

Monkey Hear: A Morphometric Analysis of the Primate Auditory Ossicles

By

Yasmin Carter

A Thesis Submitted to the Faculty of Graduate Studies,

University of Manitoba

In partial fulfilment of the degree

MASTER OF ARTS

Department of Anthropology

University of Manitoba

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ABSTRACT

Hearing plays a vital role in the life of primates and an understanding of the anatomy of the auditory ossicles is necessary for analyses of hearing sensitivity. Morphometric studies conducted on the auditory ossicles of primates are rare and those few have tended towards simple magnitude and anatomical length measures. To address this issue, a landmark analysis based on Schmidt *et al.* (2009) was conducted on ultra-high resolution computer tomography (UhrCT) scans of twenty-six primate auditory ossicle chains. The resulting data were subjected to Euclidean distance matrix analyses (EDMA) in order to discuss differences between morphology between the species represented. A percussive forager, *Daubentonia*, was included to investigate whether its unique 'hunting' style affected its ossicular morphology. Two representatives of the non-primate family Cynocephalidae were also included as an outgroup to the primates in order to provide a non-primate comparison for the morphometric and taxonomic analyses.

The results of these investigations demonstrate that the greatest variable in ossicle morphology is size. In the shape analyses, the greatest differences occurred between the landmarks measuring the maximum length of the malleus, the maximum length of the incus and the maximum width of the ossicular chain bodies. The haplorrhine–strepsirrhine split is well reflected in ossicle morphology. Clustering into biological families was strong and the scaled data reflected the accepted taxonomy, although the hierarchy within families tended to be out of order compared to the cladogram. The results of the cluster analyses indicate that although diet and activity patterns may be relevant when discussing the morphology of a specific species, the grouping is not strong enough to suggest that these patterns are an important factor in adaptation. The auditory ossicles of the percussive forager are unusual in form and are the largest of all the

species represented. *Daubentonia*'s unique method of 'hunting' would seem a likely cause of the outstanding shape differences, although this remains impossible to prove without further study. The Cynocephalidae have a unique ossicular morphology within the context of this study. Morphological evaluation of the Cynocephalidae auditory ossicles demonstrates a lack of concordance with the majority of phylogenetic hypotheses and highlights the issues with using cluster analyses to make phylogenetic-morphological assumptions. The EDMA method provided unanticipated information regarding the articulation angles of the ossicular chains, particularly that of *V.v. variegata*. The results provided by this study present opportunities for future research and suggest many new questions on the morphology of primate auditory ossicles.

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CHAPTER I – INTRODUCTION

Hearing, as one of the five senses, is vital to the life of any animal, playing a role in communication, predator detection, as well as sourcing prey for omnivores and carnivores. As an integral part of the auditory system, the ossicular chain of primates has received much study focusing mainly on human evolution, functional analyses and to a lesser degree variation and morphometrics. The precise nature of the function and movement of these three tiny bones is as yet undefined. The introductions of relatively recent technology to the field, including computed tomography, with resolution sufficient to view the auditory structures, allow a return to the anatomical foundations of functional and evolutionary studies. This in turn allows examination of the tiny bones of a number of species for variation and similarities, which may suggest common descent or adaptation. It is this opportunity that has led to the current study.

Analyses of the morphology of non-human primate auditory ossicles are rare but not without precedent and this current work builds largely on the studies of Masali and colleagues (e.g. Masali, 1964; Masali and Chiarelli, 1967; Masali, 1968; Masali, 1968; Masali, 1971; Siori and Masali, 1983; Masali 1992; Masali *et al.*, 1992). Previous morphometric studies have mainly been restricted to simple measurements such as anatomically relevant lengths and weights, largely due to constraints placed by the bones themselves, they are small as well as notoriously difficult to recover and measure. The current study is freed, to an extent, from these restrictions by the use of ultra-high resolution computed tomography (UhrCT) of *in situ* ossicular chains.

