Block 3

Living Primates: Human and Non-Human

UNIT 10 CLASSIFICATION AND CHARACTERSTICS OF LIVING PRIMATES*

Contents

Learning Objectives

After going through this unit you will understand:

- origin of primates;
- taxonomy of primates; and
- characteristics of living primates.

10.0 INTRODUCTION

The order Primates is one of the twenty orders of the class mammalia. A primate is any mammal from the group that includes the lemurs, lorises, tarsiers, monkeys, apes and humans. The members of the primate order are characterized by a set of characteristics, which define this group. A majority of the primates have nails instead of claws, a clavicle, a bony ring encircling the orbits, males with a hanging penis and scrotal testes, females with a pair of mammary glands on their chest, a well-developed caecum, a calcarine fissure in brain and an opposable thumb or big toe. Before we try to learn the details of classification of primates it would be worthwhile to understand some basic concepts of classification.

The order Primate, with its 300 or more species, is the third most diverse order of mammals, after rodents (Rodentia) and bats (Chiroptera). Although there are some notable variations between some primate groups, they share several anatomic and functional characteristics reflective of their common ancestry. Primates are a homogeneous group morphologically and it is only in the realm of behaviour that differences between primate taxa are clearly discriminant. It can be said that the most successful primates (judged in terms of the usual criteria of population numbers and territorial spread) are those that have departed least from the ancestral pattern of behaviour (Rafferty, 2011).

Prof. Rajan Gaur, Department of Anthropology, Panjab University, Chandigarh

10.1 TAXONOMY/CLASSIFICATION

Taxonomy is a branch of biology that is basically concerned with the classification and naming of organisms. The term taxonomy is a combination of two Greek roots, *Taxis* (arrangement) and *Nomia* (method). A taxonomy or classification uses names or other such labels to arrange various groups of plants and animals in "Pigeonholes" that demonstrate how all of them are related. In a way, taxonomy is the classification of plant and animals into groupings based on common biological features. It primarily deals with the orderly arrangement of the organic world and their exact naming. Very simply, taxonomy is the study of classification of organisms and the rationale behind the classification. It is in some respects similar to systematics, which, besides classification, encompasses more of evolution and biodiversity. In addition to classification, taxonomy also helps scientists to understand how various groups of organisms are related to one another.

The basis of taxonomy is the species, which are the basic units of living world. Concept of species is of concern to geneticists, biologists, palaeontologists, anthropologists, ecologists, bio-geographers, etc. But it is a concept that is understood differently by different disciplines:

- 'Evolutionary Species Concept', explains a species as "a lineage …evolving separately from others and with its own evolutionary role and tendencies" (Simpson, 1961).
- 'Biological Species Concept', defines species as "groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups" (Mayr, 1963).
- 'Phylogenetic Species Concept' describes species as "an irreducible cluster of sexual organisms within which there is a parental platform of ancestry and descent and that is diagnostically distinct from other such clusters by a unique combination of fixed characters" (Christoffersen, 1995).
- 'Genetic Species Concept' delineates a 'genetic species' as "a group of genetically compatible interbreeding natural population that is genetically isolated from other such groups" (Baker and Bradley, 2006).

With this basic background of taxonomy we are better equipped to understand primate taxonomy. However, it is also important to understand who are primates and the various features that characterise primates.

10.2 WHO ARE PRIMATES?

Primates are a diverse and very successful group of eutherian mammals (Eutheria or Placentalia is the most taxonomically diverse of three branches of extant mammals, the other two being Metatheria or Marsupialia and Prototheria or Monotremata). The word 'primate' in Latin means 'first'. It is a name of an order of class mammalia that contains prosimians, monkeys, apes and humans. Primates are an ancient group that probably separated from the primitive mammalian stock about 65 million years. It is probable that primates originated from some type of an insectivorous mammal that lived in the late Cretaceous (Fleagle, 1998; Szalay and Delson, 2013). From tiny shrew-like creatures, the primates in time have grown into an amazing variety of forms. Some of the primates are the most generalized of the mammals

while others display unmatched morphological and behavioural specializations. The living primates greatly vary in size. The smallest living primate, the pygmy mouse, weighs around 30 grams while the largest, the male eastern lowland gorilla, may weigh over 200 kilograms. The study of how the primates evolved and how they live today is termed as primatology.

With the exception of humans, almost all of the living primates are found in the tropical and subtropical parts of the world on north and south of the equator, in South and Central America, Africa, Asia and the islands of Indonesia. But the primates have always not been restricted to these parts. Fossils of many primates have been discovered from regions which are not tropical at all, such as parts of British Isles, Northern United States, tip of South America - places where no primate of today could survive (Devore & Eimerl, 1966).

Check Your Progress 1

1) What do you understand by taxonomy?

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2) Who are the primates?

