborn the cerebral skull is much better developed than the facial skull. The orbits are relatively wide and the maxilla is still undeveloped so that the face of a neonate appears low and wide.



**Figure 1.23** The changing proportions of skulls following birth.

The rate of cranial growth is most rapid in the first year of life, especially in the first six months. Head circumferences are typically:

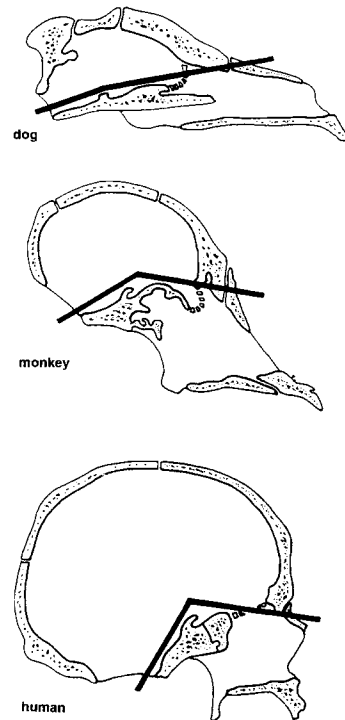
- in the newborn, around 34 cm
- at the end of the first six months, around 43 cm
- at the end of the first year, around 46 cm
- at the end of the second year, around 48 cm

### A. NEUROCRANIUM

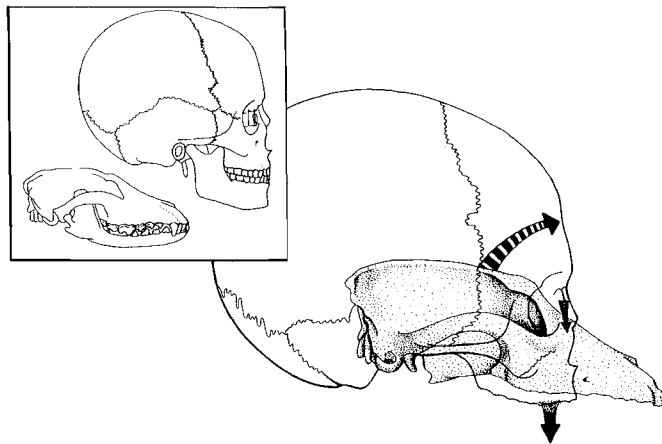
The growth of the cranium is closely connected to that of the brain, which nearly achieves its final size by the age of 10 years.

The slower growth of the base of the skull with regressive migration of the foramen magnum and the elevation of the occiput follows the more rapid expansion of the cranium.

The term “base of the skull” denotes that part which connects the skull vault and the facial skull. Its defining feature is the flexure of the cranial base, measured by ascertaining the flexion angle (Figure 1.24). In comparison to the skulls of quadrupeds, the skull base angle in humans is relatively small. This is believed to be mainly due to the upright posture, the increase in volume of the brain as well as the frontal positioning of the eyes, a consequence of stereoscopic vision (Figure 1.25). The postnatal changes in proportion to the human cranium also result in a smaller basal flexion angle.



**Figure 1.24** Angulation of the skull base in human, monkey, and dog. (From Schumacher, G-H: *Anatomie, Lehrbuch und Atlas*, Edition Zahnheilkunde. J.A. Barth, Leipzig, 1991, Vol.1. With permission.)

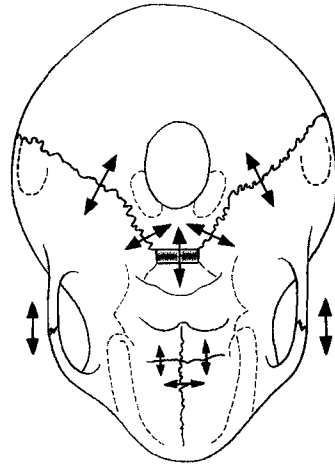


**Figure 1.25** The changing proportions of the human skull as compared with the skull of the dog. (After Enlow, DH: *The Human Face*, Harper and Row, New York, 1968. With permission of Harper Collins, Publishers, New York.)

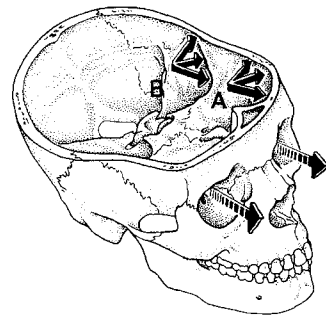
Cerebralization mainly comes about through the development of the telencephalon. The brain stem, which is topographically assigned to the region of the sphenoid bone approximately in the center of the cranial base, evinces on the contrary a relatively conservative growth, being the oldest part of the brain, phylogenetically.

The skull elongates through an increase in size of the frontal lobes and increases in width through development of the temporal lobes with consequent downward movement of the surrounding parts of the cranial base and the repositioning of the facial skull towards the front.

The growth pressure of the brain also affects the synchondroses and sutures, stimulating chondral and sutural growth (Figure 1.26). Periosteal growth is, however, also activated and effects the deepening of the skull fossae (Figure 1.27).



**Figure 1.26** The role of synchondroses and sutures in the expansion of the cranial base. (After Scott, JH and Dixon, AD: *Anatomy for Students of Dentistry*, 4th ed., Livingstone, Edinburgh, 1978. With permission.)



**Figure 1.27** Expansion of the anterior and middle cranial fossae (arrows A, B) causing a rotation of the orbital long-axis towards the midline. As a sequel, the orbit is itself displaced forwards. (After Enlow, DH: *The Human Face*, Harper and Row, New York, 1968. With permission of Harper Collins, Publishers, New York.)

For the purposes of measurement the skull is conventionally divided into three segments:

- The frontal segment is the area between the foramen caecum and the nasion. It grows until maturity under the influence of the expanding frontal sinus.
- The middle segment lies between the sella turcica and the foramen caecum. It achieves its final size at the latest at the age of 7 years. Its extension leads to the middle fossa and the middle face being pushed forward.
- The posterior segment is that part of the skull between the sella turcica and the foramen magnum. It contains the sphenoid-occipital synchondrosis which is of prime importance for longitudinal growth, and remains active up to the age of 20 years.

The steady growth of the cranial base, and especially the area nasion–sella, after the age of 7 years means that it is often used as a point of reference for growth studies.

## B. VISCEROCRANIUM

In early infancy the growth of the facial skull is slow. The lengthening of the base of the skull, accompanied by the extension of the frontal lobes, and especially of its anterior part take place at the same time as the full development of the toothbuds and the eruption of the deciduous teeth. The eruption of the 6-year molars signals another reduction in the rate of growth.

Another growth spurt is signaled by the eruption of the 12-year molars in association with the greater functional demands of the masticatory muscles and the increasing pneumatization of the nasal sinuses. The facial skull is reformed, achieving its final form only after the eruption of the permanent teeth.

The reportioning of the facial skull is attributable especially to the increase in size of the upper and lower jaws. The increase in height of the maxilla is caused by the formation of the maxillary sinus and of the alveolar process. The tooth buds in the case of the newborn are to be found in the relatively small body of the maxilla. The tooth buds of the upper first deciduous molar are found under the floor of the orbit. The formation of the alveolar process accompanies the movement of the tooth buds downwards, the palate becomes longer, wider, and its curvature increases significantly.

The growth impulse intensity in the upper and lower face differs. The upper face exhibits in the first instance after birth a faster growth, which is attributable to its connection with the cranium. This rate then diminishes considerably and becomes very slow after the 12th year.

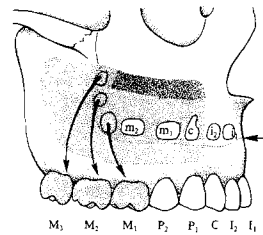
The middle face, in contrast, initially grows more slowly. Up to the age of 7 years its growth is controlled mainly through the craniofacial and maxillary suture systems as well as in part by the synchondroses and the cartilaginous nasal septum. After the seventh year periosteal growth then predominates.

