A Gateway to All Post Graduate Courses

An MHRD Project under its National Mission on Education throught ICT (NME-ICT)

Subject: Anthropology

Production of Courseware

-Content for Post Graduate Courses

Paper No. : 14 Human Origin and Evolution

Module : 24 Comparative primate osteology

Development Team

Principal Investigator	Prof. Anup Kumar Kapoor Department of Anthropology, University of Delhi
Paper Coordinator	Dr. Satwanti Kapoor (Retd Professor) Department of Anthropology, University of Delhi
Content Writer	Dr. Vijeta Department of Anthropology, University of Delhi
Content Reviewer	Prof. R.K. Pathak Department of Anthropology, Panjab University, Chandigarh

Description of Module	
Subject Name	Anthropology
Paper Name	Human Origin and Evolution
Module Name/Title	Comparative primate osteology
Module Id	24

Contents:

Learning Objectives:

1. To know about the comparative anatomy of the primates i.e. skull, facial bone, cranium vault, etc.
2. To make a comparison of the different order or suborders i.e. Prosimians, Anthropoids, Strepsirrhini, Tarsiiform, Anthropoids, Platyrrhine, Catarrhine and Hominoid Skeleton.
3. To present a brief view of primate dentition.

1. Introduction

The comparative osteology of primates has interested researchers for centuries. Extant primates are characterized along with osteology also by various myological synapomorphies, which are shared, derived features including the presence of certain muscles in the hand (i.e., opponens pollicis and opponens digiti minimi) that increase dexterity and the fact that a specific arm muscle (the biceps brachii) does not insert onto one of the forearm bones (the ulna). Such features concern the movements of the forearm and hand and are probably related to the arboreal behavior of the first primates, although some of these features are found in a few other mammals, including non-arboreal taxa such as rats (Diogo et al, 2015).

1.1. Skull: The primate skull is a three dimensional, rather spheroid structure and is the most complex organization of bones in the skeleton. The size and proportions distinguishing the primate skull from other mammalian skulls illustrates series of morphological modifications associated with an arboreal mode of life. These include an increase in visual acuity with large and more frontally oriented orbits which are surrounded by a bony ring; a reduction in smell usually accompanied by reduction of the nasal region; a gradual enlargement of the brain with commensurate increase in the neurocranium (braincase); a development of various degree of upright trunk positions which changes the position of the foramen magnum from facing backwards to a more forward position downwards; and increased use of the forelimbs for prehension and procuring food, resulting in a general reduction of jaws and teeth (Swindler, 2012).

1.2. Bone of the face: An important feature of the primate face is its angle with the basicranial axis of the skull. Typically**,** the mammalian face lies in front of the cranium, forming only a slight angle with the cranial base. The angle becomes more acute in primates, especially in the anthropoids, where the

face is positioned beneath the cranium rather than in front of it. The changes in the craniofacial relations are correlated with the greater cerebral development of primates, and the alteration in the plane of the foramen magnum is associated with the reduction of the face as well as with the orthigrade or more erect posture of the trunk. Along with changes and commensurate reduction of the olfactory areas, there has been a recession of the snout, although there is a considerable variation in muzzle development among living primates and for various reasons. The frontal bone is low and sloping in many primates, but has become more vertical, conforming to the large frontal lobes of the brain during the later stages of the primate evolution. The frontal bone develops as paired bones in all primates and remains separated by a midline (metopic) suture in many prosimians. The maxilla, or upper jaw, containing the upper teeth, is composed of two paired bones in nonhuman primates, the pre maxilla and maxilla. Only, the upper incisor teeth develop and occupy the pre-maxilla. The pre maxilla is quite variable in size, extending upward for various distances between the nasal and maxillary bones. It is reduced in modern lemurs, and apparently the small size of the premaxilla is correlated with their diminutive incisors, which, in Lapilemur, are completely absent (Swindler, 2012).