The current study has four main goals. First, to evaluate and validate the methodological frameworks specifically used for the measurement of primate auditory ossicles set out by

Schmidt *et al.* (2009). Second, to use the data gained to determine if there are any measurable differences in auditory ossicle morphology between primates at the suborder, family and species level. The third aim was to examine *Daubentonia madagascariensis* to determine what, if any, variation exists between percussive and non-percussive foragers, as percussive foragers have a unique 'hunting' style, which relies to an extent on hearing. The final goal focused on the inclusion of representatives of the order Dermoptera, specifically *C. volans* and *G. variegatus*. The Dermoptera specimens are the only non-primates in the study and they were included as an outgroup to the primates in order to provide a comparison for the morphometric and taxonomic analyses. Finally, the study conducted hierarchical analyses and compared the resulting phenograms, based on ossicular morphology to the currently accepted phylogeny.

The second chapter provides an overview of the functional anatomy of the primate auditory system with emphasis on the development and structure of the ossicles. A discussion of previous studies conducted on the auditory region is included, focusing on mechanics, evolution and functional analyses as well as morphometrics and variation. The debates surrounding the species of Dermoptera and *Daubentonia* are considered as well as their importance in this study. The third chapter outlines the materials and techniques used in the study as well as the approach taken. The first section gives a brief summary of the non-human primate sample set as well as the imaging and post-processing techniques used to generate the data. In the discussion of data collection and landmarking, the intra-observer error study is outlined along with the techniques used in the full morphometric analysis. The choices of data analysis are considered and a discussion of the methods used to explore and test the results follows.

The fourth chapter reviews the results of the intra-observer error trial before exploring the results of the morphometric analysis including the principal coordinate, cluster and phylogenetic

analyses. The fifth chapter discusses the implications of the study and examines the auditory ossicle morphology evidence for non-human primate taxonomy. The sixth chapter discusses the conclusions that can be drawn from the study and outlines possible directions for future studies.

CHAPTER II – LITERATURE REVIEW

Introduction

Most studies of mammalian and primate ossicles tend to focus solely on case studies rather than broader taxonomic trends or themes. This chapter brings together our current knowledge and provides a background to the study of the primate auditory structures, specifically the ossicles. The history of the study of the auditory system will be presented, as well as a description of the function of the outer, middle and inner ear anatomy with particular focus on the ossicles as well as potential problems. Modelling and prediction of the mechanics of the auditory system will be discussed as well as the potential for understanding primate hearing. The ossicle's place in evolutionary and comparative anatomy research is also reviewed. Finally, previous research on ossicle morphology, metrics and variation is discussed.

Functional Anatomy

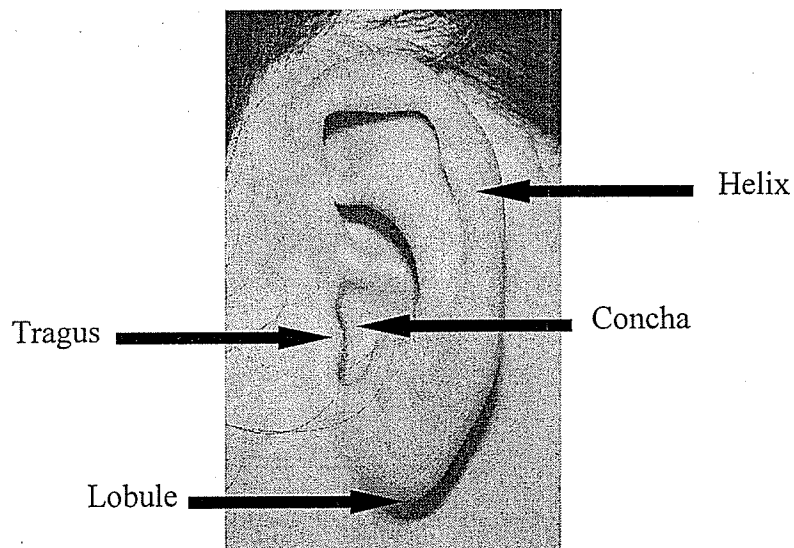
The following sections present an overview of the auditory system of primates where possible and more generally the mammalian system where not. The ear is comprised of a series of complex structures each playing their role in the conduction of sound. To understand changes in the morphology of the auditory ossicles their place in the wider context of auditory functional anatomy must first be determined. The function of the mammalian external and middle ears appear quantitatively similar. The external ear collects sound in the form of pressure waves and transfers the collected waves to the middle ear. The middle ear then transmits this power to the inner ear via the motion of the tympanic membrane and auditory ossicles (Rosowski, 1994). The main inter-specific differences then, lie in morphology rather than function.