The vertical growth of the middle face is then concomitant with the development of the nasal region. The upper ethmoidal segment has its complete growth period in early childhood under the influence of the developing olfactory mucous membrane.

The growth of the lower maxillary part is mainly stimulated by nose breathing and persists until the end of childhood. The functional impulse of nose breathing causes a widening of the lower nasal passages, this being a precondition for uninhibited nose breathing. In the case of obstruction of the nasal air passages, as for example, in excessive growth of the pharyngeal tonsils (adenoid vegetation), growth disturbances of the middle face occur. The palate is pushed downwards by resorption on the nasal side and bone apposition on the oral side.

The development of the alveolar process on eruption of the teeth leads to a further increase in size of the middle face and thus contributes to vertical growth.

The growth in depth of the middle face originates through periosteal bone apposition on the outer surface with concomitant resorption in the orbital cavities, the nasal cavity, the nasal sinuses, and the oral cavity. The main growth originates through bone apposition from on the posterior aspect to the maxillary tuberosity. The initial growth promoting stimuli arise with the development and eruption of additional teeth (Figure 1.28). Appositional growth at the maxillary tuberosity ceases after the eruption of the upper third molar (about the age of 18 years).



**Figure 1.28** Changes in the growth of the upper jaw following eruption of the teeth. (After Keith, A: *Human Embryology and Morphology*, 3rd ed., Edward Arnold, London, 1913. With permission.)

Complementary morphogenetic changes occur with regular, proportional apposition and resorption on the surrounding bones such as the lacrimal, palatine, vomer, and pterygoid process of the sphenoid bone. The stimuli controlling onset are here considered to be the compressive and decompressive forces resulting from the chewing action on the bone, these also leading to the formation of the masticatory pressure trajectories (Figure 1.14a).

The enlargement of the palate originates from the activity of the median palatine suture, and the transverse palatine suture, and goes hand in hand with the development of the alveolar process which grows downwards and outwards as well as backwards with the development of additional teeth. The incisive suture plays a very minor role in this, for it normally ossifies shortly after birth. The shaping of the palate depends not only on the alveolar process, but also on the type of breathing. Mouth breathers usually have a higher palate.

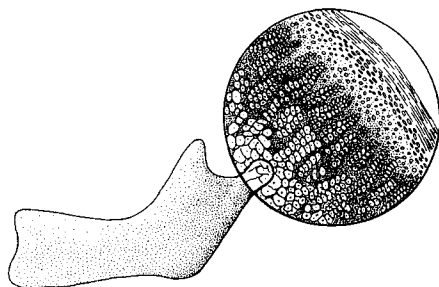
### C. LOWER JAW

The lower jaw is the bony base of the lower face. By its mode of ossification it belongs to the desmocranium. Ossification begins in the middle of each half jaw and proliferates both mesially and distally. The mandibular head and chin region are the exceptions, arising through chondral osteogenesis in secondary cartilage (Figure 1.29).

The secondary cartilage forms in the tenth week and is viewed as a cartilage growth center which is hormonally dependent, in the same way as the synchondroses. Reduced production of the growth hormone (STH) leads to micrognathia and overproduction to mandibular protrusion. Cases of unilateral disturbance of condylar growth, such as from trauma, result in lateral mandibular displacement.

The cartilage of the symphysis menti disappears with the synostosis of both halves of the lower jaw. The growth potential of the condylar cartilage persists, however, up to the age of maturity, although to

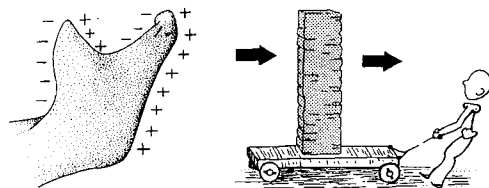
**Figure 1.29** The articular cartilage of the mandible as a growth center. (After Schumacher, G-H: *Anatomie, Lehrbuch und Atlas*, Edition Zahnheilkunde. J.A. Barth, Leipzig, 1991, Vol.1. With permission.)



a lesser degree. The lower jaw ramus extends up and backwards and the jaw angle lessens. This process is enhanced by periosteal bone deposition in the region of the angle of the jaw.

The lower jaw is displaced outwards by bone apposition on the posterior edge of its ramus including the head, by balanced resorption on its leading edge, as well as by formation of the chin (Figure 1.30). Bone deposition on the lower border of the mandible as well as the formation of the alveolar process cause downward growth at the same time. These growth movements are recognizable also from the change in direction of the mental foramen. The originally right-angled projection changes with increasing growth to point backwards and upwards, resulting in the sharper anterior edge of the mental foramen.

**Figure 1.30** The changing form of the mandible following periosteal resorption and apposition. (After Schumacher, G-H: *Anatomie, Lehrbuch und Atlas*, Edition Zahnheilkunde. J.A. Barth, Leipzig, 1991, Vol.1. With permission.)



Growth movement of the lower jaw in a downward and forward direction is partially compensated by the ventral displacement of the mandibular fossae on the base of the skull.

The lower jaw of the newborn has a relatively large corpus, the mandibular ramus in contrast being largely underdeveloped. In the corpus of the mandible the tooth buds are found. The corpus increases greatly in height on formation of the alveolar process and the strengthening of the base of the lower jaw. The increase in thickness of the base of the lower jaw is in reaction to the greater mechanical bending stresses made on the mandible.

The loss of height at the chewing level is counterbalanced by the extension of the upwardly mobile lower jaw ramus, the jaw angle concomitantly changing. At around  $140^\circ$  in newborns it is still relatively large, reducing to approximately  $120^\circ$  after eruption of the permanent teeth. The reduction of the angle of the mandible also results in an increased resistance to bending of the lower jaw.

Bone protuberances, the masseteric tuberosity and the pterygoid tuberosity, arise on the exterior of the jaw angle as well as on its inner surface with the increase in activity of the masticatory muscles. The coronoid process, to which the tendons of the temporalis muscle attach, elongates and deepens the mandibular notch.

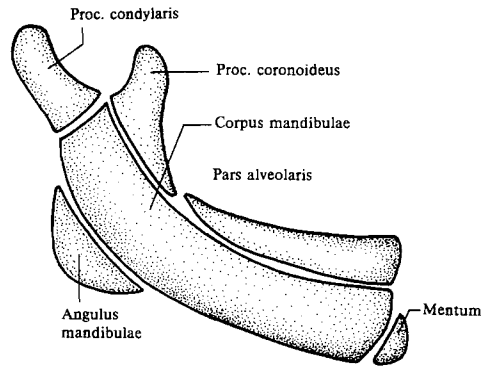
Increased bone resorption above the chin leads to the formation of a depression anthropologically known as the supramentale and as the S-Point (after Downs) in jaw orthopedics.

