

How did *Australopithecus robustus* hear?

The effect of masticatory specialization on the auditory region in *A. robustus*

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Introduction

Australopithecus robustus was first discovered in 1938 by Robert Broom, and ever since then, it has been the subject of fascination about its unique cranial morphology and specialization for powerful mastication. The species, also known as *Paranthropus robustus*, is found in East African and South African sites, and probably spanned the length of Africa about 1.8 million years ago (Wolpoff, 1994). The *A. robustus* skulls exhibit an extraordinary adaptation to powerful mastication that appears to affect every structure in the cranium. The unusual facial morphology was coined “dish-faced” because of the anteriorly projected cheekbones for the masseter muscle attachments. *A. robustus* has large masticatory muscle attachments, large posterior teeth and tall, robust mandibles. The overall effect is a skull that looks very well adapted to eating tough foods.

Beyond the masticatory specialization, *A. robustus* has been studied in the context of its diet, habitat, locomotion and brain size. While functional analysis of the cranium is limited to the masticatory apparatus, the temporal bone has maintained its status as a taxonomic indicator of the *A. robustus* species because of the trumpet-shaped external auditory meatus and large mastoids (Rak, 1994). The temporal bone has been the subject of focus in much later hominids, such as *Homo neanderthalensis*, but *A. robustus* suffers from poor preservation and small sample sizes, which limit the channels available for study. However, this complex bone has a very important, but usually overlooked function — it houses the auditory region. The study of sensory capabilities is difficult in fossil species because of the absence of soft tissue structures, but the temporal’s bony structures are modeled around these soft tissue structures. The bone is the only remnant of the hearing system in *A. robustus*.

The exact biomechanics and function of the osseous portions of the temporal auditory region may be well known for modern humans, but any changes to the morphology, as is seen in the fossil hominids, has uncertain consequences to hearing. Still, the temporal bone should not be abandoned to a non-functional area of study. *A. africanus*, a more gracile contemporaneous hominid, has been the subject of a recent study investigating hearing (Moggi-Cecchi and Collard, 2002). The study of hearing in *A. africanus* has introduced the potential for study in early hominid hearing. The study of hearing can reveal an important aspect of daily life for *A. robustus*.

Background

The temporal bone is located on the side and base of the cranium, and it is a paired bone with one on either side. The bone articulates with five bones: occipital, parietal, sphenoid, mandible and zygomatic (Gray, 1918). The majority of the auditory system is housed in the bone, and consists of both bony and soft tissue. The ear is made up of three parts: the outer ear, the middle ear and the inner ear. The outer ear consists of the pinna, which is the external ear that is visible on the side of the head, and the external auditory meatus, an opening at the center of the pinna that leads to the ear canal (Bast, 1949). The pinna is the first level of filtration for the sound arriving to the inner ear. It is a soft tissue structure that transmits the sound to the external auditory meatus. The external auditory meatus “serves as a resonator, boosting the amplitude of some frequencies and decreasing the amplitude of other frequencies” (Hauser, 1997). The most external aspect of the meatus is cartilaginous, but 2/3 of the human external auditory meatus and corresponding ear canal are bony (Bast, 1949).

Sound travels through the bony ear canal and arrives at the tympanic membrane. The tympanic membrane signals the arrival of sound to the middle ear where three bony ossicles form a linked chain connecting the tympanic membrane to the inner ear. The three bones, from most lateral to most medial, are the malleus, the incus and the stapes. The ossicles form a chain in a pneumatic chamber known as the tympanic cavity (Bast, 1949). The sound waves travel through the tympanic membrane and the ossicular chain by means of mechanical vibrations. The middle ear and tympanic cavity continue to boost the amplitude, or loudness, of the traveling signal. The ossicles, and the cavity are bony structures.

Once the mechanical vibrations are transmitted through the ossicular chain, they reach the inner ear. The inner ear is filled with fluid that houses the vestibular system and the cochlea. The cochlea is the primary hearing structure that transmits sound information to the brain (Hauser, 1997). It is a soft tissue structure whose features include the basilar membrane that moves with the sound vibrations and hair cells that follow the movement. The moving of the hair sets off the nerve cells that send signals to the brain for interpretation (Hauser, 1997). The middle and inner ear are housed in the petrous and tympanic regions of the temporal bone. The petrous pyramid is viewed from inside the cranium, and the tympanic region forms the inferior aspect of the temporal bone that is visible on the basal surface of the skull. The temporal bone

can restrict or expand the amount of space for these structures, affecting the way sound travels through the ear.

Another important and well-studied aspect of the temporal bone is the articulation with the mandible. The anterior portion of the temporal bone has a depression known as the glenoid fossa where the mandibular condyles articulate with the cranium. The temporomandibular joint is influenced by the dietary needs of the species, and affects both mandibular and temporal morphology. In fact, the morphology of the mandible, the malleus and the incus belong to the same developmental system, tracing back to the anatomical transition from reptiles to mammals (Rak, 1994). Stephen Jay Gould (1994) traced the anatomical change of jaw articulation to hearing bones in an essay called “An Earful of Jaw.” The early reptiles had three jaw bones: the articular, the quadrate and the dentary bone. The tympanic membrane was positioned at the lateral aspect of the mouth, and connected to the inner ear by only the stapes. As the early reptiles transitioned into mammals, they went through several well-documented evolutionary steps until the mammalian middle ear formed. The articular and the quadrate became the malleus and the incus, and were re-purposed as ear ossicles in the middle ear.

Thus, the ear structures and the mandible “belong to one restricted anatomic, and presumably genetic, complex” (Rak, 1994). The development of the mandible will affect the structure of the ear because of the shared ontogenetic origins. The masticatory specialization of *A. robustus* is of particular interest to the study of temporal bones because of this connection. The hyper-development of the masticatory structures affects the temporal morphology and possibly the ear structures, though the nature of the changes has not yet been qualitatively studied. With the interaction between the masticatory apparatus and the temporal structures so well-established, the effect of masticatory specialization on the auditory region can further our understanding of early hominid species.

In this study, I will investigate the influence of the masticatory system on the temporal bone, and specifically look at the relationship between highly specialized mastication and the auditory region. A highly specialized masticatory apparatus limits the development and expansion of the auditory region and in *A. robustus*, the changed morphology could indicate an altered hearing capacity. I used a comparative approach to look at the effect of specialized mastication on the temporal anatomy by selecting mammal models for the *A. robustus* and *A. africanus* comparison. The species pairings will be selected for their relevance to the

comparison between specialized masticators and their more gracile counterparts. I will qualitatively examine the morphologies for patterns that relate to hearing. My contention is that any parallels found between the comparative models and *A. robustus* can be informative about the selective pressures acting on the temporal morphology and hearing.

Selection of Comparative Models

The selection of mammal models to compare to the *A. robustus* and *A. africanus* relationship had to fit certain specifications. The two species had to be closely related, and one species had to exhibit highly specialized masticatory apparatus compared to a more generalized masticatory apparatus of the other species. Unfortunately, within the hominoid group, there were no good comparisons. However, a more distantly related primate, the Gelada baboon (*Theropithecus gelada*) was chosen as a good model for more specialized masticator species. Clifford Jolly was one of the first anthropologists to introduce baboons as a way to study humans and early hominids. In 1970, he developed the “Seed-Eater Hypothesis” for early hominid origin. His theory focused on the similarity of the *Australopithecus* adaptations to mastication and the adaptations of the Gelada baboon, *Theropithecus gelada*. Both species were well adapted to prolonged and powerful chewing, resulting in similar morphology. *Papio papio*, the Guinea baboon, functions as the non-specialized counterpart to the Gelada baboon because its gracile morphology reflects a more eclectic diet.

Shared features between the Gelada baboon and *A. robustus* include: a more vertical face, teeth positioned under the skull, a robust mandible by the molars, expanded posterior teeth, temporal origins set forward on the cranium and evidence of very powerful masticatory muscles. These cranial features indicate that Gelada baboons and *A. robustus* were meeting their environmental needs in a similar way. Jolly supported his theory with additional habitat similarities, like the open country habitat, and postcranial similarities. Gelada baboons are specialized masticators to adapt to their graminivorous diet, which involves prolonged chewing. Over 90% of their diet is grass and they are the only graminivorous primates to this extent, consuming seeds more preferentially than leaves (Jolly, 1970).

Though the “Seed-eater Hypothesis” failed to fully describe the origin of hominids, Jolly’s work set the stage for the comparison between the Gelada baboon and early hominids.

The Gelada baboon – Guinea baboon pairing can be applied to the study of heavily specialized masticators and their more generalized relatives. This pairing provided comparative data to the study of *A. robustus* and *A. africanus* that was particularly relevant because the pairing comes from within the Primate Order.

Delbert D. Davis's *The giant panda: a morphological study of evolutionary mechanisms* (1964) introduced the second pairing of comparative models. Davis related the extreme masticatory specialization of the panda, *Ailuropoda melanoleuca*, to the specialization of early hominids. Specifically, he describes the panda's postcanine teeth as "an astonishingly close parallel to [the] condition...in the fossil anthropoid *Paranthropus robustus*" (Davis, 1974). The panda has a similar degree of specialization compared to *A. robustus* because of a diet of rough, fibrous bamboo.

Davis specifies four adaptive changes in the head morphology of pandas that are seen in the *A. robustus* specimens: increased cheek tooth size, increased mass of bone tissue in the skull, elevation of the mandibular articulation above the level of the tooth row, and an increase in the total mass of the masticatory musculature. "The masticatory apparatus has undergone enormous adaptive modification in *Ailuropoda*" (Davis, 1964). Davis suggests that the morphology of *Ailuropoda* is an extension of the adaptive modifications already present in bears.

The panda, though not a primate, provides a good example of an extremely specialized masticator with adaptations to vertical chewing and grinding. Many of the bears in the *Ursidae* family could serve as a less specialized relative species. However, only one species has been studied for hearing capacity, *Ursus maritimus*, or the polar bear. Nachtigall (2007) pioneered a study of hearing in polar bears, where he found that polar bears have an acute, and wide range of hearing. The polar bear serves as the best unspecialized counterpart to the specialized panda bear anatomy because of the available hearing research.