The Outer Ear

The outer ears of primates demonstrate considerable diversity in both mobility and morphology, which frequently follows phylogenetic patterns (Coleman and Ross, 2004). The outer ear is unique to mammals and can be broken into primary subdivisions of: the pinna flange (also called the auricle), the concha and the external auditory meatus (EAM), although the transition between these divisions may not be as obvious in other mammals as it is in primates (Shaw, 1974).

The pinna flange or 'ear' is the cartilaginous and sometimes mobile, flap-like soft tissue structure that protrudes from the head. In humans, the pinna flange is separated into the helix, tragus and lobule as well as a varying number of folds and furrows (Figure 2.1). Primate pinnae are highly variable in size and complexity (Coleman, 2007).

Figure 2.1 - Photo of human outer ear labeled with terminology



Although little is known about sexual dimorphism in pinnae size, in humans there is a 9% difference in linear dimensions roughly paralleling total body size dimorphism (Shaw, 1974). An index of ear size versus head size was calculated for over one hundred primate species by Schultz (1969; 1973), who found the majority of prosimians have relatively larger pinnae than all anthropoids. The degree of pinnae movement appears to be correlated with the development of the outer ear musculature, which follows similar phylogenetic patterns as differences in the overall morphology of the outer ear. There also appears to be a gradual decrease in the differentiation and development of intrinsic and extrinsic musculature as one proceeds from prosimians to hominids (Coleman, 2007).

The concha is a funnel-like structure that connects the opening of the pinna flange to the narrower external auditory meatus (Rosowski, 1994). Although it is often included in the literature as part of the pinna flange, they are anatomically separate structures and appear to have differing functional qualities (Dallos, 1973). The external auditory meatus, commonly known as the 'ear canal,' is a tubular structure that provides restricted entrance to the middle ear, serving to protect it from external injury whilst still allowing the conduction of sound waves (Rosowski, 1994). Extant primates have an EAM that consists of a medial bony section and a lateral cartilaginous section with inter-specific variations of the ratio of each. The EAM of ceboids, lemuroids and most loroids are almost entirely cartilaginous, while that of cercopithecoids, tarsoids and hominoids are comprised mostly of bone (Coleman and Ross, 2004). In humans the EAM is approximately 30mm long with a diameter of 7mm (Dallos, 1973). In mammals the EAM is terminated by the middle ear border, consisting of the tympanic membrane (Rosowski, 1994).

The Middle Ear

The relationship between middle ear structure and performance is not completely understood, however, the main function of the middle ear appears to be to translate vibrations passed from the outer ear into pressure waves in the fluid-filled inner ear, while matching impedances between this fluid and the air. The architecture of the middle ear therefore can be assumed to reflect this purpose (Wilson, 1987).

Located within the air-filled tympanic cavity, the middle ear system of terrestrial mammals is composed of several basic elements. Firstly, the tympanic membrane for reception of sound, three ossicles coupled and supported by various ligaments, the Eustachian tube to and to equalise pressure in the cavity and the middle ear muscles that tense the tympanic membrane and ossicular chain resulting in alterations in the sound transmission (Amin and Tucker, 2006).