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10.3 PRIMATE ORIGIN

Primates are one of the better-known mammalian groups. There are about 400 living species and they have maximum diversity in lowland tropical rainforests, including mangrove and freshwater swamp forests (Heads, 2010). Though primate phylogeny is now better understood but there is hardly any consensus about their evolution with respect to where and when they originated. The earliest primates probably evolved sometimes in the late Cretaceous or in the Palaeocene (Fleagle, 2013). The earliest recognised species of Plesiadapiformes, *Purgatoriusceratops*, is commonly considered the earliest and most primitive primate (Radhakrishnan, 2006). However, it has also been suggested that the basal primate in a phylogenetic sense may be the fossil *Altanius*, from the Eocene of Mongolia and the oldest primate fossil may be *Altiatlasius*, from the Late Paleocene of Morocco (Fleagle and Gilbert 2006). Still, the interpretation of these fragmentary fossils, in particular their phylogenetic status, is controversial. Where did the primates first originate? This question has always concerned palaeoanthropologists. Anthropologists and other biologists have been debating for over a hundred years whether the true centre of origin of primates was in Africa, Asia or America. But no indisputable answer is as yet available. The issue has become more vexed with the recent developments in molecular biology. The problem of primate origins in space is related to the question of their origin in time. While dates based on fossils suggest an origin for primates in the Palaeocene, at approximately 56 million years, while the molecular clocks indicate a date of approximately 90 million years in the Cretaceous period (Janecka et al., 2007).

Several views are available for the centre of origin of primates. Fleagle and Gilbert (2006) supported Asia as centre of origin. But Rasmussen (2002) favoured Africa or India. On the other hand Bloch et al. (2007) supported North America while Arnason et al. (2008) proposed South America as the centre of origin of primates. Of the various theories, the African origin hypothesis appears to be the front runner although some also favour the Indo-Madagascar hypothesis (Heads, 2010). The debate thus remains unsettled.

In simple terms, the primate phylogeny can be considered to begin in the Palaeocene epoch spanning approximately from 65 to 55 millions of years ago with the appearance of the Plesiadapiformes in Europe and North America. The Plesiadapiformes are believed to have been a group of small mammals with primate-like characteristics. True primates or euprimates or primates of modern aspect, appeared in the Eocene epoch (spanning ~55 to 37.5 million years ago). The primate evolutionary history is not so straight forward due the general fragmentary and incomplete nature of the primate fossil record and the differences in their interpretation.

10.4 TAXONOMY OF LIVING PRIMATES

The order primate is traditionally divided into Prosimii and Anthropoidea, based on a classification system proposed by Simons (1972) and subsequently by Fleagle (1998). According to the traditional system, the prosimians included lemurs, lorises and tarsiers. They are clubbed together because they were considered morphologically more primitive than other primates. The anthropoids included the monkeys, apes and humans. However, recent biochemical, DNA hybridization, RNA sequencing and anatomical studies indicate that tarsiers are closer to anthropoids. Furthermore, the nostrils of tarsiers and anthropoids are encircled by dry skin while lorises and lemurs

