

have a relatively long trunk and a long tail and forelimbs and hindlimbs that are more similar in length but short relative to trunk length or body size, as adaptations for balance. Terrestrial quadrupeds also have forelimbs and hindlimbs that are similar in length, but their limbs tend to be longer relative to body size, since balance is not a problem on the ground. Suspensory primates usually have relatively long limbs and long hands and feet to permit them to suspend their body from a wide range of supports. They usually have a short, relatively rigid trunk.

See also Bone Biology; Forensic Anthropology; Locomotion; Musculature; Skull; Tail. [J.G.F.]

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Skhul

Rockshelter in the Wadi el-Mughara on the western escarpment of Mount Carmel (Israel). Between 1929 and 1934, excavations at Skhul by T.D. McCown (supervised by D. Garrod) recovered a number of adult and child partial skeletons of early modern humans together with a Levantine Mousterian industry. These excavations removed virtually all of the sediments from this site. All of the human fossils occur in Level B, a highly brecciated layer with generally poor faunal preservation. The lithic industry from Skhul Level B is broadly comparable to that at nearby Tabun Level C and the lower levels from Qafzeh, where remains of early modern humans were also found. Initial radiocarbon and amino-acid racemization dates placed the hominid-bearing strata ca. 45–30 Ka, but more recent thermoluminescence and electron spin resonance dates place Level B between 120 and 80 Ka. Ten individual hominids (seven adults and three children) are probably represented in Level B, and the material includes three reasonably complete adult skulls and some well-preserved long bones from the adults and children. Many of the skeletons appear to have been intentionally buried; one adult (Skhul 5) is clasping the jaw of a wild boar to his chest, and one infant (Skhul 1) is buried in a highly flexed position. The Skhul fossils were interpreted by their describers (McCown and A. Keith), together with the remains from the nearby site of Tabun Cave, as a single population in the process of evolution into an early-modern type. The Skhul material is now generally regarded as a robust early-modern population of western Asia that still retains some archaic features from nonmodern ancestors. Some workers consider the Skhul specimens, together with those from Qafzeh, to represent the ancestors of the European Cro-Magnon populations; others continue to view them as part of the same population as the Levantine Neanderthals from Tabun, Amud, and Kebara.

See also Amud; Archaic Moderns; Asia, Western; Cro-Magnon; Garrod, Dorothy Anne Elizabeth; Kebara; Keith, [Sir] Arthur; McCown, Theodore D.; Neanderthals; Qafzeh; Tabun. [C.B.S., J.J.S.]

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Skull

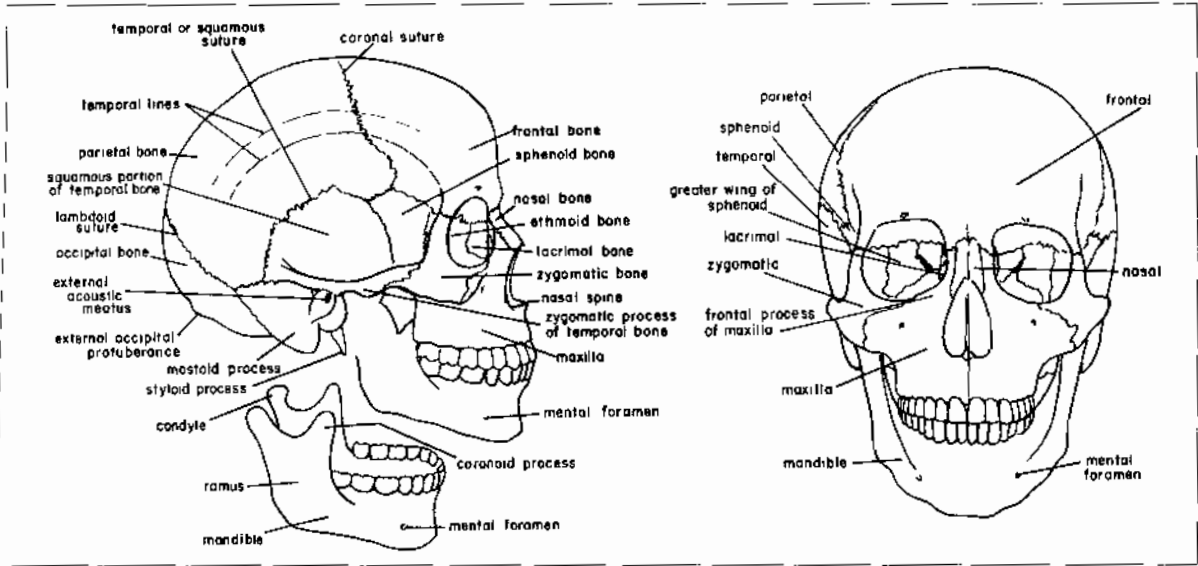
The primate skull (like that of all mammals) is composed of two elements: the cranium (including many fused bones) and the mandible or lower jaw. In turn, the cranium may be divided into two major components based on developmental and functional criteria: the neurocranium and the splanchnocranium, or viscerocranium. The neurocranium houses the brain and is made up of two parts distinguishable by the type of bone formation underlying each. The membranous neurocranium, so called because the bones develop via intramembranous ossification, forms the calvarium and comprises the frontal bone, parietal bones, the squamous (or flat) portions of the temporal bones, and the squamous portion of the occipital bone. The chondrocranium, or basicranium, develops from cartilage and comprises the ethmoid and sphenoid bones, as well as the petrous and mastoid regions of the temporal bones and part of the occipital bone. The basicranium serves as the floor of the neurocranium (and is, therefore, pierced by many nerves and blood vessels), and it also acts as a structural interface between the splanchnocranium and the neurocranium.