1.3. Bones of the orbit: The paired lacrimal bones and lacrimal canals are positioned outside the orbits in lemuriforms and lorisiforms but are located within the orbits in the Anthropoidea, though occasionally the lacrimal canal may be found on the orbital margin or slightly outside the orbit in some anthropoid genera**.** A strut or ledge of bone has developed in primates to connect the frontal bone to the zygomatic bone. It is known as the postorbital bar. The postorbital bar is presented in all living primates as well as in some other mammals. Prosimians possess only the bony bar. In higher primates, the back wall of the orbit has an additional bony partition separating it from the temporal fossa (Swindler, 2012).

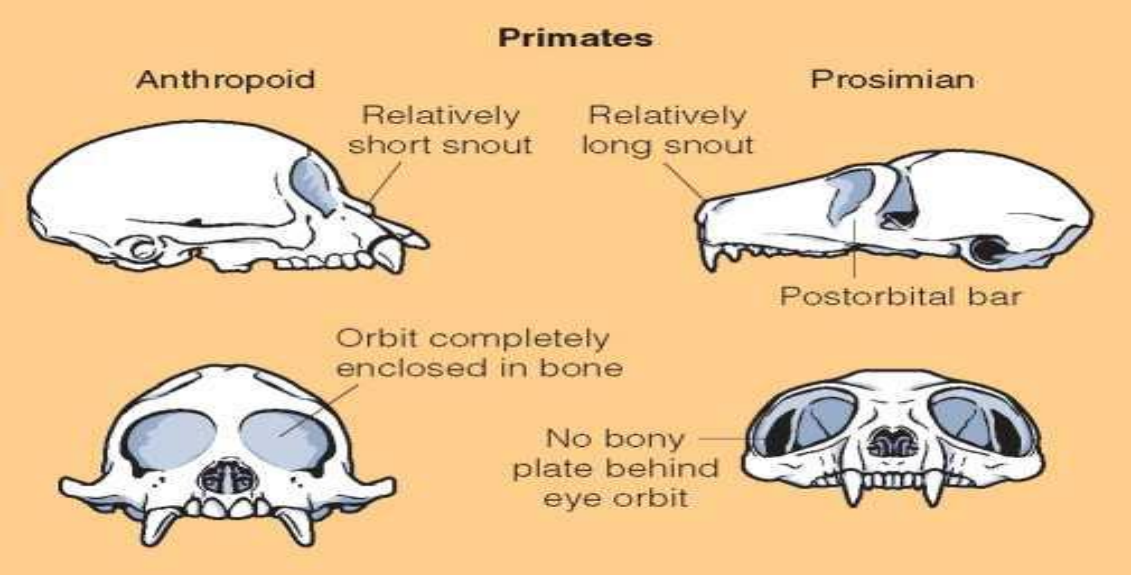

Figure-1: Bones of orbit and Snout

Source: http://www.worldhistory.biz/prehistory/89798-the-rise-of-the-primates.html

1.4. The cranial Vault: The term 'cranium' may refer only to the bones protecting the brain; in which case that portion of the skull is known as the cerebral cranium. The bones of the cranium vault are frontal, the two parietals, the ethmoid, the two temporals, the occipital, and the sphenoid bone, united by the fibrous sutures. During infancy and early adolescence these sutures allow growth of the brain, face and skull. In many groups of primates (usually in males), a sagittal crest results when temporal lines converge along the cranial vault for the attachment of the temporal muscles. Large nuchal crest, which forms a veritable bone ledge, is found in the male orangutan. Grooves, pits and foramina result from blood vessels, nerves and tendons passing on or through the bones as it develops.