The lower jaw can be divided into different functional areas on the basis of specific growth stimuli (Figure 1.31). These are:

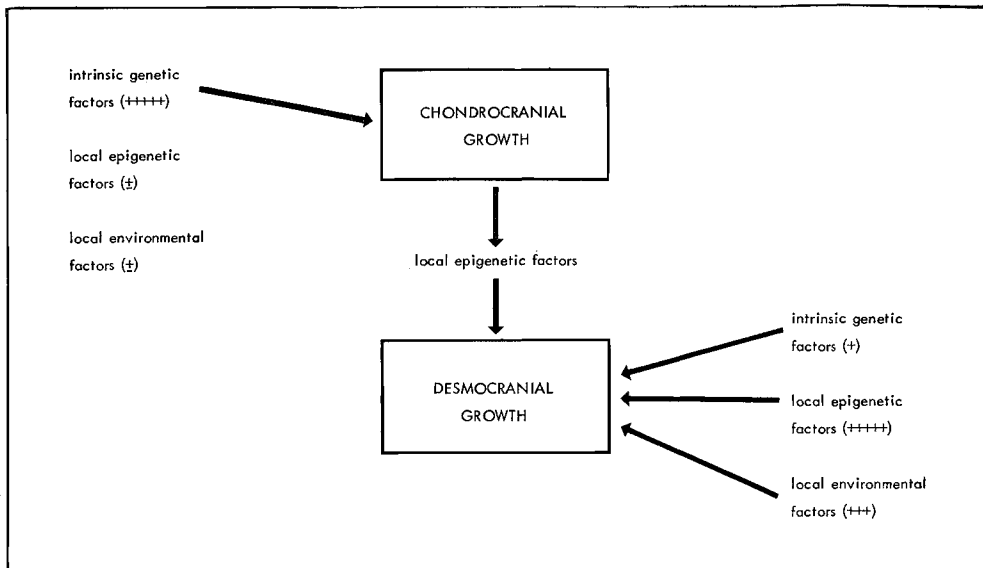
- The *condylar process*, which grows under the influence of the temporomandibular joint,
- The *coronoid process*, which extends under the traction of the temporal muscle,
- The *alveolar parts*, which form with tooth eruption,
- The *mandibular angle*, which is strengthened under the tensile force of the masseter-ptyergoid loop, and
- The *mental protuberance*, which arises under the influence of the tension of the basal arch.

## VII. REGULATORY FACTORS OF BONE GROWTH

The control of craniofacial growth is a very complicated process. The growth of the chondrocranium is in the main genetically determined and is stimulated by the growth hormone (STH). Growth of the desmocranium, on the other hand, is more under the influence of local factors (Figure 1.32). Moss (1958)



**Figure 1.31** The functional, embryological parts of the mandible as an example of the functional matrix. (After Sperber GH: *Craniofacial Embryology*, 3rd ed., Wright, Bristol, 1981. With permission.)



**Figure 1.32** Cartilage and membranous growth under the influence of genetic and epigenetic factors as well as local environmental factors. (After Limborgh, J van: The role of genetic and local environmental factors in the control of postnatal craniofacial morphogenesis. *Craniofacial Conference, Nijmegen*, The Netherlands, 1972, 47–58. With permission.)

has made a functional summary which he denotes as a “functional matrix.” There is a close connection between chondro- and desmocranial growth.

The bones of the skull are still constantly remodeled even after growth has ceased. Bone deposition and resorption behave as a self-compensatory system. If demand is constant, apposition and resorption are in equilibrium (dynamic equilibrium). Increased stimuli result in bone deposition, lack of stimuli in bone resorption (Figure 1.16). With advancing age physiological decline in bone tissue takes place (age atrophy).

### A. BIOMECHANICAL ASPECTS OF SKULL MORPHOGENESIS

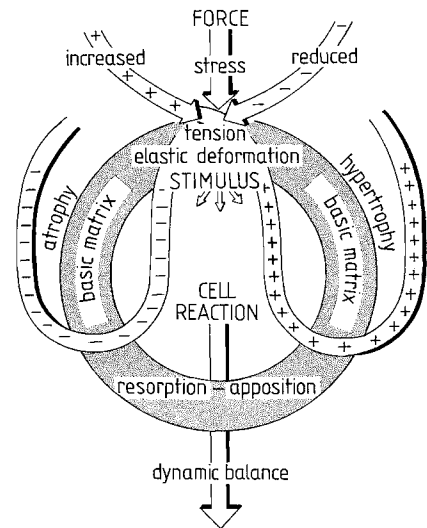
Numerous authors have attempted to elucidate the general principles and laws governing growth. It is frequently characterized as a genetically and hormonally-controlled irreversible increase of living organic substance, that can also be modified by environmental influences within the bounds of inheritance. Linzbach (1955) established the quantitative morphology and biology of growth. Wurmbach (1967) analyzed the operating forces. The publications of Bertalanffy (1951) as well as Bertalanffy et al. (1977), according to which the rate of growth depends on the interplay of anabolism and catabolism at the time in question, established the zenith of theoretical observations from a biochemical and systems viewpoint.

The origin of formative influences lies in genetically controlled growth processes. Differing growth rates of individual head system correlates lead to differing volume requirements as a function of time, which Roux (1895), for example, called “the struggle of the organs for space.”

Osteogenesis of the skull has only a few mechanisms at its disposal for the creation of pressure. These are to be found within the synchondroses and sutures, where hydraulic pressure in Wurbach's sense (1967) is produced. Bone, in contrast to cartilage, displays no swelling growth and can thus exert no moment of force. Sutural growth responds primarily to mechanical environmental influences. The appositional and resorptive processes at the periosteum are also controlled by the volume requirements of the surrounding components. According to Kummer (1980), shear stress is identifiable as the initiator of this. Genetic influences on periosteal growth have been clearly shown by Bateman (1954). Epigenetic factors emanating from the structures surrounding the bone play a major role here.

Pauwels (1965) has researched the significance of mechanical influences on bone, critically examining the theoretical hypotheses of Wolff (1884, 1892) and Roux (1895).

Deposition and resorption of bone are regulated by the tensions emanating from the bones themselves, the whole arising by means of a dynamic equilibrium (Figure 1.33). Resorptive changes predominate under a critical value and the restoration of bone tissue is a response to tensions above a certain critical value. The reactive ability of bone is seen as a regulatory system, tension being the main governing factor in the maintenance of constancy. The direction and size of demand create disturbing forces which are the agents of change.



**Figure 1.33** Scheme of bone reaction to the action of mechanical stresses of different magnitude. (After Kummer, B: Funktioneller Bau und funktionelle Anpassung des Knochens. *Anat. Anz.*, 1962, 110:261. With permission of Fischer, Jena, Stuttgart.)

Though this interplay has been well established in numerous experiments, it is still not known what causes the cells to react appropriately. Roux (1895) considered the elastic deformation of the cells as the decisive factor. Kummer (1962) considered the compression of the elementary particles of bone to be the determining process. Currently, it is believed that the electrical polarization which arises in biological systems as a result of mechanical deformation is of significance for the control of cell behavior.

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# Evolution of Form in the Craniofacial Complex

Ordean J. Oyten

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## I. PREFACE

*"Just as the clinician needs the medical history of a patient to make a logical diagnosis, so too the evolutionary history of a biological construct is essential for a logical explanation of its function and dysfunction."*

E. L. DuBrul, Origin and adaptations of the hominid jaw joint, 1992.

## II. INTRODUCTION

The goal of this chapter is to demonstrate how a comparative, evolutionary approach can yield insight and perhaps alternative thoughts about the age-old question, "Why do we (humans) look the way we do?" Towards this goal, consider three subsidiary questions: (1) What do we look like now? (2) What did we look like in the past? and (3) What can the examination of extant and fossil primates tell us about the way we look?

These are not trivial questions given the critical functions carried out by craniofacial structures and the importance of the face in establishing personal identity. Moreover, dental and medical specialists are becoming increasingly involved in procedures that affect craniofacial function and appearance. Hopefully, consideration of the evolution of form in the craniofacial complex will lead the reader to new insight about how structure and function of the face is clinically relevant as well scientifically interesting.

We begin by conducting a comparative examination of skulls from modern humans and two Great Apes, chimpanzees and gorillas, generating a list of attributes distinctive to human craniofacial anatomy. We then review the fossil record, concentrating on the past 4 million years or so. Information about functions and behaviors associated with adult and growing extant primates is subsequently used to draw inferences about the functional significance of anatomical features and changes therein seen in the fossil record. Particular consideration is given to the masticatory apparatus. In some instances, information obtained in the course of this comparative evolutionary analysis can be used to clarify or dispel mistaken notions about human craniofacial morphology; we also show how knowledge gained in this manner can provide new insight into modern human anatomy.