The splanchnocranium constitutes the rest of the skull, primarily the jaws and facial bones. The terms *splanchnocranium* and *viscerocranium* reflect the derivation of these bones from the embryonic visceral, or branchial, arches, which in primitive vertebrates line the wall of the digestive tract and support the gills. These bones develop via both membranous and endochondral ossification and, in the adult human state, are represented by the paired maxillae; inferior nasal conchae; nasal, lacrimal, zygomatic, and palatine bones; plus the single vomer and mandible. Since primate skulls are often described or measured, a system of landmarks, or defined points, has been developed to facilitate the process. Some of the most important landmarks are shown in the accompanying figure.

The primary functions of the skull are to gather and break down food for nourishment and to support and protect the brain and the soft tissues associated with the special senses of hearing, sight, and smell.

Primate Diversity in Skull Form and Function

The rich diversity of skull form evidenced by our order is best illustrated by consideration of the functional specializations of the soft tissues associated with the various skeletal regions. For example, the skull of modern humans is dominated by



Frontal and lateral views of a human skull illustrating the major bones and features. Courtesy of Brian T. Shea.

the dramatically enlarged neurocranium, which houses our most salient morphological specialization, ca. 1,500 ml of grey matter. Because our enormous cranial vaults are combined with relatively small faces, teeth, and chewing muscles, human skulls lack the marked bony ridges or protuberances, such as the sagittal crest or supraorbital torus, often seen in other primates. In other cases, relatively large braincases and small facial skulls are related to the small overall body size of a species, as in the South American squirrel monkey (*Saimiri*) or the African talapoin monkey (*Miopithecus*), both of which may be dwarfed forms derived from larger ancestors. The basis for such shape changes is the differential, or *allometric*, growth of the facial skeleton relative to the neural skeleton, so that shifts in body size during ontogeny or among adults of closely related species result in a disproportionate change in facial size relative to overall skull size.

The orbits house the eyes and associated soft tissues and are particularly well developed in nocturnal species, such as the South American owl monkey (*Aotus*). Orbital hypertro-

phy reaches an extreme in the tarsier (*Tarsius*), where the weight of a single eyeball may exceed that of the brain, and the huge orbital cones envelop the facial skeleton. In general, however, the eyes exhibit a growth pattern similar to the brain, and thus the orbits usually decrease in relative size during ontogeny and among larger adults of a series varying in body size (compare the skulls of the two small species on the left in the accompanying figure with those of the large species on the right). The degree of development of the bony midface, or snout, is influenced by numerous factors. The strepsirhine primates generally rely more on olfactory stimuli in their social and feeding behavior than do the haplorhines; they also exhibit relatively larger faces that protrude in front of the neurocranium rather than being more recessed under the skull vault. The nasal fossae in these primates are filled with bony turbinates that are covered by olfactory and respiratory epithelium. Certain extant haplorhines, such as howler monkeys, baboons, and gorillas, also have secondarily enlarged faces, due primarily to the effects of large