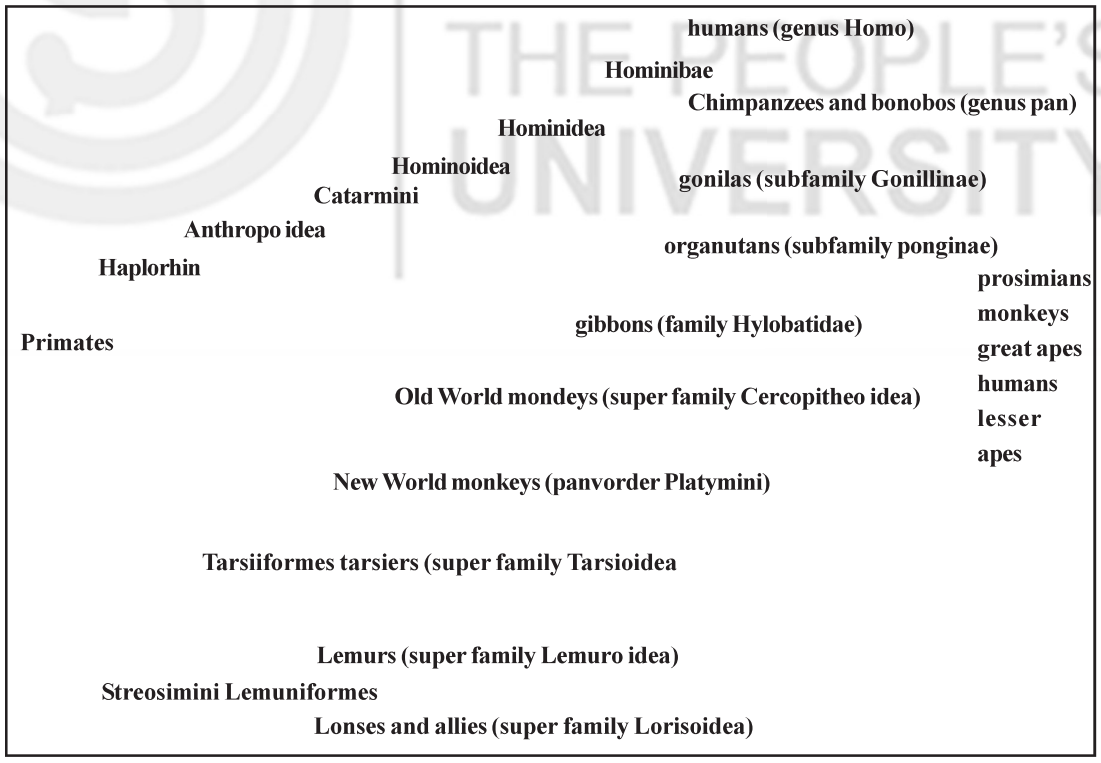


Fig. 1: Classification of Living Primates

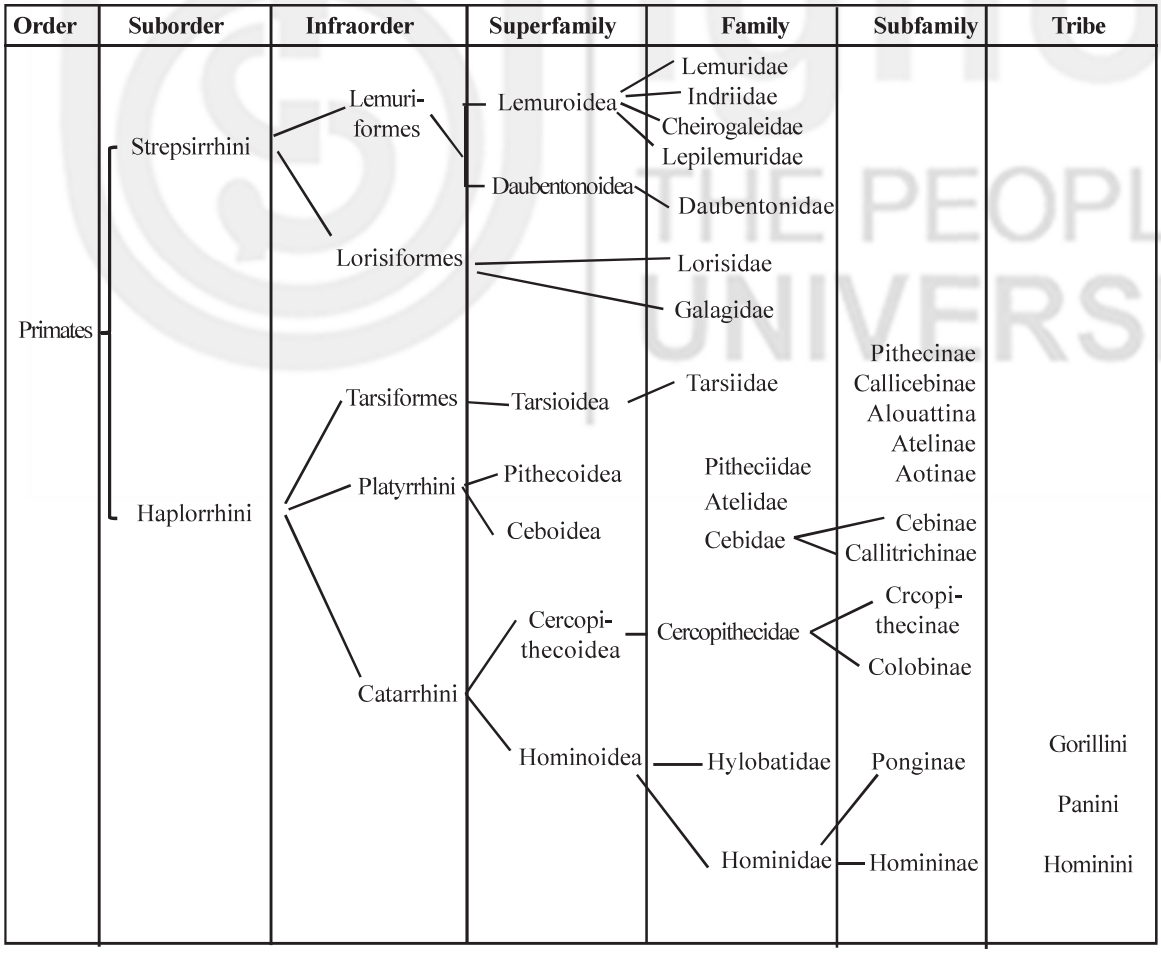
Source: Cartmill and Smith, 2011; Groves, 2001

have wet nostrils. Apart from these, there are other physical differences, for example the absence of a tapetum (a layer in the retina that helps in night vision) in tarsiers and anthropoids, due to which several taxonomists have created two new primate suborders- the Strepsirrhines (which includes lemurs and lorises) and the Haplorrhines (that incorporates tarsiers, monkeys, apes and humans). Thus, in the new system the tarsiers have been removed from prosimii and included under anthropoidea.

Another major difference between the traditional and the new classification system of primates is the position of apes vis-à-vis humans. In the traditional system (Fleagle, 1998), humans and apes were grouped under superfamily hominoidea. The great apes, which included orangutans, gorillas, chimpanzees and bonobos, were then separated into the family pongidae, while humans were grouped into the family hominidae. In recent years, this practice has lost favour. Molecular evidence has convinced most taxonomists that African apes (Gorilla and chimpanzee) are closer to humans than Asian Orangutan.

The taxonomic classification of order primates (modified after Fleagle, 2013) is summarized in Table-1. The Table below shows classification of the living primates along with their groups and commonly used names (shown on the right).