When contemplating the questions around which this chapter is organized, we follow the convention of subdividing the skull into the neurocranium and the viscerocranium, then further parceling these two basic units into the individual structural-functional components which comprise them. In our analyses, the head is treated as a three-dimensional mosaic made up of components, each of which can be individually identified and described, but whose significance can only be really understood in terms of their relationships with each other. In most instances, a top-to-bottom approach is taken, beginning with the most superiorly placed structure and working downward, ending with the dentition. A descriptive mode is used to address the first two questions, whereas a more analytical approach is used in discussion of the last question; throughout, a "form follows function" perspective prevails.

Many of the findings and interpretations offered are original, based on collective personal experience over several decades of studying craniofacial anatomy. While considered in the context of a broad body of published literature that ranges from early work by Wood Jones (1916) to recent publications by Kimble, Johanson, and Rak (1994), this effort still only provides a brief review of an incredibly complex and exciting topic. Readers interested in more detailed analyses are encouraged to consider the end-citations, especially the volumes by Rak (1983), Aiello and Dean (1990), and Walker and Leakey (1993).

## III. "WHAT DO WE LOOK LIKE NOW?"

*"The mobile mask in front of men's brains began to attract our attention when we were babies and continues to fascinate us as long as we live."*

W.K. Gregory, *Our Face from Fish to Man*, 1929.

Even a cursory comparison of a modern human skull with that of a modern gorilla or a chimpanzee shows some striking differences (Figures 2.1–2.3). The face, teeth, and jaws of the human viscerocranium seem significantly smaller; the human neurocranium, with its vertical forehead, bulbous occiput, and smoothly rounded cranial vault appears much larger; and the foramen magnum is located more centrally under the skull in humans than in the other two apes. Closer inspection yields numerous other differences and similarities among modern humans and the apes. Before proceeding however, it should be noted that, as pointed out several decades ago by Le Gros Clark (1959), "it would be wrong to say that these are the diagnostic characters whereby *man* differs from *apes*." As we shall see when the fossil record is reviewed, there are physical attributes in apes (pongids) that are also present in our fossil human (hominid) antecedents. When considered *en toto* comes the realization that modern humans still have numerous traits in common with other primates, extant and extinct, and that our uniqueness stems from the *combination* of traits we possess rather than from singular features.

Figure 2.1

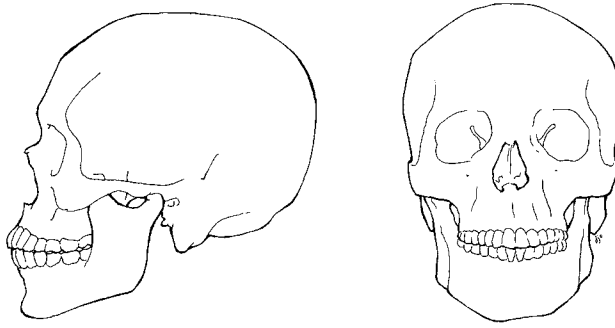


Figure 2.2

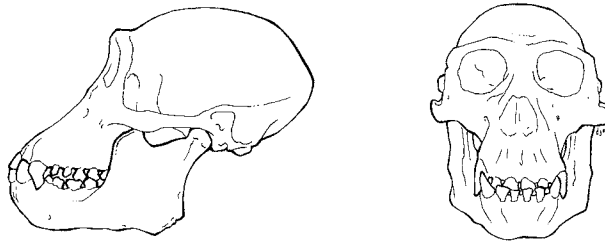
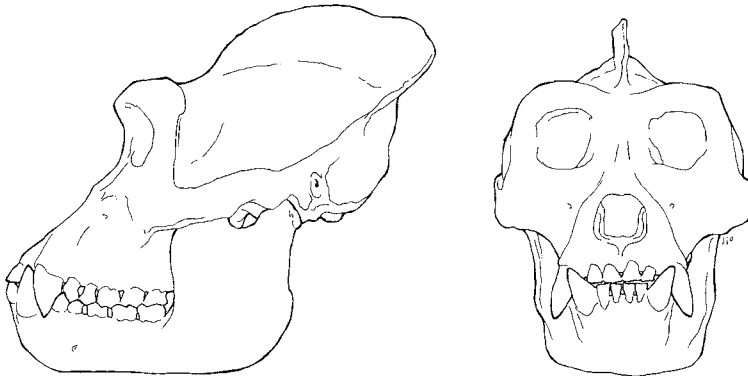


Figure 2.3



**Figures 2.1, 2.2, and 2.3** Frontal and lateral views of adult skulls from a modern human (Fig. 2.1), a male chimpanzee (Fig. 2.2), and a male gorilla (Fig. 2.3).

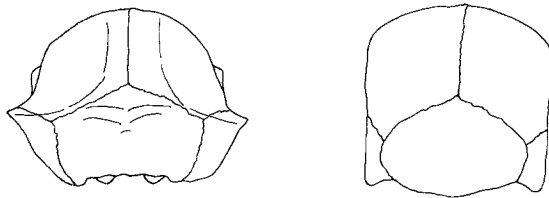
### A. NEUROCRANIUM

The average cranial capacity, i.e., the volume formed within the bony enclosure of the brain, in modern adult humans is about 1500 cc. This volume is three to four times greater than that seen in contemporary chimpanzees or gorillas. A striking feature common to adult gorillas and male chimpanzees but absent in humans, is the manner in which the lamina externa (outer table) of the neurocranium forms sagittal and nuchal crests. Besides lacking these crests, the human neurocranium is not simply a larger version of that seen in gorillas or chimpanzees; there are also significant differences in the shape of the cranial vault. For example, in humans the anterior cranial fossa is wider and spreads anteriorly so that it overlies the orbits and nasal region. The vertically rising frontal bone of forehead forms the anterior superior enclosure of this fossa. (Chapter 11 provides a discussion of the ontogeny of the cranial base and its effects on skull growth.)

Bony support of the expanded, bulbous posterior cranial fossa in humans is provided by the basi-occipital bone, which forms a good one-third of the cranial floor and which is bounded anteriorly by the foramen magnum. The large proportion of the occipital bone posterior to this foramen accounts for

much of its anterior displacement underneath the skull. In gorillas and chimpanzees the occipital squamous rises quickly to the level of the nuchal crest, cupping a relatively smaller posterior cranial fossa. Due in part to the small size of the occipital squamous, the foramen magnum in the apes is displaced more posteriorly than in humans.

The middle cranial fossa in humans is larger in every direction than in any of the great apes. The greater wing of the sphenoid, which forms the anterolateral floor and wall of the human fossa, is expanded anteriorly-posteriorly; its anteromedial aspect extends superiorly, accompanying the lesser wing to the level of the orbital roof. In chimpanzees and gorillas this delicate bone is smaller and contributes less to the bony enclosure of the orbits. The lamina externa of the greater wing provides a larger area of attachment for the middle and anterior components of the temporalis muscle in humans than in either of the apes. When compared with gorillas, the floor of the human middle cranial fossa, lateral to the sphenoid clivus and consisting of the petrous and squamous portions of the temporal bone extends laterally, roofing over most of the temporomandibular joint, less so in chimpanzees and gorillas. In both of the great apes, the walls of the middle cranial fossa formed by the lamina interna of the temporal squamous *converge* as they rise towards the parietal bones. In humans the walls *diverge*. In other words, the transverse diameter of the middle cranial fossa within the cranial vault in chimpanzees and gorillas *decreases* as one ascends the temporal squamous. This dimension *increases* in encephalized humans and continues to do so well up onto the parietal bones. Consequently, the widest part of the human neurocranium is found in the region of the parietal bosses, approximately at the boundary between the middle and posterior cranial fossae. The widest intracranial dimension is much lower in pongids, in the region where the petrous and squamous components of the temporal bones are joined (Figure 2.4.)



**Figure 2.4** Posterior views of skulls from an adult male chimpanzee and an adult human, drawn with the specimens oriented in the Frankfort Horizontal. In this position the steeply angled occiput and the flaring nuchal crest would obscure the rest of the skull in gorillas.