The tympanic cavity extends from the termination of the EAM on its lateral border to the bony cochlear wall on its medial extreme. It communicates with the inner ear via two openings in the bony wall: the oval window (*fenestra ovalis*) and the round window (*fenestra rotunda*). The Eustachian tube merges with the nasopharynx, remaining closed except during swallowing or yawning (Dallos, 1973). The bones that surround the cavity come from as many as eight different sources including the: petrosal, squamosal, ectotympanic and entotympanic (Rosowski, 1994). The floor of the tympanic cavity is unique in extant primates, in that it is almost exclusively composed by the petrosal element of the temporal bone. The rigidity this provides prevents adjacent soft-tissue structures from compressing the cavity during head movements such as mastication, which may alter sound transmission and therefore acoustic properties (Henson, 1974).

The morphology of the tympanic membrane and auditory ossicles vary greatly amongst species as do the volume, structure and number of compartments of the tympanic cavity, as well as the relative dimensions of the middle ear muscles. No correlation is apparent between the areas of the middle ear and hearing thresholds (Rosowski, 1994). Studying the inter-specific variation of the placental mammal middle ear, Nummela (1995) showed that overall middle ear size is negatively allometric to skull size. The middle ear structures, however, scale isometrically with each other through a wide range of species (Hemilä *et al.*, 1995). Generally the linear dimensions of the ossicles vary with body size, the larger the mammal the larger the ossicles. This scaling is not universal, however, and some mammals such as the golden cape mole have prodigious ossicles compared to their body size (Rosowski, 1994).

Soft Tissue

The soft tissue component of the primate middle ear comprises two intratympanic muscles and numerous ligaments (Hüttenbrink, 1992). The internal carotid artery and numerous nerves also commonly course through the middle ear region (Coleman, 2007). The entire ossicular chain is covered in a mucosal lining of the same type that lines the walls of the tympanic cavity (Dallos, 1973). The middle ear contains two muscles: the *tensor tympani* and the *stapedius*, the function of which can be interpreted as preserving the intact cartilage of the ossicular joints (Hüttenbrink, 1992). In anthropoids and strepsirrhines, the stapedius muscle arises from a sulcus or canal in the posterior wall of the middle ear cavity, while in tarsiers and tree shrews the muscle originates outside the tympanic cavity on the side of the skull (MacPhee, 1981). Both muscles are of the striated pinnate type, highly enervated, generating substantial tension with minimal displacement. These muscles are the effectors of the middle ear muscle reflex, which forms one of the vital auditory feedback mechanisms (Dallos, 1973). When contracted the stapedius pulls the head of the stapes posteriorly, almost at right angles to the

ossicular plane of rotation. The *tensor tympani*, the larger of the two, draws on the manubrium of the malleus anteriomedially, again roughly perpendicular to the plane of rotation (Dallos, 1973). Even though they are functionally synergists, the two muscles exert their force in opposing directions acting as anatomical antagonists (Fleischer, 1978).

Contraction of both these muscles results in stiffening of the ossicular chain, the exact purpose of which is debated. Dallos (1973) proposes that this stiffening results in a decrease in low-frequency sensitivity while providing a slight, less than 10dB, increase in the mid- to high-ranges. The contraction of these muscles usually occurs at higher sound pressures, with many advocating a protective mechanism to the stiffening, Fleischer (1978) disagrees with this hypothesis noting that a number of biological arguments can be made against this theory. Firstly, by the time the muscles react to the loud sound it has already occurred and the damage has been done. It is also difficult to imagine a typical situation where a primate would require such protection against excessive noise. Loud noises over 120dB are rare in nature and occur more commonly in recent industrialised human societies, hardly likely to have led to the evolution of a protective mechanism.

In humans the ossicular chain is suspended within the middle ear cavity by five ligaments, the number and morphology of which vary between primate species, although with similar functions. Three of these attach to the malleus, one to the incus and one, the so-called annular ligament, fixes the stapedial footplate to the oval window (Dallos, 1973).