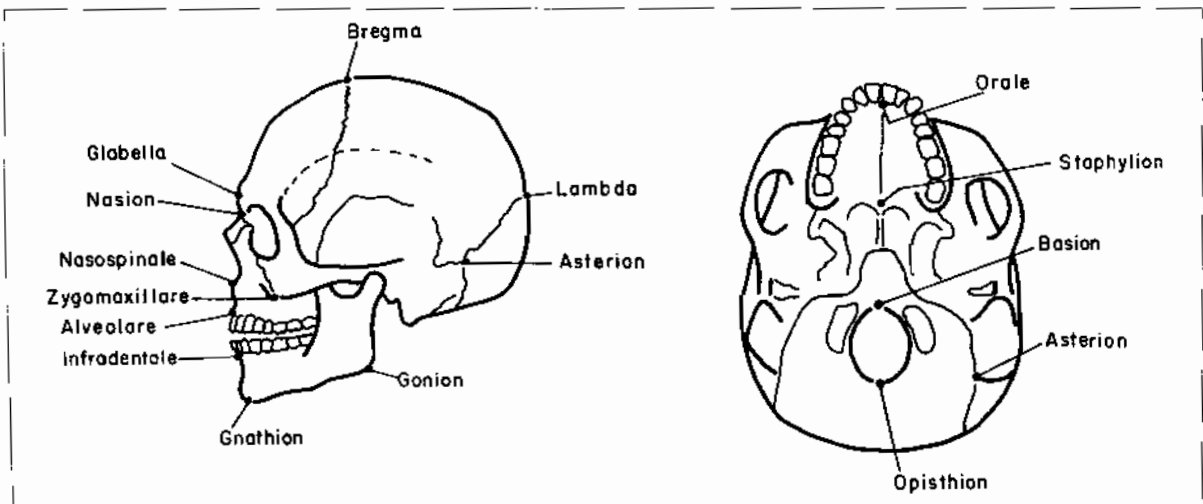
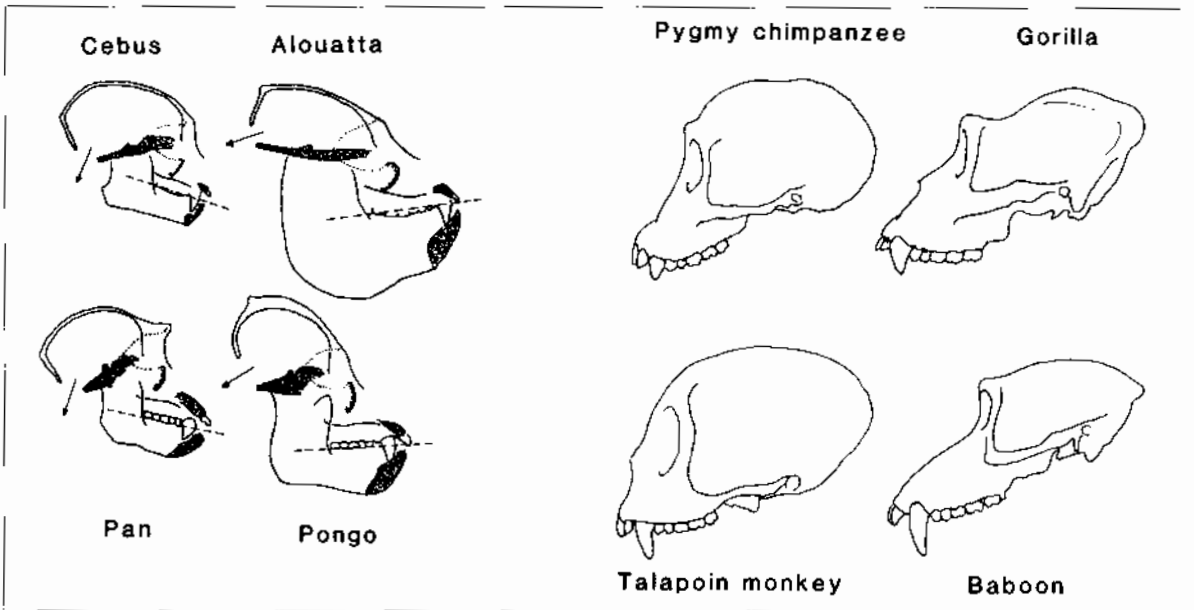


Diagram showing the major cranial "landmarks" used in skull descriptions and between which standard measurements are taken. Courtesy of Brian T. Shea.



Left: differences in the positioning of the face relative to the skull base and cranial vault in howler monkeys (*Alouatta*) and orangutans (*Pongo*) by comparison to unsexed relatives (capuchin monkey and chimpanzee, respectively). The upward or dorsal deflection of the face (airorbhynch) may be related to enlargement of structures associated with vocalization. Right: a comparison of skull shape in two pairs of closely related species differing markedly in overall body size. Above: female pygmy chimpanzee or bonobo (*Pan paniscus*, ca. 33 kg) and male gorilla (*G. gorilla*, ca. 170 kg); below: male talapoin monkey (*Miopithecus talapoin*, ca. 1.2 kg) and male savannah baboon (*Papio hamadryas anubis*, ca. 25 kg). Note the relatively enlarged faces and small braincases in the larger forms, resulting from differential growth in these regions as size increases. Courtesy of Brian T. Shea.

body size and the positively allometric increase in the splanchnocranium and the canine teeth (see Figure).