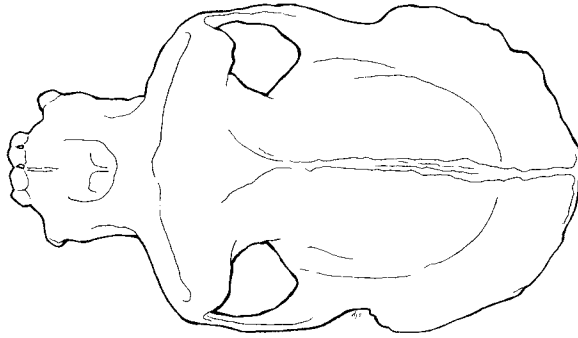
Mastoid processes are present in all three species, where they tend to be more robust in the males. In chimpanzees and gorillas the processes are triangular in shape and quite flat, whereas in humans they are ovoid and strongly convex. A highly pneumatized mastoid process can project well below the Frankfort plane, sometimes extending so far inferiorly that it breaks the occlusal plane, commonly occurring in adult humans. In contrast, the bulk of the mastoid process in chimpanzees and gorillas is located superior to this plane, where it may project posterolaterally as a continuation of the nuchal crest.

Inferior projection of the mastoid process in humans in the manner just described is related in part to flexure of the cranial base, the final neurocranial feature that will be mentioned. The geometry and mechanics of this flexure occurs in the spheno-occipital region of the cranial base, where the basilar portion is “bent” anteriorly relative to the remainder of the sphenoid body. Bending in this manner, which occurs to the fullest extent in humans, causes components attached to the cranial base posterior to the point of bending to be displaced anteriorly and inferiorly relative to the remainder of the skull. Because the basal flexure is more exaggerated in humans than in chimpanzees or gorillas, our mastoid process is positioned differently than in either of the Great Apes. In humans (and several other encephalized primates), the angle formed at the intersection of a line extending posteriorly from Frankfort Horizontal with a second line projecting through the foramen magnum along the functional axis of the vertebral column approximates  $90^\circ$ ; the external acoustic meati are in approximate alignment with the occipital condyles. In contrast, in the Great Apes this angle is obtuse and the meati are *always* located anterior to the condyles. Also, compared to humans, in the apes there is relatively little cranial anatomy located posterior to the condyles.

## B. VISCEROCRANIUM

The viscerocrania in chimpanzees and gorillas are strikingly large, especially so if the relative size of the neurocranium is taken into consideration. When viewed in profile (Figure 2.3), the contributions of large supraorbital ridges and prognathism of the mid- and lower face to robust facial appearance in the pongids is obvious. The combination of large browridges, maxillary prognathism, and a lack of bony protuberances in the nasal region in these animals gives them a decidedly concave facial profile. By comparing the three profiles (Figs. 2.1–2.3) one can infer that mesial displacement of the cheek teeth relative to the maxillary root of the zygoma accounts for some of the prognathism seen in the chimpanzees and gorillas. Other features that contribute to dentofacial prognathism in these species are the relative procumbency of the premaxillae and their dentition, the large maxillary canines, and the diastemata between the canines and lateral incisors which accommodate the protruding, enlarged mandibular canines.

When viewed from directly above with the gorilla skull positioned in the Frankfort Horizontal, the projection of the maxillary region beyond a vertical plane drawn at the anterior margins of the orbits is clear (Figure 2.5). In addition, the strong bony ridges that overlie the large canine roots, the boxy outline of the maxillary dental arch, and the canine diastemata are clearly present. In contrast, the protruding nasal bones common to humans are wholly lacking. Other ape-like features are large infratemporal fossae, which are marked anteriorly by the robust supraorbital ridges, laterally by well-developed zygomatic arches, and medially by a distinct postorbital constriction.



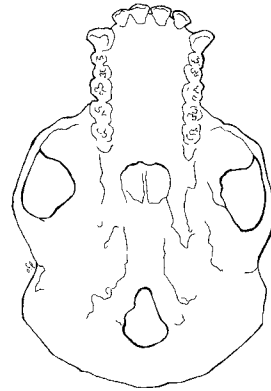
**Figure 2.5** Superior view of an adult male gorilla. The neurocranium proper is bounded by the infratemporal fossae and posterior orbital constriction anteriorly and massive nuchal crests, which encircle the vault posterolaterally.

With regard to the temporomandibular joint, in modern humans the glenoid fossa is deeper and the articular eminence is more pronounced; however, the posterior tubercle and entoglenoid process are less well developed. In contrast to the human condition, the articular surface of the joint is flat, with an anterior-superior slope in both chimpanzees and gorillas. As already indicated, in humans the temporomandibular joints are positioned *under* the cranial vault, medial to the body of the temporalis musculature; in pongids the joints are laterally displaced relative to the vault and musculature. (Chapters 5, 8, and 17 give further information about the temporomandibular joint.)

The pterygoid plates and maxillary tuberosity serve as areas of attachment for the pterygoid musculature. Based on examination of adult skulls over the years, the bony union between the pterygoid plates and maxillary tuberosity tends to be more extensive and the size of the pterygoid fossa and fissure reduced in chimpanzees and gorillas.

The chimpanzee palate is relatively shallow, especially so anteriorly; it is approximately twice as long as it is wide, with its greatest width occurring in the region of the premolars and canines; the dental arcade is arranged in parallel tooth rows (Figure 2.6). While generally larger, these shape arrangements hold true for the palate in gorillas. In contrast, the human palate is relatively deeper throughout its length and the parabolic dental arcade diverges posteriorly, making the posterior width of the palate almost equal to its length.

There are several features that can be used to distinguish between modern pongid and hominid mandibles. For example, the human lower jaw is much less robust, and the mandibular (gonial) angle is more open. Judging from Figures 2.1–2.3, this angle varies from about  $120^\circ$  in the human to  $95^\circ$  in the gorilla, with the chimpanzee falling in between at approximately  $105^\circ$ . Human mandibles characteristically



**Figure 2.6** Palatal view of an adult male chimpanzee.

have a mental eminence (chin) and they lack the bony re-enforcement or “simian shelf” that occurs on the lingual aspect of the mandibular symphysis in chimpanzees and gorillas. Mirroring the maxillary arch, the mandibular dental arcade in *Pan* and *Gorilla* has parallel sides which may be slightly convergent posteriorly; small diastemata may be seen between the enlarged mandibular canines and the lateral incisors.

The last features of the viscerocranium to be considered are the teeth. In addition to observations based on our comparative specimens, some of the descriptions which follow are derived from work by Swindler and Wood (1975) and Le Gros Clark (1959): following an ancient anthropoid evolutionary pattern, humans, chimpanzees and gorillas have the same dental formula, 2-1-2-3, i.e., in one dental quadrant they have 2 incisors, 1 canine, 2 premolars, and 3 molars. Because anthropoids have lost the more ancient first and second premolars as part of the evolutionary process, the first two permanent teeth positioned distal to the canines in modern humans and apes are properly referred to as the third and fourth premolars, abbreviated PM3/PM4.

Reflecting their premaxillary procumbency, the upper incisors tend to be more procumbent in gorillas and chimpanzees than in humans. In all three species the incisors are relatively broad, with the lingual surface of each tooth marked by raised enamel marginal ridges separated by a shallow fossa. Also common to each species, the maxillary central incisors tend to be larger than the laterals, whereas in the mandible the lateral incisors are larger than the centrals.