1.5. Basilar View of the skull: The most obvious feature from the basal view of the skull is the large hole through the occipital bone, the foramen magnum, though which the spinal cord passes to become the brain inside the cranium. There has been a trend toward more forward and downward placement of the foramen magnum in anthropoids. On either side of the foramen magnum are the occipital condyles, which fit into a pair of depressions on the first cervical vertebra. This important connection between

skull and spine permits front to back motion of the skull. The joint between the atlas and the second vertebra allows the head to glide from side to side. Thus, we nod yes at the first joint and shake no at the second joint. The bony external and middle ear regions display characteristics that are important in taxonomic and phylogenetic studies of primates. In prosimians and most Platyrrhine the bulla is inflated into a relatively large, elongated structure lying just lateral and anterior to the occipital condyles, while in catarrhines, the petrosal is not inflated as a bulla. The external auditory meatus is formed from the ectotympanic bone in primates. This feature may be expressed as a ring lying within the bulla or attached to the wall of the bulla. In tarsiers and catarrhines, the tympanic annulus remains in contact with the temporal bone but is elongated into the external auditory meatus. This type of external auditory meatus present in a specimen is one of the easiest and clearest ways of distinguishing between Old World Monkey and New World Monkey skull. The mandibular fossa or glenoid cavity for the articulation of the lower jaw is part of the temporal bone. The articular surface of the glenoid cavity is rather broad and flat in prosimians, Old World Monkeys and New World Monkeys. It is more concave in hominoids, particularly in humans, where it becomes a deep, ovoid depression. There is a post glenoid process that forms the posterior wall of the fossa in all primates except Daubentonia.

1.6. Paranasal Sinuses: Several bones of the skull (the maxillary, frontal, ethmoid, sphenoid, vomer, temporal and palatine) may develop cavities or sinuses within the tissue between the two surfaces of the bone as they mature. This process is known as pneumatisation, is initiated by outgrowths of the mucous membrane of the nasal cavity and middle ear cavity. The mucous sacs wander into adjacent bones, slowly causing bone absorption, which may continue throughout life. The pneumatic cells of the middle ear normally invade the mastoid process of the temporal bone. These bony sinuses are differentially present among primates and are all subject to considerable variation in form and size.

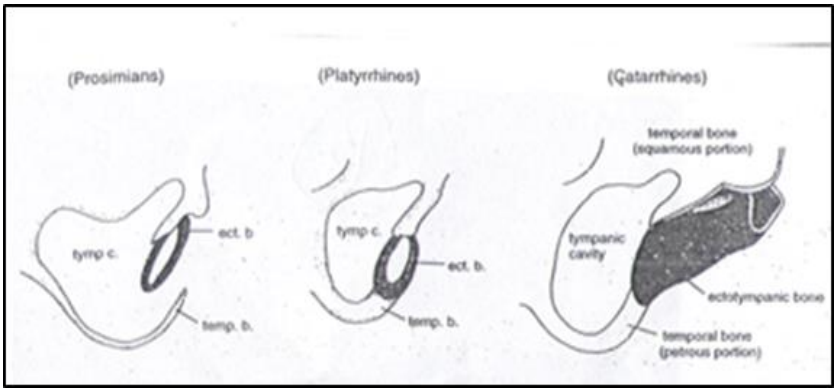

Figure-2: The structure of the bony external meatus in primates (modified from Hershkovitz, 1977)

Source: Swindler, D. R. (2012). Introduction to the Primates. University of Washington Press.

2. Prosimians and Anthropoids

The first major branch of the Order Primates is into the two Suborders: Prosimii and Anthropoidea. This distinction is made on a number of anatomical and behavioural features however the most obvious are found in the skull. There is a greater degree of midline fusion of skull bones in anthropoids: both the mandible and the frontal bone are a single bone in anthropoids and separate left and right bones in prosimians. The joint between the left and right frontal bones is a standard skull suture and immobile but the joint between the left and right mandibles is a fibrous joint that will allow a limited amount of movement. It is likely that this will affect the chewing mechanics of prosimians. Indeed the mandibular symphysis in some anthropoids is further reinforced by additional bony ridges (the so-called simian-shelf) suggesting that the mechanical stresses on the bone in this area are large. Post-orbital closure and post-orbital closure can be clearly seen. This may also be an adaptation for increased stresses on the skull during chewing. It is unlikely that protection of the eye is the sole reason, since so many other mammals that would benefit from increased eye protection do not have this bony adaptation. Prosimians possess a unique procumbent tooth comb in the lower jaw whereas anthropoids possess larger, flattened incisors (Sellers, 2000).