Structures related to the production of sound may also affect skull form. In the howler monkey (*Alouatta*), the face is flexed upward, or dorsally, on an elongated and flattened skullbase, allowing for the suspension of an enlarged hyoid bone as part of a resonating chamber used to boom signals to conspecifics. The orangutan (*Pongo*) also exhibits a dorsally deflected splanchnocranium, perhaps related to the enlarged laryngeal sac, which functions as a resonating structure, especially in males. In *Homo*, a secondary flexion or bending of the skull appears to be related to a restructuring of the pharyngeal and laryngeal region, yielding an enlarged supralaryngeal tract vital to the production of the complex and subtle sounds that make up human speech.

The dentition affects the size and the shape of the splanchnocranium and also indirectly of the neurocranium, via related soft tissues, such as the chewing muscles, and bony support structures, such as the mandible and portions of the facial region. Larger teeth basically require a larger, more heavily buttressed maxillary and mandibular framework. An interesting example is seen in the intriguing and bizarre aye-aye (*Daubentonia*) from Madagascar. Here a deep and strongly flexed, beaklike face is related to the procumbent and continuously growing incisors that aye-ayes use to pry under tree bark for grubs and insects.

The chewing muscles, along with the teeth, the bony jaws, and other stress-bearing regions of the skull, compose a functional unit that affects skull form in an important and reasonably predictable fashion. The mechanical task of this unit is primarily to break down ingested food by repetitive opening and closing of the jaws. The masticatory muscles, primarily the

masseter, temporalis, and medial and lateral pterygoids, perform this function. The degree of force produced at the bite point can be roughly determined by taking a ratio of the *lever* (or *power*) *arm* of muscular effort, which is the distance from the jaw joint to the average line of action of the muscle, to the *load* (or *resistance*) *arm*, which is the distance from the jaw joint to the bite point. If one assumes a constant force input (i.e., muscles of the same size and power), a higher lever/load ratio reflects a mechanical situation capable of producing greater forces. Increased mechanical efficiency is often produced by moving forward the insertion of the masseter muscle and thus increasing the length of the lever arm, or by decreasing the length of the load arm, accomplished by shortening of the lower face or by tucking the palate underneath the upper face.

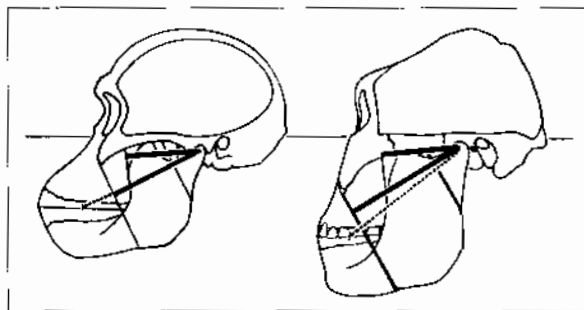
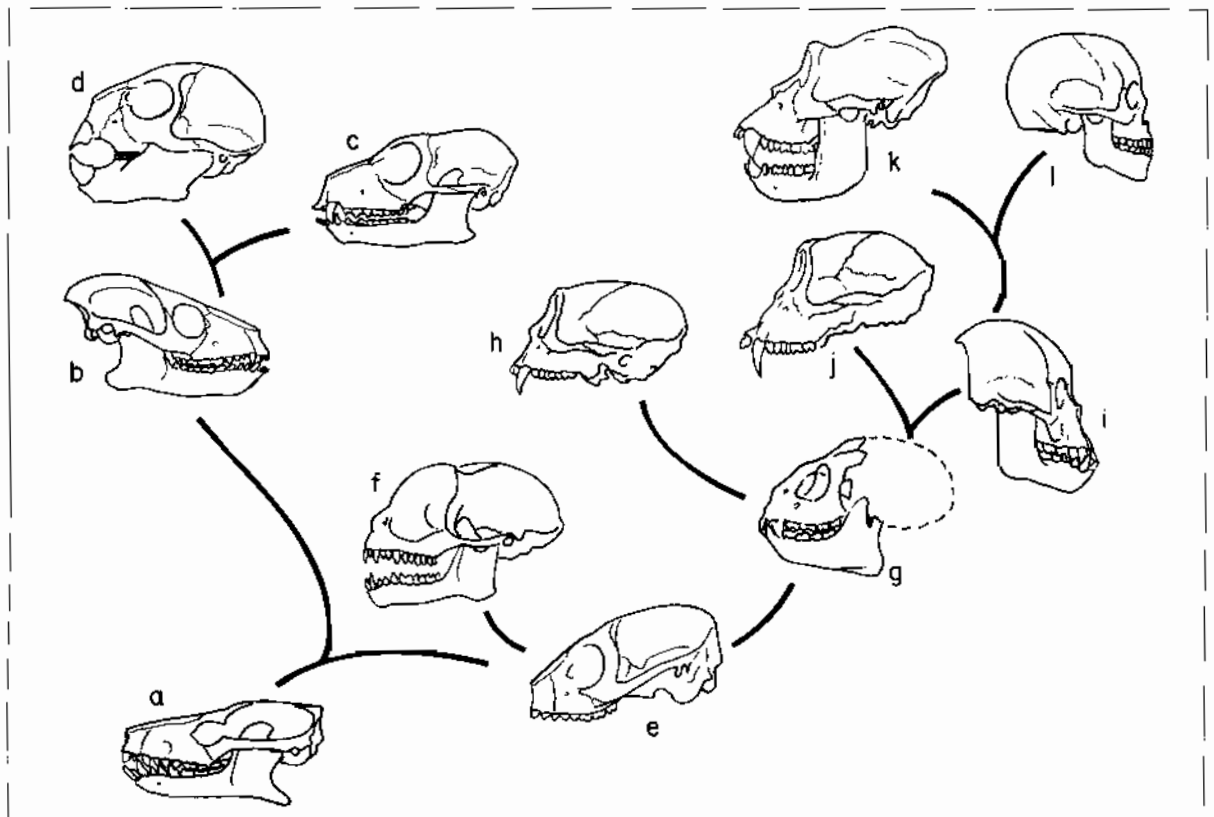