Sexual dimorphism in canine size and shape is characteristic of both chimpanzees and gorillas, but it occurs only to a limited degree in the much smaller human canines. In contrast to the spatulate shape and unremarkable size seen in humans, chimpanzee and gorilla canines are conical in shape, and crown length can easily be twice that of the adjacent teeth. While human canines wear along their occlusal surfaces just like the incisors and postcanine teeth, in chimpanzees and gorillas canine wear occurs differently. The distobuccal surface of the mandibular canines hone against the mesiolingual surface of the maxillary canines; the distolingual surface of the maxillary canines hone against the mesiobuccal surface of the third premolars. Depending to some extent on the amount of sexual dimorphism seen in the canines, the mandibular third premolars are heteromorphic and sectorial, thereby providing the cutting/honing surface for the maxillary canines. All of the premolars in humans, all the maxillary premolars, and all the fourth premolars in chimpanzees and gorillas are bicuspid, with the buccal cusps larger than the lingual cusps; in humans one cannot reliably distinguish between the premolars based on size. Humans, chimpanzees, and gorillas resemble each other in terms of cusp topography, but humans have lower, more rounded cusps on their molars. In humans, the first molars are the largest, followed by the second molars, with the third molars being the smallest; in chimpanzees and gorillas the third molars tend to be the largest, but there is considerable variability. Based on absolute size, human and chimpanzee molars overlap each other, whereas gorilla molars can easily be twice as big as those seen in the other two species.

#### IV. “WHAT DID WE LOOK LIKE IN THE PAST?”

*“In human paleontology there are often more opinions and interpretations than there are fossils.”*

L.C. Aiello, Variable but singular; *Nature* 368:399–400, 31 March, 1994.

Further to this astute observation by Aiello, it seems that the closer paleontologists get to the time of *human* origins, the greater the intensity with which these opinions and interpretations are held and defended. Because we are dealing with fossil forms of the time period leading up to the appearance of modern humans, it must be understood that my purpose is neither to elucidate the phylogeny of human origins nor to champion any particular taxonomic interpretation.

In much the same way that we compared chimpanzees, gorillas, and humans without making assertions about affinities among these species, now we dispassionately describe some of the fossil hominids known to have existed over the past 3 to 4 million years. We then speculate about the significance of the structural arrangements revealed in the fossils. Setting the stage for the last part of this chapter, we conjecture about the biologic processes that must have been involved in the evolutionary transformation of some of these fossil hominids into modern *Homo sapiens*.

### A. FOSSIL HOMINIDS

The major groupings of fossil hominids to be considered, along with their approximate periods of existence are shown in Table 2.1. *Largely because of contentiousness associated with their taxonomic classification, I have elected to exclude Neanderthals from consideration in this chapter. Information about this problematic hominid with its extraordinary craniofacial anatomy is readily available, e.g., Trinkhaus and Shipman 1992.*

**TABLE 2.1** Hominid Fossils from the Time Period Extending from Approximately 0.5 to 4.5 Million Years Ago

Genus/species	Estimated periods of existence, in millions of years ago (MA)
<i>Australopithecus ramidus</i>	4.4 – 3.5
<i>Australopithecus afarensis</i>	4.0 < 3.0
<i>Australopithecus africanus</i>	3.0 – 2.5
<i>Australopithecus robustus</i>	2.5 – 1.5
<i>Australopithecus boisei</i>	2.5 – 1.2
<i>Homo habilis</i>	1.9 – 1.5
<i>Homo erectus</i>	1.8 – 0.5
<i>Homo sapiens</i>	0.1 – present

The first broadly acknowledged hominid *Australopithecus afarensis* is known from specimens that date from the period 4 to less than 3 million years ago (Ma). Other australopithecines, *A. africanus*, *A. robustus*, and *A. boisei*, are known to have existed from 3 to 1.2 Ma, respectively. A fifth hominid, *Homo habilis* has been dated from 1.9 to 1.35 Ma; and a second member of the genus, *Homo erectus* is known from fossils aged 1.8 to 0.5 Ma. The earliest fossils from modern appearing *Homo sapiens* are known from about 0.1 Ma. Bearing in mind that we do not champion any particular phylogenetic interpretation, we generally subscribe to the idea that our lineage is one which goes *A. afarensis* > *A. africanus* > *H. habilis* > *Homo erectus* > *H. sapiens*, and which excludes *A. robustus* and *A. boisei*. A cluster of some 17 hominid fossils, discovered in Ethiopia by White et al., (1994) and named *A. ramidus* (meaning root), apparently predates *A. afarensis* by 0.5 Ma and is the most recent claim to be the earliest human ancestor.

Historically, much has been made of the purported role of bipedal posture in the acquisition of human traits. As Wood Jones (1916) averred years ago, skeletal adaptations that accommodate a vertically positioned vertebral column is an ancient primate trait that precedes the emergence of hominids. While Aiello and Dean (1990) have shown that there is no clear relationship between posture and the position of the foramen magnum, based on postcranial fossil evidence associated with *A. afarensis* at Hadar and Laetoli (e.g., Johanson et al., 1978, Kimbel et al., 1985) it is clear that habitual bipedal posture and locomotion were well established 4 million years ago, long before the establishment of tool use or emergence of our genus. In the words of one investigator, our earliest hominid ancestor, *A. afarensis*, was a “creature which climbed in the trees but also walked on two legs when on the ground” (Aiello, 1994), i.e., it was suitably adapted to habitual bipedality. Thus, few differences in craniofacial anatomy among the fossil hominids to be described can be attributed to postural or locomotory adaptations. While postural changes and the acquisition of bipedality were important events during hominid evolution, as foretold by Wood Jones (1916), we now know that these adaptations were neither recent nor unique to



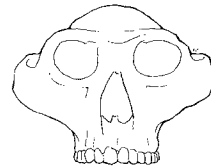
our direct ancestral lineage: humans may be the only extant habitually bipedal primate, but this was not always the case. Evolutionary differentiation of our species from other primates over the past 4 million years or so was a process that took place after several hominid forms had achieved bipedality, and this process focused almost entirely on one anatomical region, the head.

### 1. Australopithecines

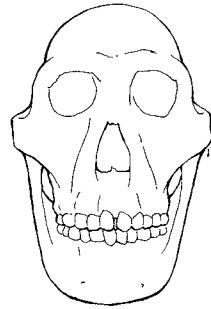
Australopithecines are known from fossils from east and southern Africa that date from as far back as 4 million years ago. Five species are generally recognized in this small-brained, large-faced genus. *A. afarensis*, the oldest dates from 4 to less than 3 Ma, and *A. africanus*, the first australopithecine to be recognized, has been dated at 3.0–2.5 Ma. Two “robust” species with massive facial features, *A. robustus* and *A. boisei* are known from fossils aged approximately 2.5–1.5 and 2.5–1.2 Ma, respectively, meaning that they must have co-existed with each other and perhaps to some extent with *A. africanus*. A sixth putative species (*A. ramidus*) has also been identified.

The following is a general summary of the australopithecines adapted from recent work graciously provided by Walker (1991). The australopithecines were upright, bipedal primates that may have spent some time feeding and/or sleeping in trees. Australopithecine limb proportions were unlike those of any living primate, including humans; however, their level of body-size sexual dimorphism approximated that seen in modern gorillas. They all had relatively small brains; their canine teeth were relatively small, but their post-canine teeth were relatively large. One of the megadontic species evolved its highly specialized dentofacial anatomy prior to the emergence of stone tools and retained these traits well beyond the temporal horizon for tool use. Evidence supporting tool use in the australopithecines is equivocal. A more detailed consideration of craniofacial anatomy in each of the australopithecine species follows (Figures 2.7–2.10).

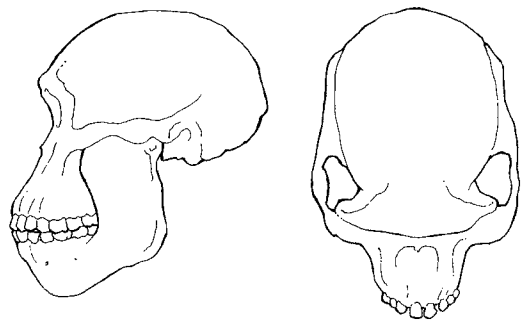
**Figure 2.7** Facial mask of *Australopithecus afarensis* (based on Hadar skull A.L. 444-2, described by Kimbel et al., 1994.)