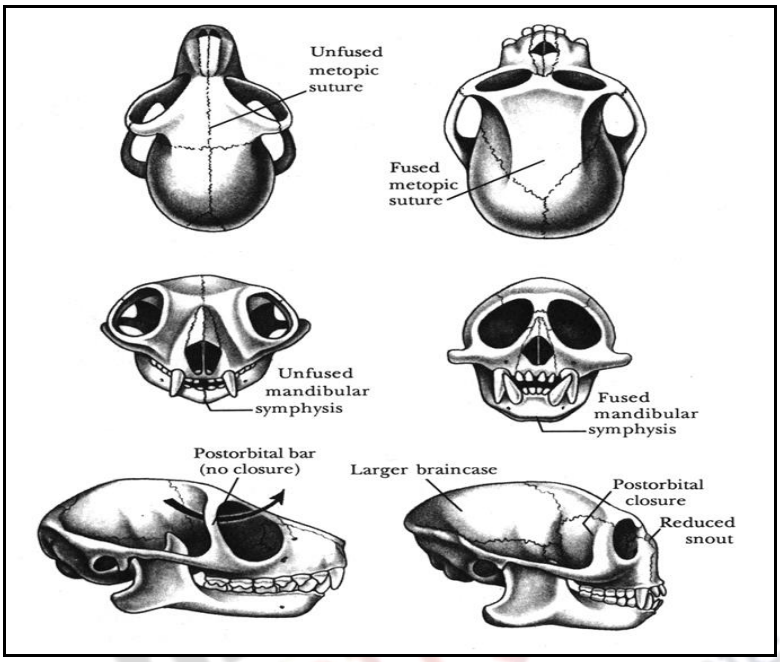

Figure-3: Skull differences between prosimians and anthropoids

Source: Sellers, B. (2000). Primate Evolution. University of Edinburgh.

3. The Strepsirrhini Skeleton

There is almost as much skeletal diversity among the extant galagos, lemurs, and lorises (modern members of the suborder Strepsirrhini; as there is in the whole order. If we include a consideration of the recently extinct lemurs, then this suborder certainly has had more variation in size, shape, posture, and locomotion than all of the living anthropoids combined. This group ranges in size from the small as 30 g. While the largest of living lemurs is not particularly impressive in size relative to hominoids and some monkeys, all of the recently extinct lemurs were larger than their surviving relatives. The largest of these, Archaeoindris, may have been nearly 200 kg, larger than most of the living hominoids. As impressive as they are in size, most of the recently extinct lemurs were even more interesting in their locomotor adaptations, with several species (Archaeolemur and Hadropithecus) converging on a more terrestrial monkey- like form, other giant forms displaying a bizarre form of arboreal morphology that included exceptionally long and curved digits and other skeletal elements. The living Strepsirrhini mostly have more typical body forms that can generally be divided into four categories:

(1) Relatively small slow bodies (e.g., those of the slow loris, Nycticebus, and dwarf lemurs, Cheirogaleus) that may represent the body plan of the most primitive ancestral primate.

(2) Small bodies built for quick movement (e.g., the bush babies, Galago, and mouse lemurs, Microcebus).

(3) Arboreal quadrupeds (e.g., ringtail lemurs, Lemur, and the "true" lemurs, Eulemur)—what most may think of as a typical lemur form.