Illustration of cranial biomechanics using the early hominids *Australopithecus africanus* (left) and *Paranthropus boisei*. The heavy solid lines represent the in-lever or power arms for the temporalis (shorter) and masseter chewing muscles, while the dashed lines represent the out-lever or resistance arms to the molar teeth. Note the higher ratio of in-lever to out-lever arms in *P. boisei*, providing increased mechanical efficiency and greater force production during chewing with the back teeth. After E.L. DuBrul, 1977, *Am. J. Phys. Anthropol.*, 47; courtesy of Brian T. Shea.



An array of skulls of extant and extinct primates, depicting the general evolutionary directions taken by some of the major taxonomic groups as well as some striking specializations. The diagrammatic linkages among these skulls reflect phylogenetic ties, but they do not represent the actual anatomical transformations among the species shown here. Several skulls are generalized, primitive designs indicative of ancestral patterns of important groups, as identified in parentheses: (a) Plesiolestes (all primates); (b) Notharctus (euprimates); (c) Lemur (lemurs and lorises); (d) Daubentonia; (e) Rooneyia (tarsiiforms and haplorhines); (g) Apidium (anthropoids); (h) Cebus; (i) Proconsul (hominoids); (j) Macaca; (k) Gorilla; (l) Homo sapiens. Courtesy of Brian T. Shea. Not to scale.

Within the hominins, the “robust” australopiths (*Paranthropus robustus*, *P. aethiopicus*, and *P. boisei*) in particular exhibit aspects of this configuration. These basic principles of cranial biomechanics also help us make sense of the differences in skull form between the two subfamilies of Old World monkeys: The folivorous, or leaf-eating, colobines with their short faces and deep jaws have higher ratios of lever/load arms compared with the frugivorous, or fruit-eating, cercopithecines with their long and prognathic faces.

Current Research and Prospects

A number of relatively new approaches and techniques in the study of primate and mammalian skull form have yielded promising results, and much additional research will be completed in these areas in the future. Experimental approaches to masticatory biomechanics have involved cineradiographic filming of jaw and tooth movement, electromyographic determination of muscle activity, measurement of *in vivo* bone strain in various portions of the face, and investigation of the histochemical properties of the chewing muscles. The integration of such information with results of studies of comparative anatomy and biomechanical modeling has resulted in significant advances in our understanding of skull function.

Another important area of work involves the genetic and developmental factors controlling skull growth and

form, since it is changes in these controls that result in evolutionary transformations of the skull. Studies in quantitative genetics, developmental abnormalities, and experimental approaches to intrinsic (e.g., developing tissue interactions) and extrinsic (e.g., hormonal) growth controls have provided new insights here. Finally, advances in evolutionary theory and the discovery of new fossil skulls of extinct primates also combine to provide important new information. Primatologists synthesize data from these and other fields in their continuing attempt to understand the form, function, and phylogeny of the skull of humans and nonhuman primates.