Table 1: Taxonomic Classification of Extant Primates
(Modified after Fleagle, 2013)



The major characteristics of various taxonomic groups of primates are given as follows:

Suborder: Strepsirrhini (earlier Prosimii)

Fleagle (2013) calls it a Semiorder while many others term it as a Suborder. It includes lemurs and lorises. The nostrils (rhinarium) of strepsirrhines is moist and bare, like that of a dog. Strepsirrhines have a reflective layer, the *tapetumlucidum*, behind the retina, which increases the amount of light for night vision. Most are nocturnal with prominent whiskers, large and mobile ears and large eyes adapted for a nocturnal lifestyle. Highly developed sense of smell. Upper lip is divided and attached to gums by a membrane. They have a protruding snout (rostrum), a tooth comb formed of lower incisors and canines, an orbital bar and a grooming claw on second digit of foot and flat nails everywhere else. Suborder strepsirrhini has two infraorders: Lemuriformes and Lorisiformes.

Infraorder: Lemuriformes

It includes all lemurs. They are restricted to the island of Madagascar and the neighbouring island of Comores. They range in body size from the 30 gram pygmy lemur to the 10kg for Indri. Lemuriformes show a broad range of dietary and locomotor adaptations. Some species, like the sifaka, primarily leap using long hindlimbs and cling to vertical branches. Others are arboreal quadrupeds, or spend substantial time on the ground. Lemuriformes has two superfamilies: Daubentonoidea and Lemuroidea.

Daubentonoidea

This superfamily has a single subfamily, Daubentonidae with a single genus *Daubentonia* (the aye-aye). This moderately sized, black animal with large ears has extreme specializations but still retains some basic features to be classified under lemuriformes.

Lemuroidea

It includes four families: Chirogaleidae, Indriidae, Lepilemuridae and lemuridae. The chirogaleids are the most primitive and the smallest of the Lemmuroids. The family Indriidae includes genera *Indrii*, *Propithecus* and *Avahi*. Lepilemuridae family consists of the genus *Lepilemur* and Lemuridae family includes *Lemur, Hapalemur, Prolemur, Eulemur*and *Varecia.*

Infraorder: Lorisiformes

The lorisiformes are all nocturnal primates who exist in forest regions of Africa and Asia. Their diets primarily consist of fruits, gums/exudates and insects. Like lemurs they have a tooth comb and a grooming claw on the second digit. The tympanic ring in the ear region of lorisiformes is fused to the later wall rather than being suspended in the bulla as in lemurs. The infraorder consists of two families: Lorisidae and Galagidae.

Suborder: Haplorrhini (termed Semiorder by some)

It is a new suborder created to incorporate tarsiers which were earlier included under prosimii in the traditional primate classification system. The haplorhines are considered the “higher” primates. This suborder includes tarsiers, monkeys, apes and humans. Scientists believe that haplorhines first appeared in the Eocene around 50 million years ago. These are the ancestors of today’s monkeys and apes. The extant haplorhines are divided into three

infraorders namely Tarsiiformes, Platyrrhini and Catarrhini. The platyrrhines and catarrhines are together termed as anthropoids.

Infraorder: Tarsiiformes

Tarsiiformes are amongst the smallest and very unusual of all extant primates. They are found in Southeast Asia. They show a mixture of prosimian and anthropoid traits. Several of the traits which they share with lower primates are primitive features such as high cusped molars, unfused mandibular symphysis, multiple nipples, grooming claws on second digit of feet. Tarsiers have very long legs and ankles. Tarsiers possess some striking and unique features also, which include the unusually large size of its eyes that is even larger than the size of its brain.

This infraorder has only one family – Tarsiidae. Currently there are three living genera of Tarsiformes: *Carlito* (from Philipines), *Cephalopachus* (mainly from Borneo and Sumatra) and *Tarsius* (manly from Sulawesi islands).

Infraorder: Platyrrhini

The platyrrhines are also known as the New World monkeys. All anthropoid primates living in Central and South America are included in this infraorder. The term platyrrhini refers to the shape of nose in these primates. Living platyrrhines are small to medium size anthropoids. Platyrrhines have broad, flat dry noses with outwardly directed nasal openings. This feature probably distinguishes them from the Old World monkeys, which generally have narrow nostrils. They lack a bony tube between eardrum and outer ear, tympanic ring fused to the side of the auditory bulla, presence of three premolars in contrast to two of Old World monkeys, absence of a hypoconulid on the first two lower molars in most members, lack ischial callosities (bare patches of skin on rump) found in some Old World monkeys, most have a well-developed tail which is prehensile and used like fifth limb in some genera, imperfect opposability of thumb and poorly developed finger grip, large and strongly opposable hallux, special scent glands in some, arboreal and mostly diurnal.

In traditional classification, platyrrhines are subdivided into two families – Cebidae and Callithricidae. But based on recent molecular systematics, it is divided into three families: Pitheciidae, Atelidae and Cebidae consisting of 19 living genera (Fleagle, 2013).

Family: Pitheciidae

This family consists of two subfamilies: Callicebinae and Pitheciinae.

Family: Atelidae

It includes two subfamilies: Alouattinae and Atelinae.

Family: Cebidae

This family consists of three subfamilies: Aotinae, Callitrichinae and Cebinae.

Infraorder: Caterrhini

The catarrhines comprise the old world monkeys, apes and humans. The word Catarrhini, like Platyrrhini, refers, to the shape of the nose. Caterrhine nostrils are narrow, close together and face downward, unlike the platyrrhine monkeys in whom the nostrils are round and laterally facing. The catarrhine

monkeys are in general larger than playrrhine monkeys. Catarrhines have only two premolars in each quadrant as compared three among the platyrrhines. They have a bony tube between eardrum and outer ear. They are mostly diurnal. Most have a well-developed grip and opposable thumb and big toe, except humans. This infraorder is usually divided into two superfamilies, the Cercopithecoidea (Old World monkeys) and the Hominoidea (apes and humans).