(4) The "vertical clinging and leaping" lemurs (e.g., the indri, Indri, and sifakas, Propithecus). Almost all of the living Strepsirrhini fall more or less within one of these categories with one amazing exception: the aye-aye (Daubentonia). Exceptions aside, strepsirrhines have a fairly typical primate skeleton: substantial clavicles and opposable, powerful big toes. All have fairly large eyes surrounded by "postorbital bars"—bony struts connecting the frontal bone to the zygomatic arch to either support or protect the relatively convergent eyes. Most strepsirrhines have long tails and typical primate molars and premolars (albeit relatively primitive). Most also have "tooth combs"—a reorganization of the lower anterior dentition (incisors and canines) in which these teeth are long and thin and aligned as an apparatus used for grooming. They also have a "grooming" or "toilet" claw—a long sharp claw generally found on the second toe. The truly defining feature of the group—the wet "rhinarium," essentially a continuity between the upper lip and nose that allows improved use of the vomeronasal organ—is a predominantly soft-tissue feature. However, the strepsirrhine emphasis on olfaction does highly influence the shape of the skull: more than any of the other primates, lemurs have fairly elongated rostra. This anatomy allows for greater olfaction—a more important sense in this group than primates such as hominoids (as exemplified by the nearly ubiquitous scent glands used by these animals)—and makes the skull longer than almost all other primates (Diogo et al, 2015).

4. The Tarsiiform Skeleton

The small number of species of this group that is found in the islands off of Southeast Asia is unique among primates in several features. For one thing, they are strictly carnivorous, feeding exclusively on insects and small vertebrates that they capture through fast visual predation. This feeding strategy has a strong effect on their bony anatomy:-

1) The tarsiers have very long ankle bones, giving them enormous leverage for leaping.

2) They also have very sharp teeth for consuming soft animals.

3) The most distinctive osteological features of the tarsiers are their orbits and huge eyes. Each is bigger, in fact, than the animal's brain. This is a consequence of both the animal's nocturnal visual predation strategy and its lack of a tapetum lucidum—the reflective layer that is found on the back of the eye of strepsirrhines and many other mammals, but not of primates such as hominoids.

4) Aside from their size, the orbits of tarsiers are notable because they are much more enclosed in the back than those of strepsirrhines. There is a debate over whether this bony septum represents a true "postorbital wall"—a defining feature separating strepsirrhines from monkeys and hominoids— or whether this is an example of convergence, but suffice it to say, this is one piece of anatomy that seems to affirm the place of this unique genus somewhere as an offshoot between strepsirrhines and anthropoids (Diogo et al, 2015).

5. The Anthropoid Skeleton

In addition to the full postorbital wall, unlike strepsirrhines, anthropoids generally have fused frontal bones (tarsiers have variability in the fusion of their frontal) and fused mandibular symphyses, that is, a single, unpaired lower jaw, while strepsirrhines and tarsiers have right and left mandibles that they can move, with varying degrees depending on genus, independently. Anthropoids also differ from "prosimians" in their possession of generally larger brains, lack of claws (with the exception of one South American monkey group), generally broad incisors, and marked sexual dimorphism in most species (most commonly seen as larger canines in males than in females) (Fleagle, 1999).

6. The Platyrrhine Skeleton

Osteologically, New World monkeys can be distinguished from other anthropoids in their retention of three premolars in each quadrant of the jaw (i.e., twelve totals while catarrhines have only eight). There are also substantial (though fairly technical) details that define this group in terms of the morphology if the bones of their ear region and specific bones of the braincase come in contact with each other. The smallest monkeys, the pygmy marmosets (*Cebuella*) who weigh ~100 g, are members of this group.

Some platyrrhines are also the only primates with truly prehensile tails. In some species (e.g., the spider monkeys, *Ateles*) this remarkable limb can support the full weight of the animal and is truly as agile as a fifth hand/foot. Some platyrrhines have completely non-prehensile tails (e.g., tamarins, *Saguinus*) while other species (e.g., the capuchin monkeys, *Cebus*) have some prehensile abilities that are not as complete as the most derived members of the group. Individual South American genera have osteological features that are unique. For instance, owl monkeys (*Ateles*) have exceptionally large orbits because these nocturnal animals (the only nocturnal haplorhines) lack tapeda lucida and thus have to collect as much light as possible by having very large eyes. Another orbital feature, a hole connecting the right and left orbits in squirrel monkeys (*Saimiri*), has less obvious adaptive significance. Possibly the most dramatic unique osteological adaptation is the hyoid (the bone at the top of the voice box) of howling monkeys (*Alouatta*), the largest of the Platyrrhines (~7–10 kg). In these monkeys, particularly in the males, this normally small bone at the top of the throat is expanded into a massive resonance chamber nearly as large as their skulls. This functions to amplify their impressively loud vocalizations (Diogo et al, 2015).