My approach was to use these two mammal models, the Gelada and Guinea baboon, and the panda and polar bear, to model the effect of specialized mastication on the temporal anatomy compared to more gracile mastication. All of the robust masticators show similar expansion of the masticatory features of the cranium that make for efficient and powerful chewing as a response to dietary pressures. In addition, the gracile masticators were chosen from the same family of species, but showed a significantly reduced expression of the masticatory anatomy. I examined specimens for morphological differences between the pairings and when possible,

explored the known hearing capacities. Using my findings, I will apply them to the *A. robustus/A. africanus* comparison in an attempt to resolve whether highly specialized mastication influences temporal anatomy in consistent trends throughout the species studied. In addition, I will discuss whether the altered temporal and auditory structures affected the hearing capacity of the robust masticators, and explore the implications for the *A. robustus*'s hearing.

Methods

October 19-20, 2009, I conducted qualitative examinations of specimens at the Field Museum of Chicago, Illinois. I examined five Gelada baboon specimens (Catalog numbers: 27039, 27038, 27187, 27185, 27184); five Guinea baboon specimens (60607, 58944, 46002, 108982, 50818); three panda specimens (36758, 31128, 39514); and four polar bear specimens (74214, 81510, 51473, 51474). I recorded observations and made sketches of the areas of interest, specifically the temporal anatomy. I used a digital camera (Canon) to supplement my observations.

When possible, I chose wild-caught specimens to more accurately model the natural mastication patterns. Drawings were transmitted to tracing paper, scanned and adjusted in Adobe Photoshop®. The labeling is courtesy of Davis (1964), Hunt (1974), and Swindler and Wood (1982).

I supplemented my study with observations of Australopithecine fossil casts from the Paleoanthropology Laboratory (Room 231) at the University of Michigan. I examined casts of two *Australopithecus robustus* specimens (SK 48, KNM-ER 407A/B) and two *Australopithecus africanus* specimens (STS 5, STW 53). I recorded observations and made sketches of areas of interest for these specimens.

Results

Theropithecus gelada

Five Gelada baboons were selected, four males and one female, which were caught in the wild in Ethiopia. The Gelada baboons exhibited a fairly consistent pattern surrounding the temporal morphology. The external auditory meatus is small and circular, and its opening faces

posteriorly and superiorly. The external auditory meatus is positioned far back in the cranium, approximately within the posterior 1/5 of the cranial length (see Figure 1-1).

The ear canal can be viewed through the external auditory meatus, and in all five specimens, the canal is compressed into a narrow ovoid shape. The compressions act from a superoposterior direction and an inferoanterior direction. Externally, the ear canal is long and narrow, directed medially and anteriorly towards the auditory bulla (See Figure 1-4). Specimen 27038, a male youth without visible third molars, has a shorter canal but this may be related to its smaller developing cranial size. The ear canal forms a wide angle to the auditory and it appears as if the canal pinches at the bend to become narrower (See Figure 1-5). The external pinching is consistent with the internal view of the canal from the external auditory meatus.

The auditory bulla is very angular, without visible inflation of the middle ear space. It does not project far from the basal surface of the cranium and its morphology is similar across all of the specimens (See Figure 1-4). An internal view of the auditory region was achieved through a large hole in the occipital region of specimen 27187 (See Figure 1-2). Additional views were obtained through the foramen magnum. The petrous region typically increased in size towards the posterior lateral portion where the petrous pyramid meets the mastoid region. Later observation of Guinea baboons will show that the petrous pyramid of the Gelada baboons is less puffy in appearance (See Figure 1-3).

The Gelada baboons displayed large mastoids, resulting in a mastoid process extending below the external auditory meatus and often looking puffy or inflated (See Figure 1-1). A hole in the bottom of the mastoid of specimen 27038 shows a well-pneumatized mastoid. The postglenoid processes are typically narrow in the anterior-posterior plane, but tall in height, extending off the base of the skull and past the opening of the auditory meatus (See Figure 1-1). In most instances, the external auditory meatus is closely sandwiched between the postglenoid process and the mastoid. Within a shallow glenoid fossa is a visible articular facet extending the width of the fossa. The articular facet is large and overhangs into the region where the ear canal bends and narrows. The curvature and width of the ear canal seems to react to the shape, size and position of the articular facets (See Figure 1-5).

Papio papio

Five Guinea baboons were selected: two males, two females and one of unknown sex. All specimens were zoo-raised in Africa. The Guinea baboons showed certain morphological similarities with the Gelada baboons. The external auditory meatus is circular and larger than the Gelada baboons' dimensionally. Its opening faces posteriorly and the external auditory meatus is positioned more anteriorly on the lateral side of the cranium. The external auditory meatus is within the posterior 1/4 of the cranial length (See Figure 2-1). Specimen 46002 has an external auditory meatus that is trumpet-shaped, but this morphology is not present in the other specimens.

The ear canal can be viewed through the external auditory meatus, and there is no visible compression. The canal maintains its dimensions through the visible portion of the ear canal. Externally, the ear canal is shorter and wider compared to the Gelada baboons'. The canal forms a sharper angle to the bulla than in the Gelada baboon, which could be a factor of the shorter canal length and larger size of the auditory bulla. There is no external evidence of narrowing towards the bend (See Figure 2-2).

The auditory bulla is larger than the Gelada baboons' and its appearance is more rounded and bulbous (See Figure 2-2). The bulla projects more greatly off the basal surface. Specimen 108982 has a removable posterior portion of the cranium, including the occipital and parietals. The removable portion allows a clear view of the internal petrous pyramid (See Figure 2-3). The petrous region is more bulging than the petrous region of the Gelada baboons, and this is confirmed with views from the foramen magnum of the other specimens. The size difference of the petrous pyramid is not significantly different between baboon species, but the rounded, puffy appearance is still more consistent with the Guinea baboons. In addition, the petrous pyramid more clearly projects off the endocranial walls. Similar to the Gelada baboon, the petrous portion expands as it hits the mastoid region (See Figure 2-4).

The *Papio* baboons exhibit very small mastoids, with only an older male (specimen 46002) presenting a mastoid process lower than the position of the external auditory meatus. The other mastoids did not project beyond the inferior wall of the external auditory meatus (Figure 2-1). The postglenoid processes are equally small in both anterior-posterior dimensions and mediolateral dimensions. They do not extend far past the external auditory meatus, either.

Since the external auditory meatus is generally opens in the posterior direction, the postglenoid process does not closely abut the external auditory meatus as is the condition found in Gelada baboons. The shallow glenoid fossae have very small or weak articular facets that generally do not extend to the auditory region (See Figure 2-2). Interestingly, the older male (specimen 46002) has a larger articular facet on the right side that overhangs into the bend of the canal and this corresponds with a sharper angle into the bulla.

Ailuropoda melanoleuca

Three panda specimens were selected, two females and one of unknown sex. The specimens were caught in the wild in China. The temporal morphology exhibited by the pandas was very consistent among all specimens. The external auditory meatus is large and ovoid. The greater diameter is superoinferior, but the external auditory meatus is angled so the superior portion is posterior to the inferior portion. The opening faces laterally. It is positioned posteriorly in the cranium, with only a large mastoid separating the external auditory meatus from the back of the cranium. The meatus is in the posterior 1/8 of a very foreshortened skull (See Figure 3-1).

The ear canal can be partially viewed through the external auditory meatus, and it appears as if the canal angles anteriorly and slightly inferiorly into the middle of the cranium and the middle ear space. Specimen 36758 is partitioned into three pieces; one slice halves the cranium down the sagittal plane and the other slice cuts through the external auditory meatus of the right half of the cranium. This affords a view of the ear canal that is short, and appears to maintain the same dimensions of the external auditory meatus. Externally, there is no view of the ear canal because of a bony bridge formed between the postglenoid process and the mastoid that travels under the ear canal and blocks the external view (See Figure 3-2).

There is no actual auditory bulla because the tympanic bone is not inflated, but rather flattened against the inferior surface of the cranium. The external inferior tympanic surface is small and smooth, without inflation or topographical change to the basioccipital. It curves around the medial base of the large postglenoid process (See Figure 3-3). An internal view of the petrous portion is visible as well in the sectioned cranium. The petrous is small, and does not project from the endocranial surface (See Figure 3-4). It is positioned posterior to the external

auditory meatus. Because of the particular sectioning of specimen 36758, the middle ear space, or tympanic cavity, can be viewed. It is a very small, restricted space and there is no evidence of inflation in this area. The internal structures cannot be viewed through the foramen magnum in the other specimens.

The pandas exhibit very large mastoids that are wide mediolaterally, tall superoinferiorly, and wide anteroposteriorly. The mastoid extends inferiorly to the external auditory meatus and curves anteriorly. It closely borders the posterior border of the meatus as well (See Figure 3-1). A bony bridge connects the large mastoid to the very large postglenoid process. The bridge runs under the entire auditory region, compacting the region into a narrow anteroposterior space (See Figure 3-2). The postglenoid process shares similarly large dimensions with the mastoid. The hooked shape molds to a rounded cylindrical mandibular condyle (See Figure 3-5). Correspondingly, the glenoid fossa is deep and large. The large postglenoid process closely forms the anterior border of the external auditory meatus, setting up a very close spatial relationship between the postglenoid process and the mastoid. These large structures occupy a very narrow (anteroposteriorly) space in the foreshortened skull (See Figure 3-5). In addition, the angling of the external auditory meatus seems to follow the curvature and position of the surrounding large structures, including the large zygomatic process of the temporal bone.