Superfamily: Ceropithecoidea

Cercopithecoids are also commonly known as Old World Monkeys. Of all the living caterrhines, they are the most numerous and diverse. Ceropithecoids are found all over Africa and Asia and some parts of Europe. It has one family, cercopithecidae and two subfamilies: Cercopithecinae and Colobinae.

Superfamily: Hominoidea

Superfamily hominoidea comprises the humans and the apes. Living hominoids are characterized by the absence of tails and by rather primitive rounded molars. In the new systematic classification of primates that also considers molecular evidence, Hominoidea comprises two families: Hylobatidae and Hominidae.

Family: Hylobatidae

Hylobatids are the smallest and most numerous of the apes and comprise the siamangs and the gibbons (*Hylobates, Symphalangus, Hoolock*). Because of their size they are occasionally referred to as lesser apes. The hylobatids are distributed in northeast India and tropical forests of Southeast Asia.

Family: Hominidae

This family includes the great apes and the humans: chimpanzees, orangutans, gorillas, bonobos and humans. Some of the main features of Hominidae include a larger brain compared to body size, sexual dimorphism, relatively larger body size, semi-upright to upright posture and the associated differences in skeletal parts.

There is an on-going debate as to how close humans are to the African great apes. In the traditional classification apes are considered in a separate family, the Pongidae and the humans are included in their own family, the Hominidae. In the new taxonomic system that considers molecular evidence, humans are combined with the great apes in family Hominidae but are separated from them at a lower classification category—the tribe. In a growing concensus among primatoloists, humans are assigned to the tribe Hominini while chimpanzees and bonobos are relegated to the tribe Panini.

Check Your Progress 2

3) Describe in brief taxonomy of living primates.

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10.5 PRIMATE CHARACTERISTICS

According to Mivart (1873), "Primates are unguiculate, claviculate placental mammals, with orbits encircled by bone; three kinds of teeth at least one

time of life; brain always with a posterior lobe and calcarine fissure; the innermost digits of at least one pair of extremities opposable; hallux with a flat nail or none; a well-developed caecum; penis pendulous; testes scrotal; always two pectoral mammae". They have incisors, canines, premolars and molars (premolars may be absent in milk dentition). They have at least one pair of grasping extremities (grasping hands or feet). Either the thumb or the big toe is opposable. One pair of mammary glands present on the chest and in males, a hanging penis and testes in a pouch of skin. Main characteristics of primates are:

- ***Pentadactyle hands and feet:*** Except spider monkey, which has four finger on each hand and five toes on each feet, all primates have retained the ancient mammalian trait of pentadactylism.
- ***Increasing refinement of hands and feet for grasping objects:*** This characteristic has been one of the main hallmarks of primate evolution. There is a trend of increasing manual dexterity. This feature has been further enhanced by the development of highly sensitive tactile pads at the tips of fingers and toes, in contrast to most other mammals.
- ***Presence of flat nails:*** Primates possess flat nail*s* to protect fingertips with dermatoglyphs (fingerprints) on fingers and toes.
- ***Presence of opposable thumbs***: Primates have opposable thumb for power grip (for holding on) and precision grip (for manipulating small objects, as in humans and some apes).
- ***Presence of clavicle and the generalized limb structure of early mammals***: Primates have retained the primitive mammalian limb structure, one upper limb bone (e.g. humerus in fore limbs and femur in hind limbs) and two lower limb bones (e.g. radius and ulna in fore limbs and tibia and fibula in hind limbs). Strong clavicles and highly flexible shoulder joints have permitted most primates to use their arms very efficiently in climbing trees. Many mammalian orders have lost various bones, particularly fusing of the two lower limb bones, as in the case of horses.
- ***Erect posture:*** All primates have a marked tendency towards erectness in their upper bodies. This can be seen in their sitting and standing postures as well as in occasional bipedalism.
- ***Reduction in the sense of smell:*** The importance of sense of smell has been reduced in primates. Consequently, the olfactory center of the brain, the rhinocephalon, has proportionally decreased in size. The skeletal structures associated with smell, the snout length and facial protrusion, have steadily and progressively decreased (the lemurs and the baboons are exceptions).
- ***Increased dependence on visual sensation:*** The orbits of primates (eye sockets) exhibit a high degree of frontation (placement toward the front of the face), which increased the overlap of visual fields thus enhancing the binocular vision and depth perception and producing what is termed as stereoscopic vision. All living members of the order primates have stereoscopic vision. Most living diurnal primates probably have some sort of colour vision, which is very helpful for a diurnal life.
- ***Relatively large brain, as compared to body size:*** There is a trend of continuous development of brain with increasing elaboration and differentiation of the cerebral cortex. The enlargement of cerebral cortex is related to improved manual dexterity and enhanced hand-eye

coordination, which is a significant aspect of primate evolution.