7. The Catarrhine Skeleton

Skeletally catarrhines have more reduced dentition than the other primates, having lost one of the premolars. Members of this clade can be distinguished from other primates in details of the ear region, but beyond this, there are not many defining osteological features of the group. These are generally the largest primates, with the smallest extant monkey, the talapoin (*Miopithecus*), at ~1 kg, which is fairly large, compared too many of the smallest strepsirrhines and platyrrhines, and the largest living members of the Catarrhini, the gorillas (*Gorilla*), are clearly the largest living taxon in the order at up to ~230 kg in the wild. One extinct catarrhine, the hominoid *Gigantopithecus*, was the largest primate to ever live at ~300 kg (Diogo et al, 2015).

8. The Hominoid Skeleton

One obvious feature often used to define this group is the lack of an external tail. While some other catarrhines have also lost their tails (e.g., the Barbary macaque, *Macaca Sylvanus*, is often called the

Barbary “ape” because this species has no tail), none of the hominoids have external tails nor did any of their common ancestors. In general, hominoids have a more orthigrade or upright posture. The hylobatids, that is, gibbons and siamangs, are highly specialized for a form of below-branch suspension that is so fast and explosive that it is often referred to as “ricochet” brachiation. Gorillas (*Gorilla*) and chimpanzees (*Pan*) exhibit a form of quadrupedal locomotion known as “knuckle walking” in which the weight of the front of the body is supported by curled fingers. The adaptations found in humans can generally be broken into two major categories:-

(1) Changes related to our bipedal locomotion (e.g., changes in our spines, hips, angles, knees) (2) Changes related to advances in our cognition (not only our large brain cases, but also modifications to our teeth and hands in response to technological advances in feeding and tool use).

9. Primate Dentition

All primates have diphyodonty, meaning they have two sets of teeth. The first set of teeth, often termed “baby” or deciduous teeth, appear early in infant development, and then are replaced by a full set of adult teeth. Teeth are found in the maxilla, the part of the upper jaw from which the teeth grow, and the mandible, the lower jaw. Each tooth can be divided into the following three parts: crown, neck, and root. The tooth crown is covered by a hard substance called enamel, and has varying numbers and kinds of cusps—the pointed or rounded biting surface of the tooth. The crown is supported by dentin, which is softer than enamel. The pulp cavity underlies dentin, and forms the central chamber of the tooth. Pulp comprises soft tissue, blood vessels, and nerves that pro-vide sensitivity to heat and cold.