Ursus maritimus

Four polar bear specimens were selected of unknown sex, coming from Canada, Alaska, and Greenland. They were wild-caught, and though they are not sexed, specimens 74214 and 51473 are small-sized, and specimens 81510 and 51474 are large. Without sectioning, the internal aspects of the polar bear are less accessible and the foramen magnum does not afford a good view of the interior aspect. Nonetheless, the external aspects are informative and fairly consistent in their differences from the temporal morphology of the pandas. The external auditory meatus is round in shape, though it is slightly smaller than the pandas'. The meatus opens laterally, and slightly anteriorly in some specimens. The external auditory meatus is positioned more anteriorly in the elongated polar bear cranium, in the posterior 1/4 of the skull (See Figure 4-1).

The ear canal can be viewed through some of the specimens' external auditory meatus, though there was frequently blockage in the canals. The canal looks short and wide, maintaining the dimensions of the meatus. The canal angles posteriorly as it travels medially towards the middle ear. Externally, the entire ear canal is visible on the inferior surface of the cranium, where it curves upward from the bulla to the meatus. It is shaped as a rounded, cylindrical tube that is gently angled posteriorly to meet the auditory bulla (See Figure 4-3). The external aspect corresponds with the view through the meatus with no visible compression of the ear canal. The canal is short and wide (See Figure 4-2).

The ear canal leads to an inflated, bulbous auditory bulla that clearly projects off the basal surface of the cranium. The connection between the ear canal and bulla is completely visible. The bulla is triangularly-shaped with the ear canal entering at the top of the triangle (See Figure 4-3). This contrasts with a curved rectangular bulla in the panda. The most notable distinction, however, is the clear inflation of the region and its elevation from the inferior surface. The internal view of the petrous region is difficult to maneuver because of the posterior, inferior orientation of the foramen magnum. Visibly, the petrous portion is not extremely inflated, but it projects from the endocranial wall in a way that is not seen in pandas (See Figure 4-5). The difference is drastic, considering the flattened and depressed appearance of the panda's petrous.

The polar bears have considerably smaller mastoids compared to the pandas. The mastoid is bulbous in appearance and is double the superoinferior height of the external auditory meatus (See Figure 4-1). Nonetheless, the mastoid is a small structure and matched by a smaller postglenoid process. The postglenoid process has a long squamosal plane on the posterior aspect. The long plane separates the glenoid fossa spatially from the external auditory meatus (See Figure 4-1). In addition, when the mandible is articulated with the cranium and the jaw is opened to the widest extent, the squamosal plane prevents the mandible from interacting closely with any part of the auditory region. The postglenoid process moves the action of the temporomandibular joint away from the auditory region (See Figure 4-4). The glenoid fossa is smaller and shallower than the pandas' but morphologically, the shape is similar as it curves to enfold a cylindrical mandibular condyle. Interestingly, specimen 51473, one of the smaller craniums, exhibits asymmetry of the glenoid fossae. The left glenoid fossa is smaller and shallower, and the left external auditory meatus is larger than the right meatus.

Australopithecus robustus

Two casts of *A. robustus* were selected. Specimen SK 48 comes from Swartkrans, South Africa and is dated to 1.8 mya. Specimen KNM-ER 407 A/B consists of two pieces, essentially the right and left temporals, and comes from Koobi Fora, Kenya. The skull fragments are dated to 2.6 mya (Tattersall, 1997). The two specimens do not afford a good view of the auditory region because of their fragmentary nature and the damage done to the SK 48 specimen. However, some observations could still be made about the temporal morphology.

The right temporal of KNM-ER 407 has the best preserved external auditory meatus. The external auditory meatus is small and somewhat ovoid, with a greater diameter superoinferiorly. The opening faces laterally and somewhat posteriorly (See Figure 5-1). SK 48 has a preserved right ear canal that is long, compared to the *A. africanus* specimens that will be described later. It is narrow and angled anteriorly towards the tympanic and petrous structures (See Figure 5-3). KNM-ER 407 supports this observation of the ear canal. It cannot be determined if the ear canal narrows or pinches medially, or if the canal bends towards the middle ear. KNM-ER 407 provides a view of both of the petrous pyramids inside the cranium. They are long, narrow and angular (See Figure 5-2). The morphology resembles the less inflated morphology of the Gelada baboon. In Guinea baboons, the petrous region inflated significantly towards the border into the mastoid region, but this inflation is not present in *A. robustus*.

The surrounding structures also suffered from damage, but KNM-ER 407 exhibits a broad, large base of a mastoid. The bottom of the mastoid has been broken, but judging from the present base, the mastoid is well-pneumatized and large. It does not project greatly below the inferior surface of the cranium, but the anteroposterior and mediolateral dimensions are large (See Figure 5-1). Though SK 48's mastoid is damaged, it appears to correspond with the greater volume and inflation of the KNM-ER 407's mastoid (See Figure 5-3). The two *A. robustus* specimens exhibit different morphologies of the postglenoid process. KNM-ER 407 does not have a clear postglenoid process. The posterior aspect of the glenoid fossa makes up the anterior wall of the external auditory meatus, and forms a ridge along the inferior aspect of the meatus that functions as a postglenoid process (See Figure 5-1). SK 48 has a small postglenoid process on the inferior surface of the right temporal that may be sectioned due to breakage, potentially indicating a larger postglenoid process when complete. Nonetheless, the postglenoid processes

are small and closely abut the ear canal and external auditory meatus. This places the action of the temporomandibular joint right next to the external auditory meatus and the other auditory structures. The glenoid fossa is deep and large (See Figure 5-3).

Australopithecus africanus

Two casts of *A. africanus* specimens were selected. Specimen STS 5 comes from Sterkfontein, South Africa and is dated to 2.15 mya (Herries, 2003). Specimen STW 53 comes from Sterkfontein, South Africa also and is dated between 2 and 1.5 mya. The skulls are more complete than the *A. robustus* specimens. The specimens have much better preservation of the temporal morphology, though because they are casts, the internal morphology remains unknown.

The external auditory meatus is large and circular, with the opening facing laterally. The meatus is positioned in the posterior 1/3 of the cranium in a very anterior placement (See Figure 5-5). The ear canal is short and wide compared to the *A. robustus* specimen (See Figure 5-4). The difference in dimension and length of the ear canal parallels the difference between the Gelada baboon and Guinea baboon. The canal is angled slightly anteriorly as it travels towards the tympanic cavity. STS 5 reveals a slight bend towards the tympanic structure. The interior petrous pyramid is not visible.

Both specimens have small mastoids, with a noticeable reduction in inflation compared to the *A. robustus* mastoids (See Figure 5-5). STS 5 has a very small postglenoid process that moves the action of the temporomandibular joint away from the external auditory meatus and ear canal. The postglenoid process only extends halfway down the height of the external auditory meatus (See Figure 5-5). STW 53 has an even smaller postglenoid process that appears as a slight hump anterior to the external auditory meatus and is largest laterally. However, the more medial aspect of the glenoid fossa, where there is no postglenoid process, turns into the anterior wall of the ear canal (See Figure 5-4). The glenoid fossa is smaller and shallower than the *A. robustus* specimens, though still fairly large (See Figure 5-4).

Analysis

Non-hominid comparative models

The qualitative investigation of the specimens revealed certain trends that encompassed the species pairings. The masticatory morphology underwent extreme adaptive modifications in the robust masticators, and this is seen in the musculature, dentition and overall robusticity of the craniums. However, the temporal morphology also seemed to undergo certain changes that are reactions or responses to the masticatory adaptation. These trends are generalized, but reveal changes in the robust masticators' temporal anatomy in comparison to the generalized masticators'. Eight major temporal changes to the heavy masticators' anatomy are:

1. Position of the auditory region is shifted posteriorly towards the back of the cranium.
2. The ear canal is compressed in a general anteroposterior direction.
3. The ear canal is limited in expansion potential by surrounding structures.
4. The auditory bulla, or tympanic cavity, is smaller in volume.
5. The internal petrous pyramid is smaller in volume.
6. The mastoid is larger and more projecting.
7. The postglenoid process is larger and more projecting.
8. The glenoid fossa responds to more joint and has larger articular surfaces for the temporomandibular joint.

Though the temporal structure has not been studied in depth as far as the relation between the bony structures and hearing capacity, it has often been suggested that the larger tympanic cavities are associated with better hearing ability (Wang and Tedford, 2008; Pavlinov and Rogovin, 2000; Elbroch, 2006; Hunt, 1974). In addition, the expansion in volume of many of the auditory structures allows for the possibility of hearing a larger range of frequencies because of the increased surface area for sound wave capture. In both the study of primates and the study of carnivores, authors have made reference to the link between expansion of the auditory structures and better hearing ability. Hunt (1974) associated an increase in middle ear cavity volume to increased auditory sensitivity in the Carnivora order, which includes the panda and polar bear. Fleagle (1999) describes the inflation of the bulla as poorly understood, but observed that the more inflated bullae seem to increase frequency perception.

The robust masticators exhibit decreased space for the auditory structures. To adjust for the expansion of masticatory-related structures, the auditory region is shifted posteriorly (See Table 1). Compression of the ear canal limits the sound waves that can reach the tympanic membrane, get transmitted through the middle ear and into the inner ear's cochlea. The ear canal acts as the first filter of audible sound waves and "maximal sensitivity is largely determined by the resonant frequencies of the ear canal" (Hauser, 1997). Though the effects are not well-known, the anteroposterior compression of the ear canal relates to the reduced space for the auditory region and could have potential repercussions in for hearing capacity. The surrounding structures, the postglenoid process and the mastoid, increased greatly in size and as an effect, appear to function as blocks against potential expansion of the auditory space. The large structures sandwich the auditory region, resulting in the compression of the ear canal (See Table 1).

External qualitative examinations of the auditory bullae and tympanic structures show a decrease in the available space for the middle and inner ear. The decrease in the volume of the middle ear, as seen from both ectocranial and endocranial views (See Table 1), could potentially result in reduced hearing capacity if large volumes equate to increased hearing capacity. Even without a full CT scan of the temporal region, the smaller volume can be seen by the size of the external structures that set the maximum limits of volume. The expansion of the mastoid however, could provide compensation for the loss of middle ear volume since the mastoid air cells are connected to the volume of the middle ear. The mastoid's function is not understood, even in humans. Various theories have attempted to describe the function of the mastoid as a gas reserve (Doyle, 2000); a temperature and gas regulator (Magnuson, 2003), an acoustical enhancer (Onchi, 1966); an insulator for the inner ear structures (Diamant, 1962); or a non-functional feature that lightens the weight of the bone (Krantz, 1964). There is no known consensus about the mastoid's function, so this potential explanation has no supporting evidence without further investigation.