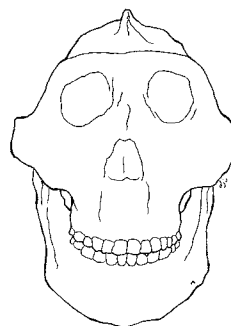


**Figure 2.8** Facial view of *Australopithecus africanus* (based on Sterkfontein 5, “Mrs. Ples,” from South Africa.)



**Figure 2.9** Lateral and superior views of *A. africanus*. Compare with like views of “robust” australopithecines, Figures 2.10, 2.12, and 2.13.





**Figure 2.10** Facial view of *Australopithecus boisei* (based on Olduvai hominid 5, “Nutcracker man,” and the Peninj mandible, from East Africa).

### **a. *Australopithecus afarensis***

This fossil species includes the well-known partial skeleton “Lucy” as well as the Hadar skull which was hailed as the “Son of Lucy” on the March 31, 1994 cover of *Nature*, the British science journal. Aged at 3.0 Ma, and with a maximum cranial (biasteronic) breadth of 106.0 mm (Kimbell et al., 1994), the Hadar specimen holds the dual distinctions of being the youngest *afarensis* and the largest *australopithecus* skull yet discovered. *A. afarensis* is a sexually dimorphic, transitional form that is “apish with human features” which, prior to discovery of the Hadar skull, had an estimated cranial capacity of 380–450 cc, comparable to that of modern chimpanzees or gorillas (Johanson and Edey 1981). Using a regression calculated on the basis of the biasteronic measurement reported by Kimble and his colleagues, the Hadar skull has a predicted cranial capacity of 700 cc, with outside limits of 600 and 850 cc (Walker, personal communication). As can be judged from recently published photographs and descriptions of the Hadar skull (Kimbell et al., 1994), the cranial vault in this male *A. afarensis* is fronted by an expansive supraorbital torus that is thickened laterally and continuous with laterally flaring robust zygomatic processes. The supraorbital torus continues superiorly-posteriorly without interruption with a low, flat frontal squamous. The well-developed zygoma connects posteriorly with a proportionately large zygomatic process of the temporal bone, encircling a substantial infratemporal fossa. Anteriorly the temporal lines rise only part of the way up the sides of the cranial vault, not reaching high enough to form a frontal trigone, a trait which is otherwise common to “robust” australopithecines. Posteriorly, the temporal crests converge to form a low sagittal crest.

There are several pongid-like traits present in *A. afarensis* viscerocrania. For example, canine diastemata and bony eminences over the canine roots are clearly seen. Parallel-rowed cheek teeth, almost flat mandibular fossae, conical-shaped canines whose crowns project beyond the occlusal planes, an anteriorly flattened palate, and a convex premaxilla with procumbent incisors are all ape-like traits. However, the relatively large diameter post-orbital constriction, polymorphic non-sectorial third premolars, zygomatic processes which rise from the maxillae in the region of the fourth premolar/first molar, molar cusps that are more rounded than sharp and which flatten with wear, an anteriorly displaced foramen magnum, and a cranial capacity that may be around 700 cc are all hominid attributes.

Judging from descriptions provided by Johansen and his colleagues (e.g., Johansen et al., 1978, Kimbel et al. 1985, and White et al., 1981), the *A. afarensis* mandible has a squat, robust appearance. Its ramal height is relatively short, while its ramal depth (anterior margin to posterior margin) is relatively large given the total anterior-posterior length of the mandible. Separated from the condyle by a shallow mandibular notch, the coronoid process does not rise above the plane of the condyle. Consistent with its apish middle and upper face, the anterior dentition is procumbent and set in an alveolus that projects buccally beyond the inferior border of the mandibular corpus, i.e., there is no mental protuberance. In the occlusal plane, the mandible appears V-shaped, with a tooth row that varies from parallel-sided in some specimens to slightly divergent posteriorly in others. The vertical height of the mandible in the region of the canines is notably greater than in the area of the third molars. The gonial angle varies from slightly open to almost vertical.

### **b. *Australopithecus africanus***

This bipedal hominid (Figures 2.8, 2.9) had a cranial capacity in the range of 450–500 cc. Based on the spatiotemporal distribution of fossils, this hominid overlapped geographically and possibly chronologically with “robust” australopithecines. Often referred to as the gracile form, this australopithecine shared with the “robust” forms similar cranial capacities, evident bipedality, parabolic tooth rows, and diminished canines.

Gracile (slender) australopithecines had a relatively steeply rising frontal squamous, positioned posterior to a moderate supraorbital torus, giving the appearance of an incipient forehead. Because the temporal lines do not converge along the midsagittal plane on the surface of the neurocranium, there is no hint of sagittal cresting; nuchal crests are equally diminished. The zygomata flare out somewhat with anteriorly directed planar surfaces, but they are less hypertrophied; the anterior-posterior oriented zygomaticotemporal processes (“infraorbital plates”, Rak, 1983) are more gracile. This australopithecine had a smaller infratemporal fossae and a narrower, less dish-in appearing face than *A. afarensis* or the “robust” forms.

The premaxillary component or “muzzle” in gracile australopithecines may seem to protrude more than in the robust form (Leakey and Lewin, 1991). This characterization is misleading, however, because this protrusiveness is restricted to the relationship between the premaxilla and the zygomaticomaxillary complex that immediately surrounds it. *A. africanus* is not facially more prognathic than *A. robustus* or *A. boisei* (Figures 2.10–2.12). Rather, because the anterior roots of the zygomata are less robust and do not originate so far anteriorly on the maxillae, part of the face, i.e., the muzzle seems to be more protrusive in the gracile form. Further contributing to an overall protrusive appearance, there is more dentoalveolar procumbency in the gracile australopithecines.

Figure 2.11

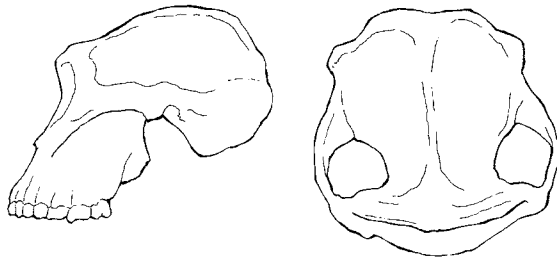
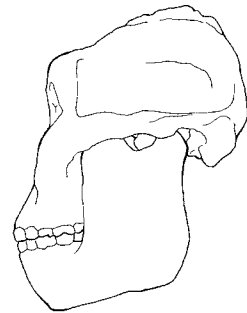


Figure 2.12



**Figures 2.11 and 2.12** Lateral and superior views of *A. boisei* (Fig. 2.11) based on KNM ER 406, from Lake Turkana; and lateral view of *A. boisei* (Fig. 2.12), from Olduvai. Note the inferior projection of the maxillary complex, the forward position of the zygomatic take-off, and the massive mandible.

The height of the maxillary complex (the distance from the inferior orbital margin to the occlusal plane) is noticeably less in the gracile form than in the “robusts.” Given this difference, ramal height in the gracile form is much shorter and the jaw joint is positioned closer to the occlusal plane. Gracile australopithecines also have a noticeably weaker mandibular corpus, and a more open gonial angle. The mandibular fossa in *A. africanus* is planar, with a very shallow glenoid fossa and a low articular eminence. (DuBrul, 1992 provides an extensive comparison of the jaw joint in australopithecines.)