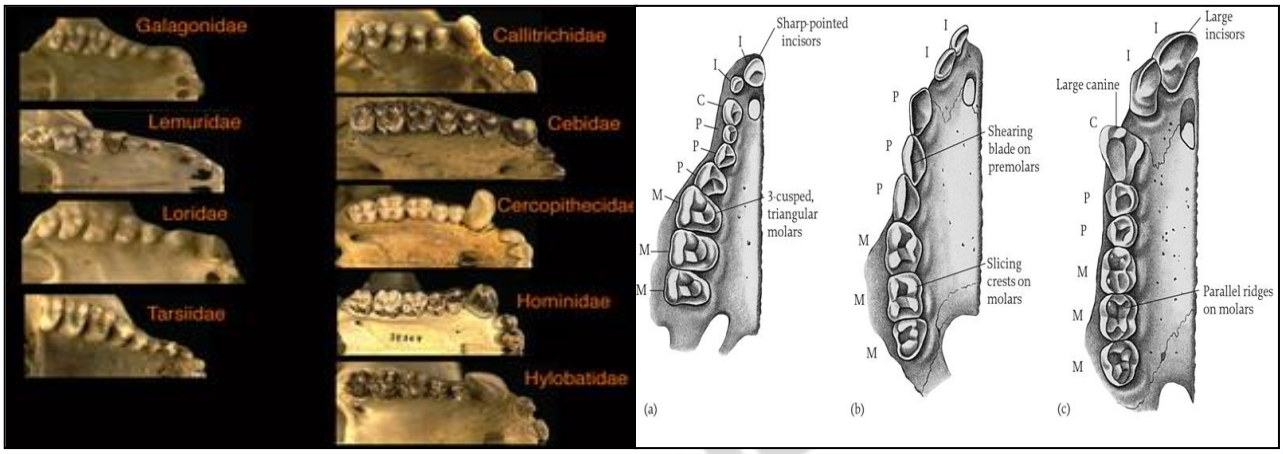

Figure-4: Differences in Dentition in Primates

Source: http://hominidteethanddiet.weebly.com/primate-dentition.html

All primates are characterized by heterodonty, meaning they have different kinds of teeth. Specifically, most primates have the following four kinds of teeth (from front to back): incisors, canines, premolars, and molars. These teeth can be categorized into two parts: anterior dentition (incisors and canines) and posterior dentition (premolars and molars). Paleoanthropologists use the dental formula to describe the number of each kind of tooth in one half of the maxilla and mandible of a species. In each quadrant of the mouth (moving from the midline along the toothrow to the back of mouth), most primates have 2 incisors, 1 canine, 2 or 3 premolars, and 3 molars. This combination is known as the dental formula. Lemurs, lorises and bushbabies (collectively known as strepsirhines) have various dental formulas but generally have 2 incisors and a canine (which on the lower jaw are arranged in a specialized comb-like structure known as a toothcomb), 3 premolars and 3 molars. New World monkeys (platyrrhines), except for the small marmosets and tamarins that have only 2 molars, have the same formula, but do not have a specialized toothcomb. Old World monkeys, apes, and humans (called catarrhines) all have 2 incisors, 1 canine, 2 premolars, and 3 molars (http://elearning.la.psu.edu/anth).

10. Hands of the Primates: Primate hands represents one of the original and fundamental adapatations of primates. Hands are grasping stuctures and are generally palmgrade in their orientation to a support.

Some primates use digitigrade., knuckle-walking, suspensory grasps or fist-walking hand postures. Grasping hands must flex all five digits at the metacarpophalangeal and interphalangeal joints, while simultaneously opposing the first digit or thumb. Rotation of the hand, pronation or internal roatation, aligns the palm with the support, usually a branch. Hand rotation, either pronation or suprination, an ecternal roatation, occurs primarily at the elbow joint between the radial head and the capitulum with little mobility at the wrist joints. Wrist joints primarily function to flex and ectend the hand. Another distinctive wrist feature in primates is where the wrist bones contact the ulna. The styloid process at the distal end of the ulna is long and contactsthe triquetrum and pisiform wrist bones in most primates. In apes, the styloid process is reduced in length and does not conctct these two wrist bones. A pad, or fibrocartilagineous meniscus, is located bewtween the ulnar styloid and the triquetrum in apes, preventing articulation between these bones. The reduction of the styloid process results in greater abduction at the wrist in apes (Gebo, 2014).