The final limiting factor for the auditory region is the temporomandibular joint and its effect on the space available for the auditory structures. In the Gelada baboon, the articular facets showed that the mandibular condyles edged into the region where the ear canal met the auditory bulla. The expansion of the auditory bulla is limited by the movement of the mandibular condyles during chewing because of the close proximity of these structures (See

Figure 1-5). In the panda, both the proximity of the temporomandibular joint and the placement of the bulla at the base of the postglenoid process show that the auditory structures are positioned nearly on top of the joint action within the cranium (See Figure 3-5). Without expanding into the endocranium, the auditory structures reduce in volume. The changes to the temporal anatomy show a reduction in the volume of the auditory structures in the robust masticators that could have significant effect on their hearing capacities.

Australopithecines and the Comparative Models

The australopithecine observations show that, though not all of the eight temporal changes are present in the *A. robustus*, most of the changes are applicable to this hominid. *A. robustus* is a robust masticator that responded to selective pressures for powerful mastication in many of the same ways as the Gelada baboon and the panda. The temporal changes are hard to fully document because of the small and damaged fossil sample, but the general trends of the non-hominid robust masticators seem to describe the *A. robustus* condition as well:

1. *Position of the auditory region is shifted posteriorly towards the back of the cranium.*

Neither of the two specimens, SK 48 or KNM-ER 407 provides a good estimation of the position of the external auditory meatus on the lateral side of the cranium. The SK 48 cranium is crushed from the rear forwards (Wolpoff, 1994), but it is the more complete specimen. The KNM-ER 407 lacks a complete enough cranium to make positional determinations.

2. *The ear canal is compressed in a general anteroposterior direction.*

KNM-ER 407 has the best preserved external auditory meatus. The shape of the opening is ovoid, compressed anteroposteriorly to create a taller, narrower opening. In addition, an image of SK 83, an *A. robustus* specimen from Swartkrans, shows an ovoid external auditory meatus (Wolpoff, 1994). The SK 83 meatus looks as if it is being compressed from a superoposterior and an inferoanterior direction. These directions of compression are paralleled in the Gelada baboons. Though the ear canal cannot be viewed through the meatus, it is likely to either

maintain the dimensions of the external auditory meatus or narrow further. In addition, Yoel Rak found that three *A. robustus* specimens (SK 46, SK 848, and 52/SKW 18) had external auditory meatus “that form a trumpet shape which...tapers towards the middle ear from a mean diameter of 13 mm to 8.7 mm” (Rak, 1979). In contrast, the *A. africanus* were found to have parallel-walled meatus.

3. *The ear canal is limited in expansion potential by surrounding structures.*

Expansion of the ear canal is limited the mastoid and the glenoid fossa. The large mastoid lies closely alongside the external auditory meatus, and generally curls anteriorly around the meatus. The mastoid surrounds the posterior and inferior aspects of the external auditory meatus. The postglenoid process is small in both of the specimens, but KNM-ER 407 shows that the deep glenoid fossa is right next to the ear canal. The anterior aspect of the ear canal is formed in conjunction with the posterior aspect of the glenoid fossa. The shared bony wall means that the temporomandibular joint is restricting expansion of the ear canal. Both anteriorly and posteriorly, the ear canal is restricted.

4. *The auditory bulla, or tympanic cavity, is smaller in volume.*

The tympanic cavity or middle ear space cannot be viewed because there is no auditory bulla in *A. robustus* and the potentially visible inferior portion of the tympanic bone is missing or damaged in the specimens.

5. *The internal petrous pyramid is smaller in volume.*

KNM-ER 407 shows both of the internal petrous structures. There is no comparative data available from the *A. africanus* specimens, but the internal petrous of the *A. robustus* is long and narrow, with a closer morphology to the Gelada baboon’s petrous pyramid than to the Guinea baboon’s inflated petrous pyramids (See Table 1).

6. *The mastoid is larger and more projecting.*

The mastoids of KNM-ER 407 are definitely larger and bulbous compared to the *A. africanus* specimens. However, the mastoids do not extend their dimensions superoinferiorly like the Gelada baboons and the pandas. Instead, the mastoids increase their anteroposterior and mediolateral dimensions to create a large pneumatized structure. Additionally, though the mastoid region of SK 48 is damaged, the *A. robustus* specimens from Swartkrans are known to have larger mastoid processes (Wolpoff, 1994). SK 83 also exhibits a large mastoid process.

7. The postglenoid process is larger and more projecting.

Both of the *A. robustus* specimens have postglenoid processes, but they are small compared to *A. africanus* specimens'. In the Gelada baboon and the panda, the postglenoid process increased in size, bringing the action of the jaw joint close to the ear to limit the volume for the auditory structures. In *A. robustus*, the two morphologies (See Figures 5-1, 5-3) also bring the action of the jaw directly near the auditory structures, though the postglenoid process does not increase in size or projection. The restriction on the auditory structures is relevant to *A. robustus*, but despite the similarity in mechanics, this trend cannot be applied to *A. robustus* morphology.

8. The glenoid fossa responds to more joint stress in its structure and has larger articular surfaces for the temporomandibular joint.

The glenoid fossa of *A. robustus* is larger and deeper than the *A. africanus* specimens, indicating a response to strong forces going through the temporomandibular joint during chewing. In *A. robustus*, the absence of the postglenoid process brings the action of the jaw joint directly next to the auditory structures. There are no visible articular surfaces, but as the mandibular condyles fit into the glenoid fossa, they are right next to the auditory structures. This creates a situation in which the chewing motion closely, if not directly, interacts with the auditory region. In the Gelada baboon and the panda, the glenoid fossa was also very near to the auditory structures (See Table 1).

The unique temporal architecture found in the *A. robustus* encompasses some, but not all of the eight major temporal trends found in non-hominid robust masticators (See Table 2). The limitations of fossilization prevent certain observations of the auditory region, and the postglenoid process is the only temporal change that is not applicable to *A. robustus*. Nonetheless, the majority of the changes are paralleled among the robust masticators. As with the other species, there is a likely correlation between the size of the auditory structures and the hearing capacity. The effect is unknown, but *A. robustus* shows characteristics of decreased space for auditory structures similar to the Gelada baboon and the panda.

The external auditory meatus is smaller in *A. robustus* compared to the large circular external auditory meatus in *A. africanus* (See Plate 5). The smaller external auditory meatus filters the sound waves entering the auditory region, and its smaller size reduces the capture of certain sound wave frequencies. The ear canal, as inferred from the shape of the external auditory meatus, is compressed in a general anteroposterior direction. Additionally, as Rak found, the *A. robustus* ear canals narrows as it moves medially to the middle ear. This condition was seen in the baboons, where the Gelada baboon has narrowing of the canal while the Guinea baboon showed parallel-walled ear canals. Data on the tympanic cavities is not available and though, the only data available on the internal petrous pyramid comes from *A. robustus*, it can be described as angular and narrow.

The mastoid increases greatly in size, closely bordering the auditory region posteriorly. The mastoid also surrounds the external auditory meatus inferiorly as it curls forward to encompass the inferior border of the meatus. The auditory region is constricted as a result. However, the more important limiting structure surrounding the auditory region is the glenoid fossa. With small postglenoid processes, the glenoid fossa directly leads into the auditory region. Expansion in the anterior direction would be severely limited because jaw function would have to be reduced or the auditory structures would be crushed. These two structures, the glenoid fossa and the mastoid, sandwich the auditory region (See Table 2). The structural changes to the temporal anatomy do suggest a reduction in volume for auditory structures, as was seen in the Gelada baboons and the pandas.

Non-Hominids Hearing

Hearing research provided the next step in exploring the effect of heavy mastication on hearing ability. The field has been limited to certain species of interest, but there are some available auditory data relevant to this study for the four species: the Gelada baboon, the Guinea baboon, the panda, and the polar bear. The research is limited, but sets the basis for possible associations developing between the architecture of the ear and its function.

The Gelada baboon and the Guinea baboon were not individually tested for hearing capacity, though baboon hearing studies are not uncommon in the literature. Stebbins (1973) conducted a study of the hearing in the Cercopithecinae monkeys. He tested seven species of Old World monkeys and found “the differences between species are no greater than the intraspecies differences on the audiometric measures we have taken, so that we are able to present our findings for the subfamily Cercopithecinae as a whole” (Stebbins, 1973). His testing group included the Guinea baboon, but not the Gelada baboon. The subfamily Cercopithecinae’s auditory range extended from below 60 Hz to 40-45 kHz, wider than the human auditory range. Their hearing was most sensitive at 1 kHz and 8 kHz. While this may be a close approximation of the Guinea baboon’s hearing range, it does not necessarily relate to the Gelada baboon.

The Gelada baboons have a very complex communication system that has been well-studied. Bruce Richman (1976) studied the distinctive vocal sounds used to communicate between Gelada baboons and found that a number of calls concentrate below 2 kHz which is in the low-frequency hearing range for Cercopithecoids. There is a link between the auditory range of an animal and the vocal range, because an animal must be able to hear and communicate with other members of the species. For example, humans show high sensitivity in the 2 – 4 kHz range, which contains relevant acoustic information in the spoken language (Martinez, 2004). The complex nature of the Gelada baboon’s communication relies on sensitivity to the more subtle sound distinctions within the vocal range of frequencies.