Evolution of Primate Skull Form

Our knowledge of cranial anatomy in the earliest primates is based largely on fossil remains of Paleocene forms such as *Palaechthon nacimienti* from North America and *Plesiadapis tricuspidens* from western Europe. These examples illustrate that the first primates were more similar to their mammalian contemporaries than to their later primate descendants or to any primates alive today. The skulls of these Paleocene primates generally resemble those of living treeshrews, with a long snout projecting in front of the relatively small braincase. Such a skull is designed to accommodate a large masticatory apparatus, with a long dental arcade and well-developed chewing muscles anchored to the skull vault, the zygomatic arches, and

the lower jaw. The long face also reflects an acute sense of smell, whereas the eye sockets are relatively small, less frontated, and without the supportive postorbital bar characteristic of later primates. This combination of features has been used by some to argue that the earliest primates were nocturnal animals.

The fossil evidence indicates that plesiadapiforms had an ossified auditory bulla, a bony shell-like casing that envelops the chamber of the middle ear and its ossicles from below. According to some authors, this bullar capsule is formed by the petrosal bone, a derived homology that unites all of the primates as a monophyletic group. Other mammals have analogously evolved ossified bullae by incorporating different cranial elements into a middle-ear covering, such as the ectotympanic bone, whose primary function is to provide a collar for the tympanic membrane. Some mammals lack an ossified bulla entirely but encase the ear region with membrane or cartilage. The evolution of a bony auditory bulla may be related to the development of a hearing mechanism sensitive to low-frequency sounds.

The second major radiation of primates occurred during the Eocene epoch and produced a new type of cranial organization. Eocene adapiforms, such as *Notharctus*, and omomyids, as exemplified by *Rooneyia*, are characterized by a reduced snout, relatively larger brains, more frontally directed orbits, and a postorbital bar developed from processes of the frontal and zygomatic bones. The postorbital bar stabilizes the zygomatic arches by solidly fusing them to the braincase, providing a lateral truss that resists the twisting generated during unilateral mastication in a face that is shorter and with more frontated orbits than found in Paleocene primates.

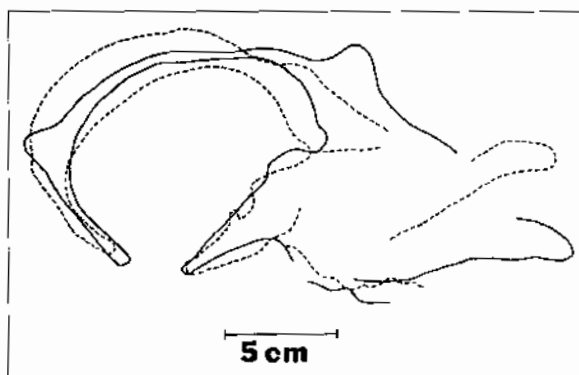
The early omomyids were perhaps the first primates to adopt a diurnal activity pattern. Their skulls reflect this change from a dominance of the olfactory/tactile sense and corresponding enlargement of the portions of the brain associated with the sense of smell, the primitive primate pattern that characterized the plesiadapiforms and that persists among many extant strepsirhines. One of the important skeletal features reflecting this change in omomyids is the loss of the deep posterior recess of the nasal cavity that forms part of the separation of the eye sockets in most mammals. In the modern haplorhines, this space is occupied by the medial walls of the orbits, which have become frontated and closely spaced, enhancing the capacity for stereoscopic vision. An orbital septum, or bony plate enclosing the posterolateral portion of the orbital space, is an important novel development in this group.

Anthropoids mark another adaptive transition in the evolution of the primate skull that is documented by such Oligocene forms as *Apidium*. In addition to a larger braincase, their faces are proportionately shorter and more vertical, the mandibular symphysis and frontal bones are rigidly fused early in life, and a greatly modified zygomatic bone extends laterally around the orbital fossa to form a postorbital partition that, in its detailed construction, is unique among the mammals. One explanation of this suite of features is that they signify a more active, forceful use of the incisor teeth in harvesting foods, powered by masseter and temporalis muscles of larger size and strength. With a fused man-

dibular symphysis, large loads can be carried by the solidly rooted, large, spatulate incisors that are typical of anthropoids, and power generated by muscles on either side of the head can be added together to increase the force of molar biting. Possibly to balance these forces and protect orbital contents from injury, the zygomatic bones have expanded in size and become firmly joined to the skull. The effect of this is to produce the postorbital plate, or septum, and reinforce the junction between the facial skull and the neurocranium. This basic anthropoid groundplan of skull form served as a foundation for marked diversification during Oligocene, Miocene, and Plio-Pleistocene times, yielding a broad array of extinct and extant monkeys, apes, and hominins.