- ***Reduction in number of teeth:*** Primates have reduced number of teeth, as compared to primitive mammalian dentition, with a maximum of two incisors, one canine, three premolars and three molars in each quadrant of jaw. They have retained a simple generalized cusp pattern on molars. This allows them to exploit different food sources.
- ***Presence of mammary glands:*** Most primates have one pair of mammae on the chest.
- ***A trend towards smaller litter size, longer gestation periods and prolonged period of juvenile growth:*** The gestation period increases from at least 4 months in case of more primitive small prosimians such as *Microcebus* and *Galago* to nine months in case of humans. The consequence of long gestation period is that offsprings are born more mature and therefore, have a greater chance of survival. Reduced litter size (usually just one in most primates) permits more individual attention to young and allows more mobility with young clinging to the mother. There is a trend of increase in the postnatal growth period from lower to higher primates, which may vary from less than 1 year among nocturnal prosimians to roughly 15 years in case of man (Buettner-Janusch, 1969).
- ***Increase in the natural life span:*** There is a trend of marked increase in the natural life span of all primates. Tiny mouse lemurs (*Microcebus*) are known to survive for 8 years while equivalent-sized rodent mice rarely survive beyond 2 years. Large monkeys, such as baboons, the males of which may weigh up to 90 lbs, have may live up to 30 years, while domestic dogs of comparable size may have a life span of only 10-12 years. The average life span of humans ranges between 70 to 80 years.
- ***Complex social behavior:*** The vocalizations, visual displays and specific social behaviours, such as infant care and grooming, are very complex and diverse among primates. It would not be wrong to state that the primates are the most social of all the mammals.

It may be noted that all the above characteristics may not be found in each and every member of the order. But several of these traits occur in most living primate groups.

Check Your Progress 3

4) What are the characteristics of primates?

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10.6 SUMMARY

The order Primates is one of the twenty orders of the class Mammalia. There are roughly 400 species of living primates which are distributed, with the exception of humans, in the tropical and subtropical parts of the world on north and south of the equator, in South and Central America, Africa, Asia and the islands of Indonesia. The primates are characterised by a set

of traits such as possession of nails instead of claws, a clavicle, a bony ring encircling the orbits, males with a hanging penis and scrotal testes, females with a pair of mammary glands on their chest, a well-developed caecum, a calcarine fissure in brain and an opposable thumb or big toe. All these traits may not be found in each and every member of the order primates. Dates based on fossils suggest an origin for primates in the Palaeocene, at approximately 56 million years ago. The separation of the ape-line from the Old World monkey lineage is thought to have happened in the Miocene epoch (~22.5 million years ago). Order Primate, these days, is considered to have two suborders: Strepsirrhini (which includes lemurs and lorises) and the Haplorrhini (that incorporates tarsiers, monkeys, apes and humans). The humans and great apes are now placed together in the family hominidae separate from gibbons and siamangs which are grouped under family hylobatidae. The gorilla and chimpanzee are grouped into subfamily homininae along with humans distinct from orangutan that is placed in the subfamily ponginae. Apart from anatomical features, the recent primate classification has also taken into consideration the molecular evidence.

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10.8 ANSWER/HINTS TO CHECK YOUR PROGRESS

1) Taxonomy is a branch of biology that is basically concerned with the classification and naming of organisms. The term taxonomy is a combination of two Greek roots, *Taxis* (arrangement) and *Nomia* (method). For more details kindly refer section 10.1

2) Primates are a diverse and very successful group of eutherian mammals. The word 'primate' in Latin means 'first'. It is a name of an order of class mammalia that contains prosimians, monkeys, apes and humans. For more details kindly refer section 10.2

3) The order primate is traditionally divided into Prosimii and Anthropoidea. According to the traditional system, the prosimians included lemurs, lorises and tarsiers. The anthropoids included the monkeys, apes and humans. However, recent biochemical, DNA hybridization, RNA sequencing and anatomical studies indicate that tarsiers are closer to anthropoids. Several taxonomists have created two new primate suborders- the Strepsirrhines (which includes lemurs and lorises) and the Haplorrhines (that incorporates tarsiers, monkeys, apes and humans). For further details kindly refer section 10.4

4) Primates are unguiculate, claviculate placental mammals, with orbits encircled by bone; three kinds of teeth, at least one time of life; brain always with a posterior lobe and calcarine fissure; the innermost digits of at least one pair of extremities opposable; hallux with a flat nail or none; a well-developed caecum; penis pendulous; testes scrotal; always two pectoral mammae. (Mivart, 1873). For more details kindly refer section 10.5.

UNIT 11 COMPARATIVE ANATOMY OF HUMAN AND NON-HUMAN PRIMATES*

Contents

Learning Objectives

After going through this unit, you would be able to:

- understand factors affecting primate anatomy;
- describe the trends of primate evolution;
- know the characteristic of apes and man; and
- explain the comparison of morphological and anatomical features of man and apes.

* Dr. Ajeeet Jaiswal, Assistant Professor, Department of Anthropology, Pondicherry University, R.V. Nagar, Kalapet, Puducherry.