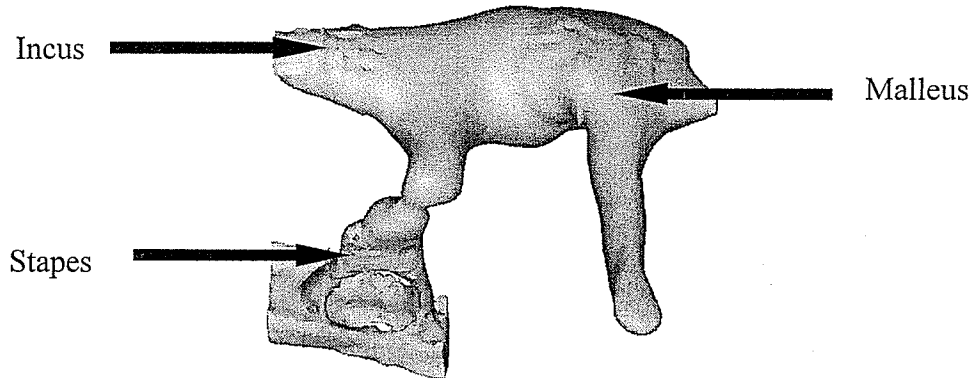
The lateral border of the middle ear is comprised of the tympanic membrane (*membrana tympani*), commonly called the 'ear drum.' This cone-shaped membrane is attached to the ectotympanic ring by its own fibrous border, the annulus, either on the inner border of the *sulcus*

tympanicus or its medial crest (*crista tympanica*) (Dallos, 1973). The outermost ossicle, the malleus, attaches to the apex of the tympanic membrane known as the *umbo*. The membrane is comprised of three layers; the outermost layer is continuous with the lining of the EAM, while the innermost is continuous with the lining of the tympanic cavity (Dallos, 1973). The middle layer consists of two groups of fibres, one radially orientated and the other concentrically arranged. These fibres result in the majority of the membrane being taut, giving its characteristic shape and structural stability, and consequently are named the *pars tensa* (Coleman, 2007). Helmholtz (1885) in his work on hearing proposed that the tympanic membrane is curved so that, when straightened, the fibres could force the *umbo* to move against a large force and therefore magnify small acoustic pressures sufficiently to displace the ossicles.

The Ossicles

The ossicular chain is comprised of three bones: the malleus, incus and stapes (Figure 2.2). This chain links the tympanic membrane with the inner ear. Together these bones form a functional unit with the joints between adjacent bones being relatively firm. In some mammals, notably the chinchilla and house mouse, the malleus and incus are so tightly bound as to appear fused (Rosowski, 1994). The ossicle joints are unique as they are constantly in motion and cannot be voluntarily controlled (Masali and Cremasco, 2006). With the exception of the stapes, these skeletal elements are unique to mammals and derive from the first branchial arches (Amin and Tucker, 2006).

Figure 2.2 - Diagram of Auditory Ossicle Chain terminology (*Loris tardigradus* pictured)