The Gelada baboon’s behavior as it gathers seeds can play an important role in the hearing capacity. Gelada baboons disperse over a wide range to find and gather seeds (Dunbar, 1992; Iwamoto, 1979) As a result, they developed a wide series of calls to continue

communicating when separated by distance, and low-frequency sensitivity facilitates long distance communication. “An increase in low-frequency sensitivity could result in a considerable expansion of the distance over which primates can adequately communicate” (Coleman, 2004). Lower frequency sound waves travel further distances without loss compared to high frequency sounds (Bortolotti, 2008). If their vocal communication takes place at lower frequencies, their hearing would adjust to specialize in picking up the subtleties at the lower frequencies. For the Gelada baboon, the low-frequency sensitivity is an environmental adaptation. On the other hand, the Guinea baboons feed on leaves that can be gathered in groups, so their behavioral adaptation does not require a complex communication system, especially when body language can be more heavily relied upon. This may fit better into the general Cercopithecinae pattern of higher frequency sensitivity at 8 kHz.

The Gelada baboon condition can be compared to the blue monkey, *Cercopithecus mitis*. Brown and Waser (1984) found that blue monkeys produce a specialized, low-frequency boom call and exhibit enhanced low-frequency sensitivity. Anatomically, the blue monkey also provides a parallel of the Gelada baboon condition. Hauser (1997) suggests that the longer ear canal of the blue monkey relates to the increased sensitivity to low frequencies. Hauser compares the length of the ear canal to humans and rhesus monkeys, who have shorter ear canals. The blue monkey’s boom call is centered at 125 Hz. The Gelada baboon has a longer ear canal than the Guinea baboon, and potentially an increased ability to hear low frequencies.

Though the evidence is indirect, it is reasonable to suggest that the hearing capacity of the Gelada baboons is shifted to lower-frequency sensitivity compared to the Guinea baboon. The temporal morphology could be in response to selective pressures from the environment and behavior. However, the other possibility is that the Gelada baboon has similar hearing capacities as the Guinea baboons, and the temporal morphology is just an adjustment to maintain the same hearing capacity with the changed masticatory anatomy.

The hearing research on the Ursidae family is not much better than the situation with the baboons. Central to the choice of polar bear as the gracile bear species was a study by Paul Nachtigall of the hearing range of polar bears. Nachtigall (2007) studied the auditory range of three anaesthetized polar bears and found that they had sensitive hearing over a wide frequency range. Their most sensitive range is between 11.2 kHz and 22.5 kHz, though they remained fairly acute over the broad range of 1 kHz to 22.5 kHz (highest tested frequency). Nachtigall

suggests that the auditory range of the polar bear was larger, and further study was limited by technology. The acute hearing was related to the polar bear's hunting ability because the polar bear must be able hear the calls and noises of its prey. Nachtigall determined that one way to estimate the hearing of a species was to examine the calls of its prey. Ringed seals are prey to polar bears and their calls fall within 2 kHz to 8 kHz, which is within the polar bear's range of acute hearing. Polar bears exhibit a wide range of hearing, though the most sensitivity is achieved at the high frequencies.

Pandas have not been directly studied for hearing, but as a frequent zoo animal, there have been studies of the effect of noise on panda's stress levels. The stress levels are studied through measurements of locomotion, restlessness, scratching and vocalizations of agitation, and glucocorticoids excreted in urine. Owen (2004) found that pandas reacted most strongly to low-frequency noises. The males were able to significantly discriminate noise amplitude (loudness) for low frequencies, but not for medium or high frequencies which demonstrates an increased sensitivity to low-frequencies. Females' increased glucocorticoid levels also showed sensitivity to low frequencies, more than medium or high frequency noises.

In a similar situation to the Gelada baboon's environmentally forced communication system, the pandas encounter each other in a closed habitat of thick bamboo "with limited opportunity for visual contact" (Kleiman and Peters, 1990). As a result, pandas are found to be more vocal than other carnivores. The lack of visual cues and a complex system of auditory communication could suggest a greater emphasis in low frequency hearing and communication. Kleiman and Peters studied the eight major acoustic signals of the giant panda, and found that they centered in the 0 – 2 kHz frequency range. Corresponding to the low-frequency vocal range, the panda is likely to have low frequency sensitive hearing in order to communicate effectively.

Australopithecine hearing

Though *A. robustus* cannot be tested for hearing capacity, there has been some degree of investigation relating to Australopithecine hearing and certain osteological investigations on auditory structures. The difficulty in studying hearing in extinct specimens is that the full

function of each auditory structure is unknown. Equations have been developed that try to estimate the hearing capacity strictly from an anatomical viewpoint.

John Rosowski (1991) developed an equation that measures sound power as it travels through the middle ear and inner ear. However, his model oversimplifies the transmission of sound power by assuming the direction of transmission is linear and not affected by the muscles in the ear. Melchiorre Masali and Margherita Cremasco later developed a morphometric model to calculate “the fraction of sound energy transmitted from air to the endocochlear fluids under normal conditions” (Masali and Cremasco, 2006). The model was used on Neanderthal specimens and it was found that Neanderthal fell within the modern human range.

Unfortunately, the model requires measurements of all three ear ossicles and cannot be applied to Australopithecines because of the limited sample of ossicles. At most, one *A. robustus* specimen, SKW 18 has been found with both a malleus and an incus (DeRuiter *et al*, 2006), though nothing was published on them.

However, one ossicle can provide clues into the hearing capacity of these early hominids. Jacopo Moggi-Cecchi and Mark Collard (2002) found a stapes in the middle ear cavity of STW 151, an *A. africanus* juvenile. The researchers focused on the footplate area because it directly transmits the sound energy to the inner cochlea. The STW 151 footplate dimensions fell within the great ape range of variation. The great apes exhibit a wider range of sensitivity to sound extending into higher frequencies. Chimpanzees have two peaks of high sensitivity at 1kHz (low frequency) and 8 kHz (high frequency), whereas humans show high sensitivity at 1 kHz (low frequency) and a loss of sensitivity into the higher frequencies (Martinez *et al*, 2004). Moggi-Cecchi and Collard supplemented their STW 151 measurement with oval window measurements from other *A. africanus* specimens. “The size of the oval window is a reasonable proxy for the area of the footplate” (Moggi-Cecchi and Collard, 2002). The values fell within the great ape range as well, indicating that *A. africanus* may have been more sensitive to high frequency sounds than modern humans.

No study has replicated Moggi-Cecchi and Collard’s analysis to the same degree or with a different hominid species. However, there is one notable ear ossicle, an incus, that has been associated with *A. robustus*. In 1979, Yoel Rak published two papers regarding an incus bone found with SK 848, an *A. robustus* specimen from Swartkrans, South Africa. His study of the SK 848 revealed that “its unusual morphology is far beyond the range of normal variation

characteristic of the incudes of modern man and the great apes” (Rak, 1979). The unusual morphology is significant because the ossicles are highly stable and fully formed at birth, removing the possibility of environmental changes to the morphology (Hershkovitz, 1977). More significantly, Rak noticed that the acute angulation of the articular surface on the incus is characteristic of the rodent *Dipodomys merriami*. *D. merriami* has an ear that is highly specialized for low frequencies. In addition, the short process of the SK 848 incus is also shared with *D. merriami*, and “may indicate that, as in *D. merriami*, the ossicles were loosely suspended in the tympanic cavity” (Rak, 1979). Neither modern man nor the great apes exhibit these two characteristics.

In a later study, Rak (1994) suggests that the deviant morphology of the SK 848 incus is a result of pleiotropy and is non-adaptive. He does not speculate further on the functional significance of the changed morphology or its potential influence on hearing capability. However, there is little difference between the chimpanzee and human incudi, and they have different hearing capabilities. In addition, Segall (1944) examined the mallei of the panda and the polar bear, finding that there were many similarities in the morphology: prominent vertical ridge on the lower facet, broad base of the manubrium, small muscular processes, well-developed lamina, and “the upper and lower facets of the articulation plane form an obtuse angle with each other” (Segall, 1944). Despite these similarities, the panda and the polar bear also potentially have different hearing capabilities. The morphology of the SK 848 incus does appear more visibly deviant from human incudi morphology than the panda malleus morphology is different from the polar bear morphology (Rak, 1994; Segall, 1944). It is likely that morphological change of the ossicle would affect hearing, perhaps more drastically than the changes seen between chimpanzee and human hearing. Though the *A. africanus* species has a stapes and the *A. robustus* species has only an incus for comparison, it is reasonable to suggest a morphological difference between *A. robustus* and *A. africanus* ossicles that may also indicate a hearing difference.

As with the Gelada baboon and the panda, the evidence supporting *A. robustus*'s low-frequency sensitivity is indirect and not solidly conclusive. However, the behavioral parallels between the Gelada baboons and the pandas, relating to the complex vocal communication system, could be compared to what is known of *A. robustus*'s diet and habitat. A recent study by Sponheimer and colleagues found that *A. robustus* had a diverse diet ranging from fruits and nuts

to sedges, grasses and seeds, and perhaps even animals. The specimens showed evidence of a diet that varied by season and possibly by year, likely depending on weather patterns like rainfall. Sponheimer and his colleagues suggest that *A. robustus* may have been “migrating between more wooded habitats and more open savannas” (Sponheimer *et al*, 2006). In an earlier study, Sponheimer and Julia Lee-Thorp studied the diet of *A. africanus* and determined that *A. africanus* also consumed a variable diet. *A. africanus* is thought to have inhabited relatively wooded habitats, but the evidence shows that though they ate fruits and leaves associated with woodlands, they also ate grasses, sedges and grazing animals associated with grasslands (Sponheimer and Lee-Thorp, 1999).

A comparison of the diets of *A. robustus* and *A. africanus* shows that they ate similar food items, though “[*A.*] *robustus* may have included a higher proportion of tough, fibrous foods in its diet” (Sponheimer and Lee-Thorp, 1999). Environmentally, the *A. africanus* may have spent more time in the woodlands, while the *A. robustus* may have spent more time in the grasslands, but likely both occupied and traveled between the two habitats. Unfortunately, there is no conclusive link between vocal and auditory communication and environment, especially with so many unknown variables. Long-distance communication favors lower frequencies, and this is modeled by the food-collecting behavior of Gelada baboons, but the food-gathering methods of *A. robustus* or *A. africanus* is unknown.