11.0 INTRODUCTION

A primate's survival is reflected in its behavioural ecology, how it uses its environment, its anatomy and its evolutionary history. A simple triangular model (Figure 1) illustrates this relationship. Behaviour, anatomy and the environment are at the corners of the triangle. Behaviour affects anatomy and the environment, while the environment affects anatomy and behaviour. Evolutionary history affects all three. For example, behaviour such as locomotion determines where a primate moves and how it is capable of moving its body. Most of these abilities are the result of a long history of adaptation to enhance survival in a given, usually arboreal environment. Heads, teeth and bodies are thus mosaic structures that reflect a species' evolutionary past as well as their current survival abilities. Consider, for example, the body of humans as a series of upper body adaptations that reflect our arm-swinging ancestral past, while our hips and legs reflect a more recent evolutionary modification for bipedalism. The same is true for our teeth and our heads. In short, primate and human bodies are true time capsules of our ancestral past (Gebo, 2014).

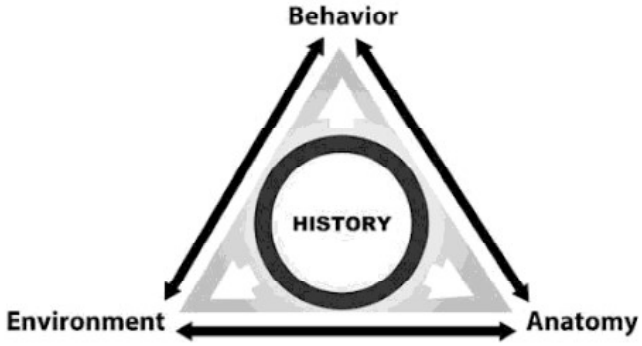

Fig. 1: Simple Triangular Model of PrimaeAdaptation

Source: Gebo, 2014

Understnding primate adaptations is important since this information allows us to comprehend survival abilities and it helps us to sequence the morphological changes that explain primate phylogeny. Adaptation and phylogeny go hand in hand in the science of primatology. By definition, an adapttion is a characteristic that allows an organism to survive and reproduce in its environment. A niche is an organism's way to make a living; in other words, a niche is how an organism finds the resources needed to survive and compete against other organisms. When it comes to species, we often seek to examine how a single group is creatively modified into an array of different forms. We call this species explosion an adaptive radiation and it means that closely related organisms have evolved to exploit different ecological niches. Adaptive radiations are the heart and soul of biology (Gebo, 2014).

Check Your Progress 1

1) How primate behaviour is influenced by environment and anatomy? Explain with suitable example.

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11.1 PRIMATE EVOLUTIONARY TRENDS

Although this unit focuses on the comparative anatomy of human and non-human primates, it is helpful to include a brief overview of primate evolutionary trends. Structurally, primates are not easily distinguished as a group chiefly because of the fact that, as an order, we and our close relatives have remained quite generalized. Unlike the specialized dentition of rodents or the specialized limbs with great reduction of digits found in artiodactyls (cows, deer, camels, pigs) primates are characterized by their extreme structural specializations.

For this reason, we cannot point to a single anatomical feature that can be applied exclusively and universally to the primates. On the other hand, there is a group of evolutionary trends (Clark, 1971) which, to a greater or lesser degree, characterize the entire order. Keeping in mind, these are set of general tendencies and are not synonyms with progress. In evolutionary terms, we are using "trend" only to reflect a series of shared common characteristics (i.e., general homologies).

A common evolutionary history with similar adaptations to common environment challenges is reflected in the limbs and locomotion, teeth and diet and in the sense, brain and art behaviour of the animals that make up order. Following is a list of those evolutionary trends that tend to set the primates apart from other mammals.

11.1.1 Limbs and Locomotion

- Retention of five digits in the hands and feet-pentadactyle.
- Nails instead of claws.
- Flexible hands and feet with a good deal of prehensility (grasping ability).
- A tendency toward erectness (particularly in the upper body).
- Retention of the clavicle (collar bone).

11.1.2 Teeth and Diet

- A generalized dental pattern, particularly in the back teeth (molars).
- A lack of specialization in diet. This attribute is usually correlated with change in pattern of teeth.

11.1.3 Senses, Brain and Behaviour

- A reduction of the snout and the proportionate reduction of the smell (olfactory) areas of the brain.
- An increased emphasis on vision with elaboration of visual areas of the brain. A trend related to the decreased dependence on smell. Except for some specialized nocturnal forms, colour vision is most likely present in all primates.
- Expansion and increasing complexity in the brain.
- A more efficient means of foetal nourishment, as well as longer period of gestation (with single births the norm), infancy and extension of the whole life span.
- A greater dependency on highly flexible learned behaviour is correlated with longer periods of infant and child dependency. As a result of both these trends, parental investment in each offspring is increased so that although fewer young are born, they receive more efficient rearing.
- Adult males often associate permanently with the group.

11.2 MORPHOLOGICAL AND ANATOMICAL FEATURES OF APES

Apes are a group of anthropoid primates native to Africa and Southeast Asia. In traditional use, apes are excluded from humans and are differentiated from other primates in terms of locomotion. Apes are divided into two extant branches or super families: Hominoidea (gibbons or lesser apes) and Hominids (great apes).

11.2.1 The Apes: Characteristics of the Apes: General

- They have no tail.
- Only apes (and humans) have five cusps on their teeth, known as Y-5 pattern. Monkeys have four cusps to their teeth.
- Locomotion is by several means, in the trees and knuckle-walking on the ground (Quadrupedal).
- The arms are long in comparison with their hind limbs.
- Their rib cages are flattened from front to back.
- Their brains are larger than those of monkeys, which allow them to learn quite complex behaviour patterns.
- The upper lip is free of the gums. This allows the apes to have mobile and expressive faces, so they use facial expression for communication.