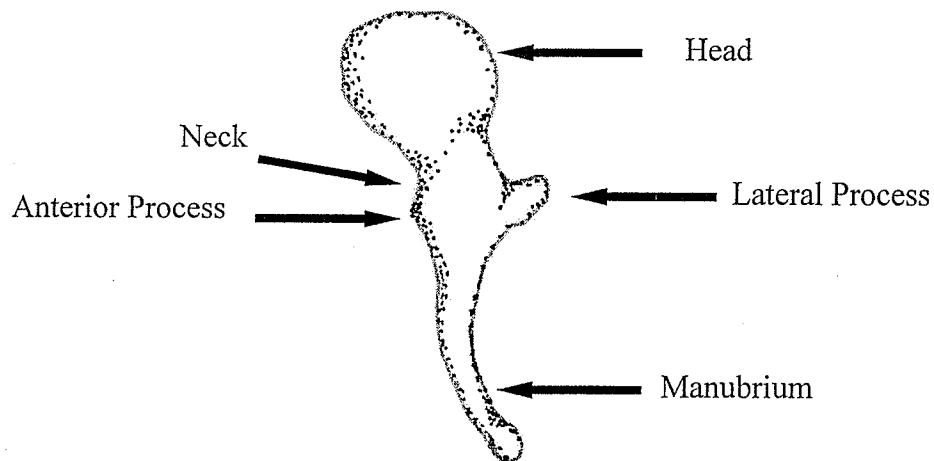


Early anatomical knowledge of the organisation of the ear was limited to those structures that were readily visible. According to O'Malley and Clarke (1961), Alessandro Achillini first noticed the presence of the bones of the human middle ear in the second half of the fifteenth century. It was not until the publication of *The Fabrica* by Vesalius of Padua in 1543, however, that the malleus and incus were identified and named for the first time. The discovery of the stapes is generally attributed to Giovanni Filippo Ingrassia of Naples. Cassebohm, in 1730 was probably the first to take measurements of the ossicles. Carus (1818) and Meckel (1821) studied the embryology and comparative anatomy of the auditory ossicles in the early nineteenth century (Arensburg *et al.*, 1981). The study of ossicle development and embryology was taken up again in the early twentieth century, and detailed descriptions of numerous species including primates soon followed. The literature now contains a solid description of the ear morphology of most major taxonomic groups (Hyrtl, 1845; Doran, 1878; Parker, 1886; van Kampen, 1905; Cockerell

et al., 1913; Schultz, 1969; Hinchcliffe and Pye, 1969; Lay, 1972; Fleischer, 1973; 1978; Henson, 1974; HersHKovitz, 1974; 1977; Hunt and Korth, 1980).

The primate malleus (Figure 2.3) is the largest and most external of the ossicles, consisting of a head (*capitulum mallei*), three processes: the manubrium (*manubrium mallei*), the anterior process (*processus gracilis*), the lateral or short process (*processus brevis*) and sometimes a neck (*collum mallei*). It is commonly referred to as the 'hammer' (Dallos, 1973).

Figure 2.3 - Diagram of malleus terminology (*Macaca nigra* 1 - LACM 90765 pictured. Illustration by Yasmin Carter)



The head of the malleus is enlarged and rounded and incorporates the articular surface that connects with the matching facet of the incus, forming the stiff malleoincudal joint (Dallos, 1973). The articular surface is commonly divided into a pair of medial and lateral facets, separated by a small ridge. The malleus attaches to the umbo via the manubrium, commonly known as the handle. Excluding humans and most hylobatids, many primates have a short

tubercle situated midway along the manubrium for attachment of the tensor tympani muscle (Coleman, 2007). The head is connected to the roof of the tympanic cavity by the delicate superior ligament (Dallos, 1973).

All catarrhines and some prosimians possess a constricted area of the manubrium located between the head and lateral process known as the neck (Coleman, 2007). The neck is absent in nearly all platyrrhines, except for a few species of *Callithrix*, who also demonstrate a spherical protuberance (*orbicular apophysis*), on the posterior side of the manubrium, which is rare in primates but commonly seen in bats, rodents, marsupials and insectivores (Hershkovitz, 1977).

Manifest in all primates, the anterior process extends anteriorly from the inferior angle of the head, providing attachment for the anterior ligament (Dallos, 1973). The anterior process is one of the most variable ossicular structures. In humans, the adult form is a small tubercle; in children it is a longer process, which may even form a short synarthrosis with the tympanic bone. The most prominent anterior process seems to occur in bats and shrews. In non-human primates the anterior process varies from a small tubercle to nearly absent (Rosowski, 1994). Associated with variations in the prominence of the anterior process are variations in the orientation of the manubrium relative to the horizontal plane and the long crus of the incus, known as the axis angle (Fleischer, 1973; 1978). In mammalian species with a reduced anterior process, the manubrium and long process of the incus are nearly parallel and both are perpendicular to the horizontal plane (Rosowski, 1994). Fleischer (1978) proposed that the anterior process is a distinguishing functional feature, since mammals with prominent anterior processes tend to be insensitive to sounds below 1kHz and more sensitive to sounds at higher frequencies. Projecting from the root of the manubrium, the lateral process is absent in all platyrrhines but well