In addition, “visual messages can transmit a greater quantity of information than messages of other channels” (Nöth, 1995). The loss of visual communication could necessitate a more complex auditory communication system that make up the amount of transmitted information. However, the behavior in terms of long-distance communication needs is also unknown about Australopithecines in general. Thus, despite available information about the environment and diet of Australopithecines, no distinction or inferences can be made about ecological pressures forcing certain behaviors, communication styles or auditory capacities.

Discussion

The observations of the Gelada baboons and pandas show some unexpected similarities beyond their heavy mastication apparatus. Though the degree of specialization in the panda is more extreme than the specialization of the Gelada baboon, the adaptations to a tough diet

requiring powerful chewing follow a similar pattern. *A. robustus* fits well into this pattern of heavy masticatory anatomy. Degrees of specialization are difficult to determine objectively, but *A. robustus* and the panda are well-matched in how drastically their craniums changed to accommodate the specialized mastication.

In response to the increased masticatory structures, the temporal structures underwent certain changes that fall into a somewhat consistent pattern among all three robust masticator species (See Table 1). The generalized masticator species, the Guinea baboon, the polar bear and *A. africanus*, represent family-specific morphologies that differ clearly from each other. The robust masticators hyper-emphasize the masticatory structures already present in the family. However, the focus and improvement of the masticatory structures has consequences on the rest of the cranium. Because of proximity, interaction and certain ontogenetic connections, the temporal bone is affected by the changes. Considering the differences between the species used for comparison, on the basis of morphology, the species are relatively and surprisingly similar. *A. robustus* falls into the trends fairly well, with a majority of the trends applying to the temporal changes seen in its morphology (See Table 2).

Behavioral similarities between the Gelada baboon and the panda supplement the morphological similarities. Both species developed a complex vocal communication system because of environmental selection for food-gathering methods that disable visual communication. The studied vocalizations center on the lower frequencies that can travel longer distances better than high frequencies, and can be important to species that need to communicate information when distanced from other individuals. Sensitivity to low-frequencies is a likely and necessary consequence of lower frequency vocalizations. However, for *A. robustus*, there is not enough information about their behavior in their habitats, and there is no certainty about whether long-distance or non-visual communication was important. The available information about *A. robustus* traveling between woodlands and grasslands is not enough of a parallel with the Gelada baboon or panda behaviors to conclude, or even indicate, the possibility of a behavioral parallel.

With only one half of the comparison applicable to the *A. robustus* condition, the issue of relevance is at the forefront of the discussion. The concern is that the panda is not a good model for *A. robustus*. Davis discussed comparative anatomy extensively in relation to pandas, suggesting that there is uniformity among the structure of vertebrates. With structural uniformity

already well-established, Davis focused on the observable differences in structure between related forms (Davis, 1964). The inclusion of non-primate pairings in this study utilizes both aspects of comparative anatomy, structural uniformities and structural differences, to investigate the mechanisms responsible for the differences in temporal anatomy. Limiting the study to just the Primate Order drastically reduces the information that can be gained about the effects of specialized mastication. The panda has, arguably, the closest degree of masticatory specialization to *A. robustus* found in the mammal kingdom. However, despite the shared evolutionary history as vertebrates, the Gelada baboon and the panda are very different and very distantly related species. Additionally, while *A. robustus* is in the Primate order with the baboons, the phylogenetic connection is still distant. The Gelada baboon and the panda may be responding similarly to:

1. Diet – their diet requires a heavy masticatory apparatus with morphological consequences
2. Environment – they may have different methods of food-gathering, but these methods remove visual communication to influence how they vocally communicate in the environment.

However, there is no certainty that if *A. robustus* had a similar environmental situation, where visual communication was not possible, then the species would respond with complex vocal communication systems centering on lower frequencies. In addition, it is not clear whether the dietary pressures that drove masticatory change drove the hypothesized low frequency hearing in the Gelada baboon and the panda, or whether the environmental and behavioral pressures are driving the low frequency hearing. However, it is possible that both selective pressures worked in conjunction to a similar end result in the Gelada baboon and the panda. If the low frequency sensitivity is a result of changed temporal morphology alone, there is a possibility that *A. robustus* would also have lower frequency hearing, at least in comparison to *A. africanus*.

Conclusions

The comparative analysis of the Gelada baboon, the Guinea baboon, the panda and the polar bear has revealed some trends in how specialized mastication affects the temporal morphology and the auditory structures housed in the temporal bone. In addition, the paralleled morphological changes found in *A. robustus* provide some information to a relatively

underdeveloped area in early hominid studies. There are indications about the possible hearing capacity of *A. robustus* linked to its unique masticatory specialization. *A. robustus* may be more sensitive to low frequencies compared to *A. africanus*. The selective force acting on the robust masticators as they adapted to tough or hard diets is very similar between species, but without a conclusive link between morphology and function, it is unknown whether morphology alone can force low-frequency hearing. Environmental pressures on how food is gathered and how individuals interact could equally force low-frequency hearing, but already within the Gelada baboon and the panda comparison, it can be seen that they are responding to different conditions. The environmental pressure for Gelada baboons is for long distance collection of seeds, whereas the environmental pressure for pandas is for loss of visibility in a bamboo-dense forest. It is significant to note that within the parameters of comparative analysis, *A. robustus* is neither a baboon nor a bear in phylogeny or behavior, and this may be significant.

This study has revealed a number of questions about the life of *A. robustus*, and potentially illuminated one small aspect of our knowledge, which is a better understanding of the morphological changes that took place in the temporal morphology of *A. robustus*. The next step to further the investigation of hearing in *A. robustus* and the effect of specialized mastication on hearing capacity would be the use of CT scans to look at the internal structures, like the actual tympanic cavities and the area housing the cochlea. Further research on the effect of changes to the osteological features of the auditory region could go a long way in improving our knowledge of hearing. Finally, more testing on the hearing of living mammals could find some as-yet-unrealized relevance to early hominid studies.

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Table 1 - Summary Table of Observations for non-hominid specimens

	Gelada baboon	Guinea baboon	Panda	Polar bear
External auditory meatus (EAM) appearance	Small, circular	Large, circular	Large, ovoid (compressed anteroposteriorly)	Large, circular
EAM position on skull	Posterior 1/5	Posterior 1/4	Posterior 1/8	Posterior 1/4
EAM orientation	Opening is posterior/superior	Opening is posterior	Opening is lateral	Opening is lateral
Ear canal (internal view from EAM opening)	Compressed from superoposterior and inferoanterior directions	Canal maintains dimensions, no compression	Canal maintains narrow EAM dimensions	Canal maintains round dimensions
Ear canal (external)	Long, narrow and pinched medially; forms wide angle with bulla	Short and wide with no pinching; forms more acute angle with bulla	Not visible; hidden by bony bridge between mastoid and postglenoid process; short	Short, wide and curved slightly posterior and slightly inferior from the EAM
External auditory bulla or tympanic structure	Angular, does not project much off basal surface	Rounded, projects off basal surface	Flattened, flush to basal surface, curved rectangle shape	Inflated, triangular shaped, projects off basal surface
Appearance of internal petrous	Angular	More inflated, rounded	Flattened and depressed into endocranial walls, small	Not very inflated, but projects off endocranial surface
Appearance of mastoid	Large, inflated	Small, not very projecting	Large, projecting with anterior curvature	Medium-sized, not very projecting, bulbous
Appearance of postglenoid process	Tall, but narrow (A-P); projecting	Small, not very projecting	Large, hooked, very projecting	Smaller, less projecting; long squamous
Appearance of glenoid fossa	Shallow glenoid fossa, with large overhanging articular facet	Shallow glenoid fossa with weak articular facets	Deep glenoid fossa that is very curved	Shallower glenoid fossa, similar curved shape

Table 2 - Summary Table of *A. robustus* temporal changes

Trends for Robust Masticators	<i>A. robustus</i>
1. Position of the auditory region shifted posteriorly	————
2. Ear canal compressed anteroposteriorly	present
3. Ear canal limited by expansion of surrounding structures	present
4. Tympanic cavity is smaller	————
5. Internal petrous pyramid is smaller	present
6. Mastoid is larger	present
7. Postglenoid process is larger	not present
8. Glenoid fossa is larger, deeper	present