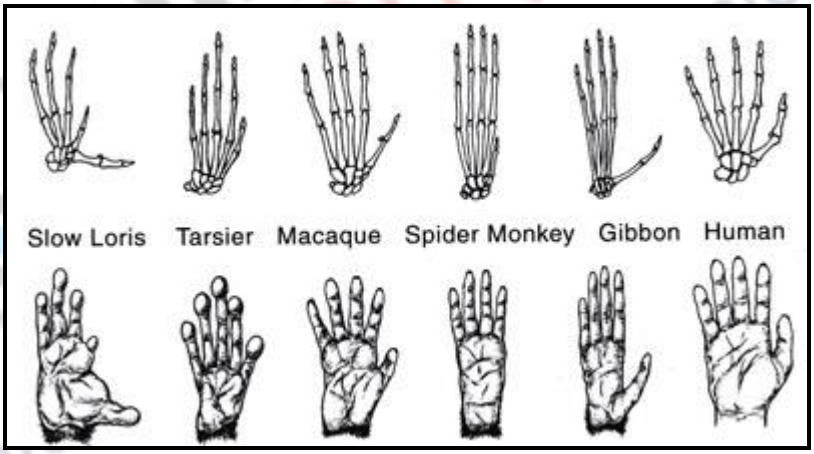

Figure-5: Comparative Osteology of Hands of Primates

Source: http://elearning.la.psu.edu/anth/022/lesson_2/anatomical-features

10. Primate Pelvis

The most significant changes to the pelvis in humans compared to other apes are in the ilium (top portion of the innominate bone) in humans is shorter and broader curves around the trunk, whereas in apes it is flat against the back of the trunk. Greater sciatic notch is very wide in apes, a function of their

long, tall ilium. Anterior inferior iliac spine is prominent in the hominin pelvis, absent or small in apes and Sacrum, in apes is narrow and long, usually incorporating 6 or more sacral vertebral bodies.

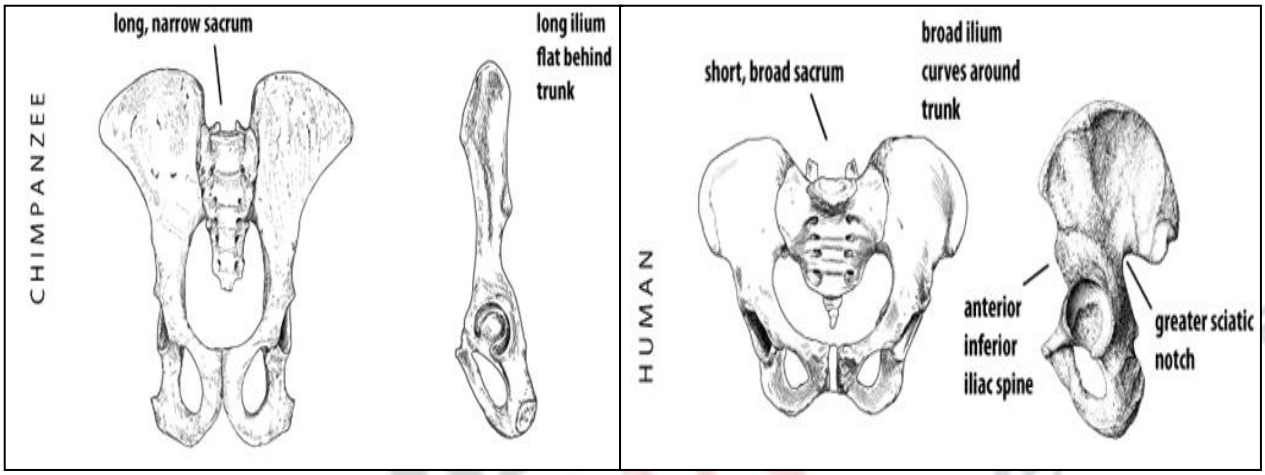

Figure-6: Comparative Pelvis of Chimpanzee and Humans

Source: http://johnhawks.net/explainer/laboratory/bipedality-pelvis/

11. Summary

The comparative osteology of primates has interested researchers for centuries. The first major branch of the Order Primates is into the two Suborders: Prosimii and Anthropoidea. There is almost as much skeletal diversity among the extant galagos, lemurs, and lorises (modern members of the suborder Strepsirrhini. The small number of species of Tarsiiform group is found in the islands off of Southeast Asia is unique among primates in several features. The other groups also differentiates from each other osteologically are Anthropoid, Platyrrhines and Catarrhines. One obvious feature often used to define Hominoid group is the lack of an external tail. All primates have diphyodonty (they have two sets of teeth) and heterodonty (they have different kinds of teeth) and distinctive pelvis.