### **c. *Australopithecus robustus* and *A. boisei***

Up until recently it was felt that these two “robust” forms (Figures 2.11, 2.12) from southern and eastern Africa constituted a single species, a view that is probably still held by many. Fossil specimens from Olduvai Gorge in Tanzania, include the largest known hominid teeth. The “robust” forms, whether from eastern or southern Africa, share with *A. afarensis* a hyperrobust, dish-in face dominated by massive, forward-facing zygomata (a nasomaxillary basin bounded by infraorbital plates in the parlance of Rak, 1983) whose large temporal processes wall-in huge infratemporal fossae, a pronounced supraorbital torus, and sagittal crests. Cranial capacity in the “robusts” has been estimated at 500 cc, marginally larger than that of *afarensis*. There are several features that distinguish *afarensis* and the “robust” australopithecines. For example, in both “robust” species, the mandibular fossa is marked anteriorly by

a distinct articular eminence and posteriorly by a deep glenoid fossa. *A. robustus* and *A. boisei* also have massive cheek teeth — three to four times as large as in modern humans — yet their anterior dentition, including the canines are relatively small, even falling within modern human range; their dental arcades are parabolic. Canine diastemata are reduced or absent, and in the East African “robusts” the canine eminences have been made indistinguishable by their incorporation into the bony structure of the nasomaxillary basin characteristic of this species.

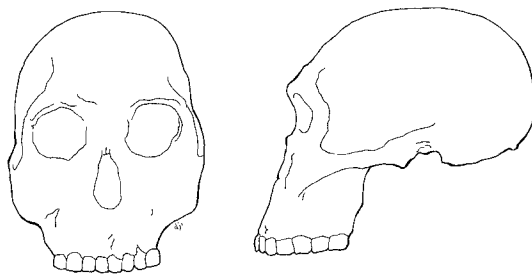
The mandibular corpus and ramus of the “robusts” are huge, with those attributed to *A. boisei*, such as the Peninj mandible being among the most massive seen in any hominid (Figures 2.10, 2.12). The ramus is exceptionally tall, an arrangement that positions the jaw joint well above the occlusal plane. Ramal depth is so great that its dimension equals or exceeds half the total anterior-posterior length of the mandible; this arrangement positions the anterior-most area of attachment of the masseter muscle well out onto the mandibular body. A shallow mandibular notch separates the coronoid and condyloid processes, but in the “robusts” the anterior process projects above the plane of the condyles. The mandibular corpus is exceptionally thick buccolingually and in its vertical height, which is greater in the region of the canines than at the third molars. On the lingual surface, distinct mandibular tori extend from side to side across the mandibular symphysis, which is transversely thickened. In contrast to *A. afarensis* and *A. africanus*, the anterior dentition is positioned vertically, though crowded into the anterior aspect of the dental arch. Like *afarensis*, there is no discernible mental eminence in the “robusts,” even though transverse thickening in the symphysis gives this region a flatter, more vertical appearance. The gonial angle approximates 90°.

## 2. Homo

*Homo*, the genus to which modern humans belong, is a taxon with closely guarded membership (Remember the quote by Aiello and the comments used to open this part of our chapter). For purposes of this discussion we will consider two closely related species, *H. habilis* and *H. erectus*.

### a. *Homo habilis*

A poorly known, highly variable species with many features in common with the australopithecines, *H. habilis* also has several attributes that are more modern and human-like. According to one expert in the field, few paleontologists actually know what *H. habilis* is (A.C. Walker, personal communication). Fossils attributable to this species have thus far only been identified in East Africa. Cranial capacity in this species averages in the realm of 650–700 cc, with one specimen attributed to *H. habilis*, KNM-ER 1470 measuring almost 800 cc (Figure 2.13). Accompanying this cranial volume, which is almost 50% greater than that measured in the australopithecines, is one of the striking features of *H. habilis*: an enlarged neurocranium that rises behind unobtrusive supraorbital ridges and which is bounded posteriorly by a rounded occiput. The orbits are still positioned in front of the neurocranium, with little, if any, of the anterior cranial fossa projecting over them. Given this brain–orbit relationship, a considerable postorbital constriction prevails.



**Figure 2.13** Frontal and lateral views of *Homo habilis* (based on KNM ER 1470 from East Africa).

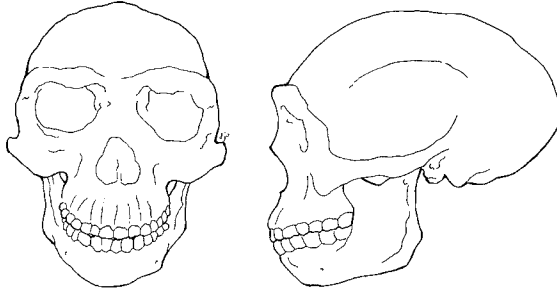
The zygomata are reduced in *H. habilis*, but because the planes of the right and left malar surfaces are directed anteriorly and the pyriform aperture is relatively flat, the face is somewhat dished-in, but with a protrusive premaxilla, as in gracile australopithecines. Perhaps more similar to “robust” australopithecines, the midface projects downward, creating a vertically-elongated maxillary complex and a correspondingly lengthened ramus.

While the proportions of the anterior and posterior dentition relative to each other are more human-like, the teeth are somewhat oversized. Continuing trends seen in the australopithecines, *H. habilis*

canines are more spatulate, they do not project below the occlusal plane, and they do not require skeletal adaptations like diastemata or eminences.

**b. *Homo erectus***

Our closest known fossil antecedent, *H. erectus* had an estimated cranial capacity in excess of 900 cc. As might be expected in a species whose brain size approaches the lower limit of normal variation in modern humans, the size of the viscerocranium no longer overwhelms the neurocranium; a shift has begun away from a large face coupled with a small brain (Figure 2.14).



**Figure 2.14** Frontal and lateral views of *Homo erectus* (based on Pithecanthropus, "Peking man," from China).

In addition to differing from *H. habilis* on the basis of morphological features, more of which are described below, fossils attributed to *Homo erectus* have been discovered in disparate regions of the world, from Asia to Africa (though no conclusive specimens have yet emerged from Europe); only modern humans are a more widely distributed hominid.

The neurocranium in *Homo erectus* is elongated along its anterior-posterior axis, with marked expansion in the occipital region. Nuchal lines, but no real crests are present along the posterior inferior border of the occiput, approximately equidistant between lambda and the foramen magnum. Temporal lines rise up the lateral walls of the vault, sometimes ascending about two-thirds of the height of the parietals. Ovoid, convex mastoid processes begin their protrusion from the cortical surface of the outer table at or near the Frankfort plane. While possessing distinct supraorbital ridges that are separated from the cranial vault by a sulcus, a portion of the orbits are covered by the anterior cranial fossa. The zygomata are unremarkable in size, and their malar surfaces are directed laterally more so than anteriorly. The take-off for the zygomatic root is between the first and second molars, and there is a distinct fossa anteromedial to this area. The premaxilla is procumbent, but with a vertically oriented dentition. In contrast to earlier hominid forms, the maxillary components and the adjacent nasal bones that form the lateral and superior margins of the nasal aperture project outward from the facial plane, giving the nasal region a protrusive appearance and contributing to a convex facial profile. Compared with australopithecines, midfacial height in *H. erectus* is truncated, along with the vertical length of the mandibular ramus. The mandible is less robust overall, and still lacks a mental eminence. The anatomy of the mandibular fossae is very human-like. Each fossa is bounded anteriorly by a slight articular eminence, posteriorly by a deep glenoid fossa, and medially by an entoglenoid process. A post-glenoid process separates the mandibular fossa from the bony opening of the external auditory meatus.

The dental arcade in *H. erectus* is parabolic and devoid of any diastemata. With shovel-shaped incisors, spatulate canines, bicuspid premolars, rounded-cusp molars, and tendencies for third molar reduction or agenesis, teeth in this species resemble modern human populations. On the other hand, the second molars usually are larger than the first molars, a more primitive trait.

Readers wishing to learn more about *Homo erectus* are encouraged to see the volumes by Walker and Leakey (1993) and Rightmire (1990).

## V. "WHAT CAN THE EXAMINATION OF EXTANT AND FOSSIL PRIMATES TELL US ABOUT THE WAY WE LOOK NOW?"

*"Man's position in the scheme of things is likely to become more clear if it is viewed against the background of the evolution of the Primates as a whole."*

W.E. Le Gros Clark, *The Antecedents of Man*, 1959.