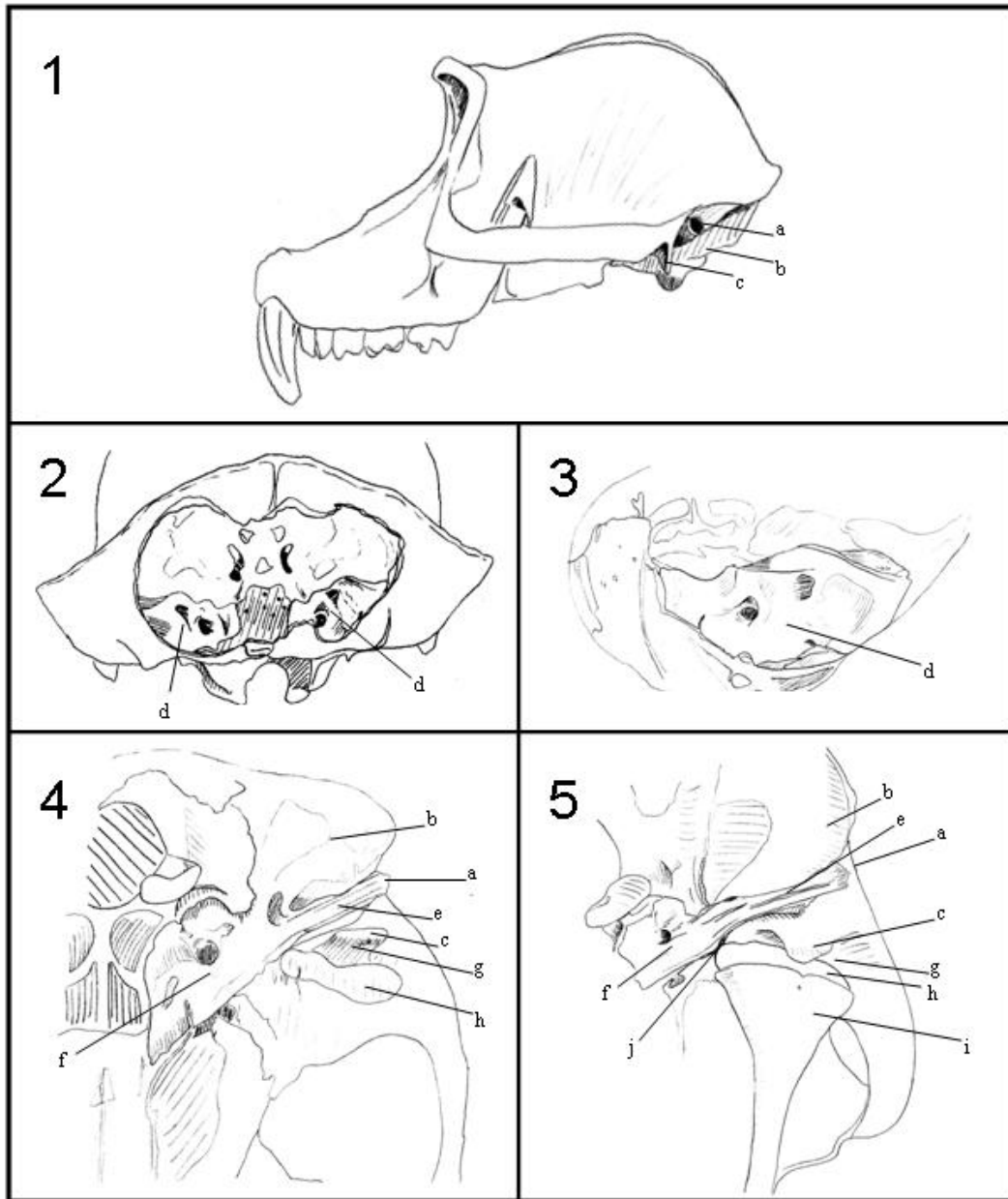


Figure 1-1: Lateral view of Gelada cranium. **Figure 1-2:** Posterior view of cranium with a hole in the occiput. **Figure 1-3:** Close-up view of left petrous pyramid. **Figure 1-4:** Inferior view of right temporal region. **Figure 1-5:** Posteroinferior view of temporal region interacting with mandible. *a. external auditory meatus; b. mastoid; c. postglenoid process; d. petrous pyramid; e. ear canal; f. bulla; g. glenoid fossa; h. articular facet; i. mandibular condyle; j. overhang of articular facet into auditory region*

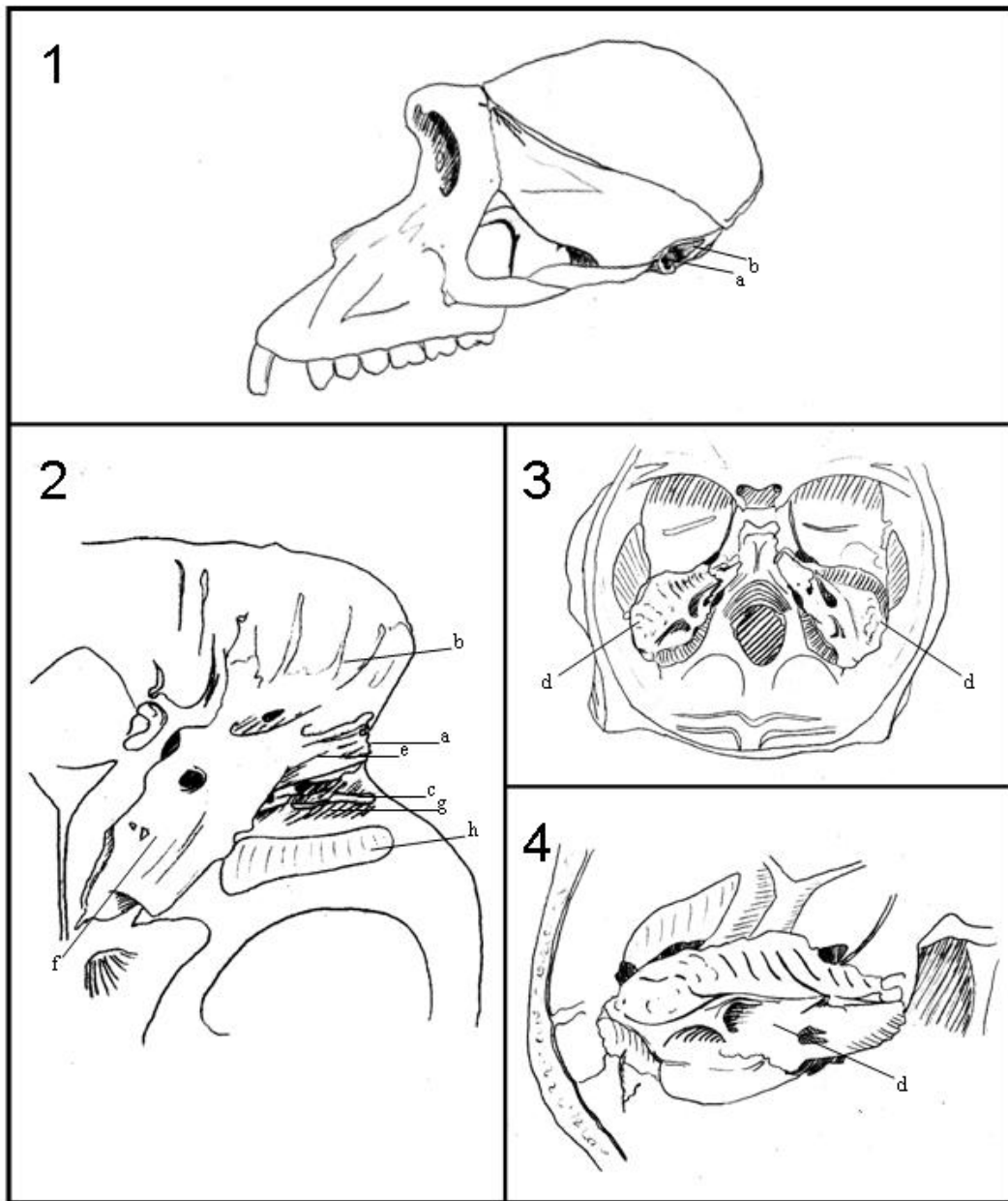


Figure 2-1: Lateral view of Guinea cranium. **Figure 2-2:** Inferior view of right temporal region. **Figure 2-3:** Posterosuperior view of endocranium with skull cap removed. **Figure 2-4:** Close-up view of left petrous pyramid. *a. external auditory meatus; b. mastoid; c. postglenoid process; d. petrous pyramid; e. ear canal; f. bulla; g. glenoid fossa; h. articular facet*

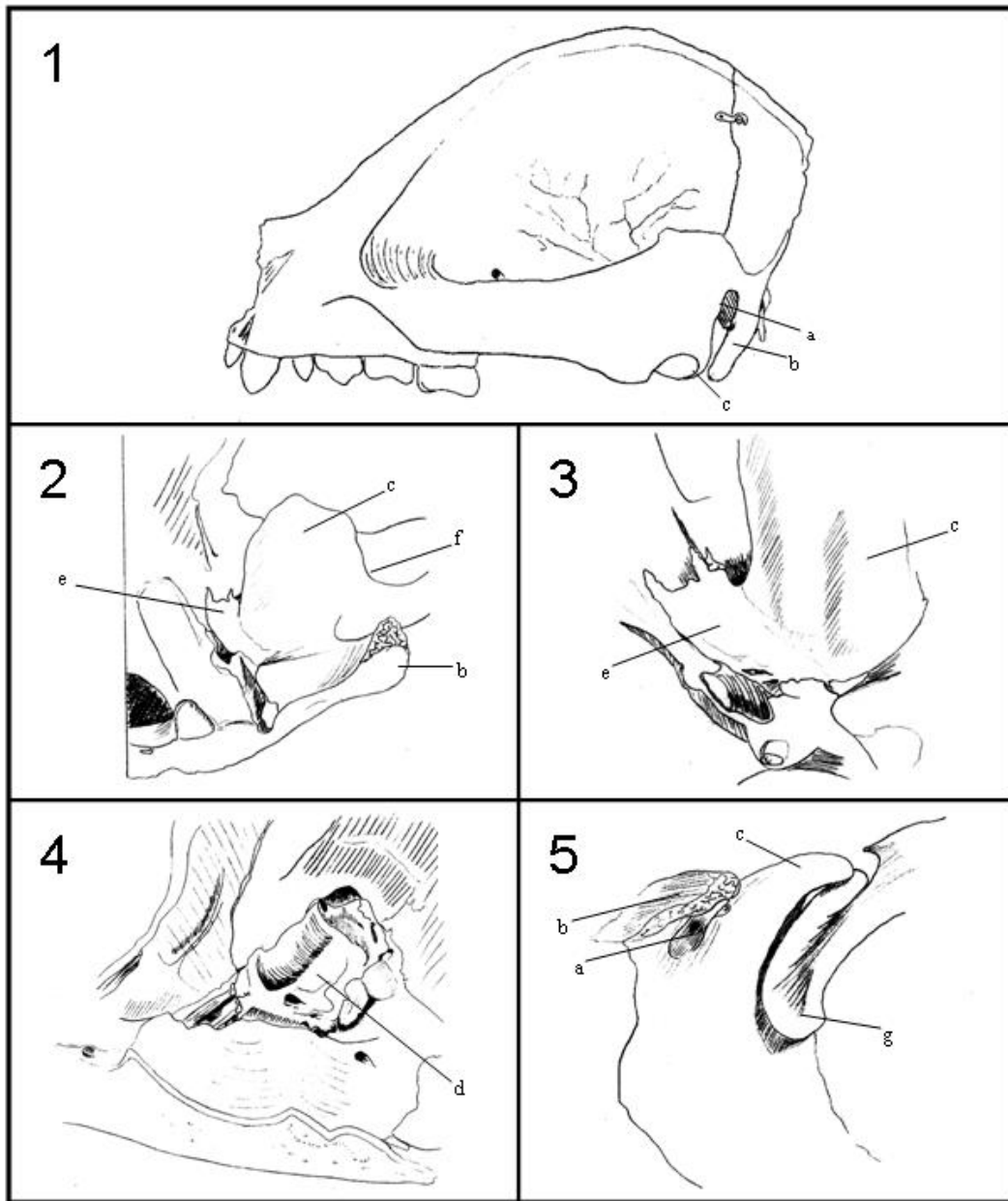


Figure 3-1: Lateral view of panda cranium. **Figure 3-2:** Inferior view of left temporal region. **Figure 3-3:** Close-up of inferior tympanic structure. **Figure 3-4:** Endocranial view of right petrous pyramid. **Figure 3-5:** Lateral view of left temporal interacting with mandible. *a. external auditory meatus; b. mastoid; c. postglenoid process; d. petrous pyramid; e. tympanic structure; f. glenoid fossa; g. mandibular condyle*