Recent fossil discoveries of Miocene hominoid skulls, combined with a new perspective on the phylogenetic significance of certain cranial features, have rekindled debates over the origins of the African-ape clade. Previous schemes have characterized great-ape crania as either *klinorhynch* or *airorhynch*, depending on whether the facial skeleton is directed more ventrally or dorsally relative to the cranial base. While it has always been appreciated that the Asian orangutan has a particularly airorhynch skull relative to the other large-bodied hominoids, recent studies have raised the possibility that this feature is probably a shared primitive character of most known Early and Middle Miocene hominoid crania. In this view, a more klinorhynch skull represents a shared derived feature uniting humans, African apes, and certain Miocene forms perhaps specially related to this African clade (*Dryopithecus* and *Graecopithecus*, also known as *Ouranopithecus*, have been suggested as such possibilities). Moreover, certain other cranial features that have played a key role in phylogenetic and evolutionary debates, such as supraorbital-torus form, paranasal-sinus development, and nasoalveolar-clivus morphology, may covary with facial position and size to some extent, thus providing additional information of phylogenetic significance.

Another late-twentieth-century development has been the attempt to identify cranial features that link chimpanzees and hominins to the exclusion of gorillas, thus corroborating recent biomolecular phylogenies. However, much additional comparative data, an increased understanding of trait polar-



Outlines of hemisected skull of female gorilla (solid line) and male orangutan (dashed line) to show differences in positioning of the face, base and braincase. After Shea, 1985; courtesy of Brian T. Shea.

ity and homoplasy, and new fossil evidence from particularly the African-ape lineages are required before this suggestion can be accepted on the basis of cranial anatomy.

Evolution of the Human Skull

The evolution of skull form in our own lineage has been the subject of intense interest and debate since the discovery of the Taung child, formally named *Australopithecus africanus*, by R.A. Dart in the 1920s. This skull exhibited a counterintuitive mosaic of features, considering that common preconceptions, fueled by the fraudulent Piltown skull, predicted that early hominins would have large, humanlike brains combined with primitive, apelike faces and teeth. The Taung skull was followed by even more impressive fossil remains from South Africa, and, from the late 1950s onward, the sediments of East Africa have yielded an unprecedented series of well-preserved skulls of humans and our close relatives. Combined with additional material from Asian and European sites, these African fossils permit us to sketch a fairly detailed, if ever-changing, scenario of human evolution over the past several million years based on craniodental remains.

Although specific phylogenetic connections are difficult to determine, particularly in the period 3.5–1.5 Ma, we can discern three primary groups of hominins, which are placed in the closely related but divergent genera *Australopithecus*, *Paranthropus*, and *Homo*. The australopiths (hominins other than *Homo*) are characterized, particularly in later and larger forms, by massive chewing teeth, well-developed sagittal crests, and large, heavily buttressed faces adapted to generating great chewing forces and withstanding the resultant bony stresses. Relative brain size exhibits no apparent increase through time within this group, although the australopiths are more highly encephalized than the great apes. Authorities have interpreted the most salient aspects of skull form in the australopiths as evidence of an increasing specialization on some type of hard-food items, such as roots and nuts, perhaps a dietary adaptation related to exploitation of drier and more open-country environments. It has never been clearly demonstrated that these specialized herbivorous hominins used any of the primitive stone tools found in eastern and southern Africa in the Plio-Pleistocene, and they disappear from the fossil record by ca. 1.4 Ma.

Another lineage of early hominins, in all likelihood derived from a primitive early australopith like *Australopithecus afarensis*, exhibited quite different skull morphology and general adaptations. In this group, the chewing teeth and associated masticatory apparatus became smaller and more gracile, while the brain literally exploded in an evolutionary sense, undergoing a three- to fourfold increase in overall size in a 3 Myr period. Skulls of the genus *Homo* combine a large and rounded cranial vault devoid of sagittal cresting with a smaller and flatter (orthognathic) face. The evidence of skull form and the archaeological record clearly suggest that, by ca. 2.5–2 Ma, our own genus had embarked on what would be a most successful evolutionary pathway, one characterized by behavioral flexibility and an adaptation to the natural environment based on culture.

Some interesting elaborations on this basic *Homo* pattern are seen in the well-known Neanderthal crania: The