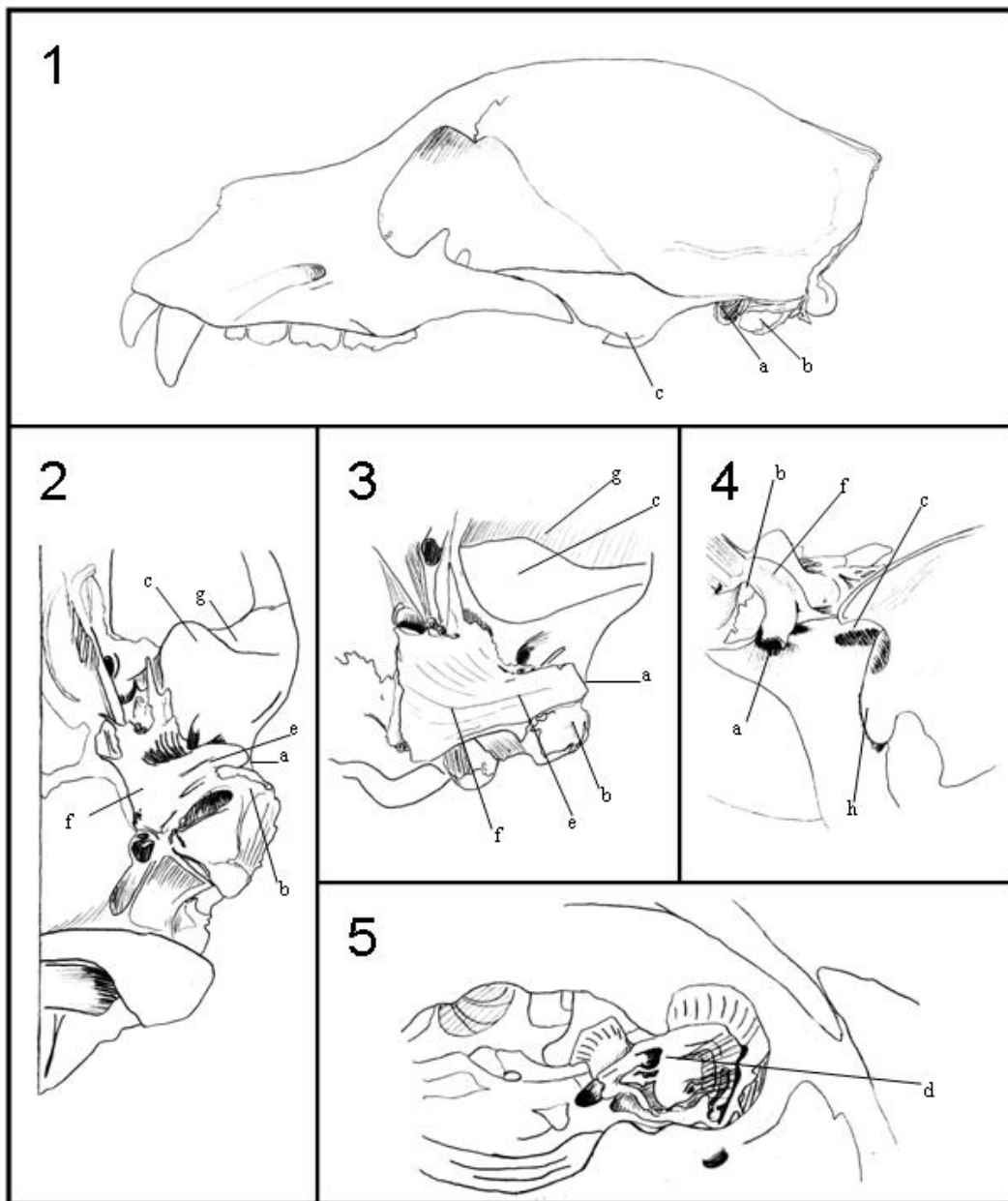


Figure 4-1: Lateral view of Polar bear cranium. **Figure 4-2:** Inferior view of left temporal region. **Figure 4-3:** Close-up of left auditory bulla. **Figure 4-4:** Lateral view of left temporal interacting with mandible. **Figure 4-5:** Posterior view of right petrous pyramid through the foramen magnum. *a. external auditory meatus; b. mastoid; c. mastoid; d. petrous pyramid; e. ear canal; f. bulla; g. glenoid fossa; h. mandibular condyle*

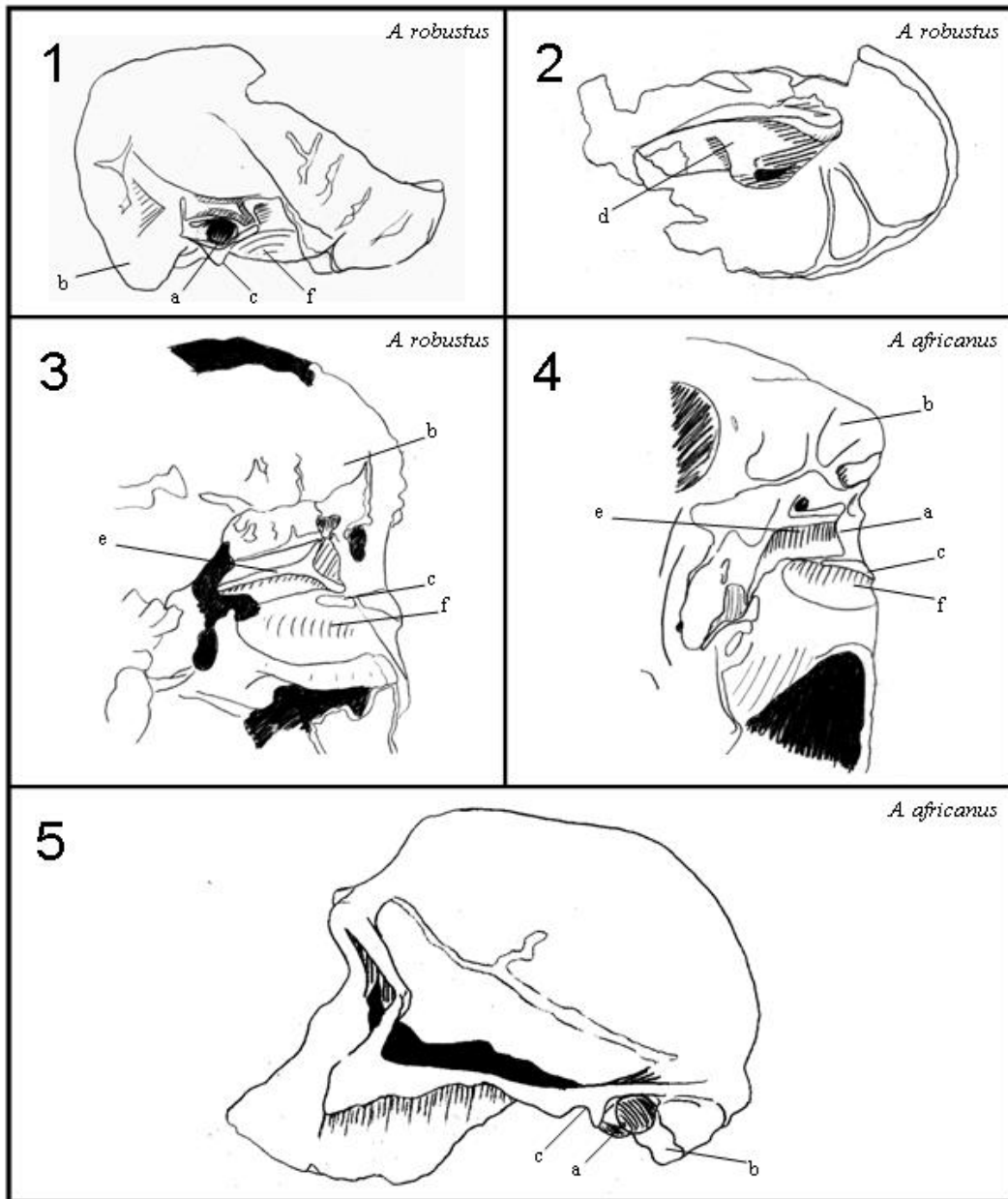


Figure 5-1: Lateral view of *A. robustus* (KNM-ER 406) right temporal fragment. **Figure 5-2:** Endocranial view of KNM-ER 406 right petrous pyramid. **Figure 5-3:** Inferior view of *A. robustus* (SK 48) temporal region. **Figure 5-4:** Inferior view of *A. africanus* (STS 5) temporal region. **Figure 5-5:** Lateral view of STS 5 cranium. *a.* external auditory meatus; *b.* mastoid; *c.* postglenoid process; *d.* petrous pyramid; *e.* ear canal; *f.* glenoid fossa