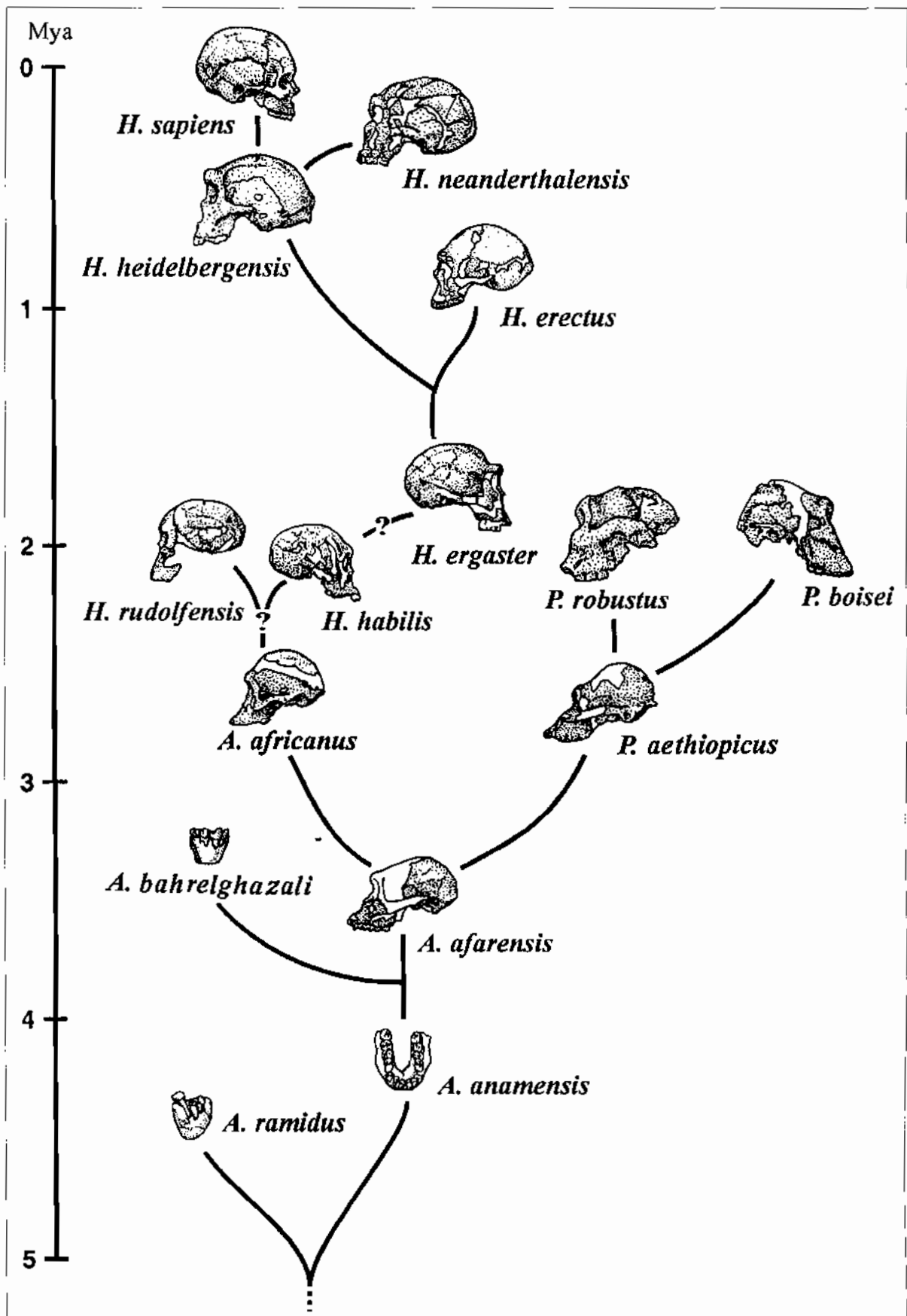
faces are enlarged and protruded in the nasal region and dominated by a heavy supraorbital torus, or browridge. Some have interpreted this morphology as evidence of cold adaptation in glacially isolated hominins, while others have suggested a link to use of an enlarged anterior dentition as part of a cultural tool kit.

In any case, a plentiful fossil record has revealed some haunting reflections that clearly inform us of the evolutionary pathways that culminated in our own species, *Homo sapiens*. Only time will tell whether this aberrant and highly encephalized species will avoid the fate of our closest cousins.

See also Adapiformes; Allometry; Anthropoidea; Australopithecus; Bone Biology; Dwarfism; Functional Morphology; Gigantism; Hominidae; Homininae; Hominoidea; Homo; Morphology; Omomyidae; Ontogeny; Paranthropus; Plesiadapidae; Ponginae; Primates; Sexual Dimorphism; Skeleton; Teeth. [B.T.S., A.L.R.]

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Evolution of hominin skulls. Two or three broadly defined phylogenetic trends are indicated by the fossil record. From a pattern similar to that of *Australopithecus afarensis* increasingly large masticatory muscles and chewing teeth produced the strongly buttressed, deep faces of the robust lineage, which became extinct. A general decrease in tooth size, musculature, and face size, coupled with a dramatic increase in the size of the braincase, marked the *Australopithecus africanus*–*Homo sapiens* lineage, although the intervening details of phylogenetic and morphologic evolution are unresolved.