11.2.2 Gibbons

- These are the smallest of the apes, the largest being no more than 11.5 kg.
- They live in the dense tropical forests of Southeast Asia.
- They are acrobatic brachiators 75 per cent of the time, the rest is spent quadrupedally or bipedally.
- They show no sexual dimorphism. (Apes vs Humans & Skeletal Differences, n. d.)
- Face and Ischial callosities are devoid of hair covering.
- Digital formula: 3>2>4>5>1.
- Digits except thumb are provided with nails.

11.2.3 Orangutan

- They live in thick tropical rain forests in Sumatra and Borneo.
- They are fruit eater.
- They have reddish hair coating on the body.
- They brachiate and often hang by their arms, which are very long. They have long curved hands.
- They tend to be too heavy to swing from one tree to another, so they have to come down on to the ground where they knuckle - walk to the next tree.
- Live in small group of 2-4 members.

- Each night they make a new nest to sleep in.
- Digital formula: 3>4>2>5>1.
- Their thumb is short and other fingers are long bear flat nails.

11.2.4 Chimpanzee

- Found in forest fringe and open woodland habitats in Africa.
- They are knuckle walkers on the ground and in the trees and they brachiate and can walk on two legs.
- Their main diet is fruit, supplemented by insects such as termites. They do not eat meat very often but it is greatly relished when they do.
- Their visual sense is highly developed; each animal looks different and is recognized by facial features.
- They live in troops of about 20 animals; children remain with their mothers for 4 or 5 years. During this time they learn from their mothers many complicated behaviors, including how to raise young babies.
- These are highly intelligent animals, able to fashion tools out of a piece of stick, throw stones when frightened, or pickup sticks to defend themselves.

11.2.5 Gorillas

- They are found in Africa
- These are the forest dwellers and spend most of their lives on the forest floor.
- They forage for food, mostly eating a type of celery and many leaves and shoots rather than fruit.
- They are nomadic, travelling daily to new feeding areas in groups of about 12-20 animals.
- They show sexual dimorphism; the males are bigger and have large canine teeth.
- They make nests each night.
- Fore limbs are considerably longer than hind limb (Apes vs Humans & Skeletal Differences, n.d.).

11.3 COMPARISON OF MORPHOLOGICAL AND ANATOMICAL FEATURES OF MAN AND APES

11.3.1 The Skull

The skull consists of a rounded brain case which surrounds and protects the brain and also provides attachment for muscles, especially those used for chewing. In an ape, the foramen magnum (the hole through which the spinal cord passes) lies towards the rear of the skull, so large neck muscles are needed to prevent the head from sagging forward. These are particularly strongly developed in male gorillas and run from the nuchal crest on the rear of the skull to the large spines (parts that stick out the back of each vertebra) of the thoracic vertebra.

In a human skull the foramen magnum is more or less in the center of the skull. As a result the skull is balanced on the first neck vertebra. So little muscle muscular energy is used to support it and the neural spines are correspondingly small (Apes vs Humans & Skeletal Differences, n. d.).

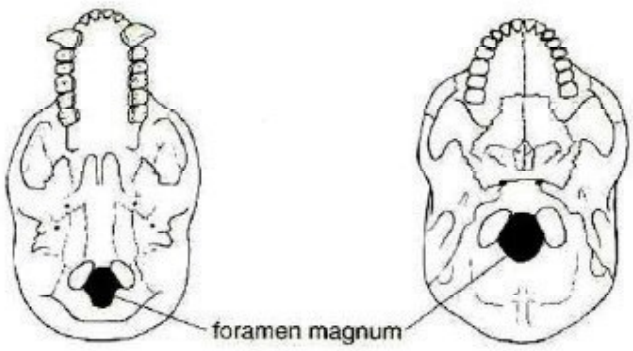

Fig.2: Position of Foramen Magnum in ape (left) and Human Skull (Right)

Source: Jaiswal, 2013

Characteristics of Modern Human Skulls

- Small mandible with prominent chin.
- Small zygomatic arch gap through which jaw muscles pass.
- No sagittal crest so reduced jaw muscles.
- Vertical face with no snout/muzzle.
- No brow ridges and forehead is vertical.
- Large brain size (cranium capacity). Enlarged particularly in the frontal and occipital regions, associated with increased reliance on vision and advanced thinking including speech.

Characteristic of Gorilla Skulls

- Large mandible with no real chin.
- Prominent snout/muzzle.
- Massive zygomatic arch - gap through which jaw muscles pass.
- Large saggital crest- attachment of strong jaw muscles.
- Nuchal crest- attachment of strong neck muscles.
- Receding forehead.
- Large brow ridges.
- Smaller cranium capacity (Apes vs Humans & Skeletal Differences, n. d.).

11.3.2 Teeth and Jaws

The teeth are much smaller with reduced enamel thickness in humans. This is probably due to the development of tools as weapons and food cutters, the size of teeth would be less important.

- There is a noticeable reduction in the size of the incisors.
- There is no sexual dimorphism in humans.
- The tooth row (dental arcade) is parabolic (bow shaped) in humans but is U-shaped in apes.

- In apes the lower canine fits into a gap or diastema between the upper canine and first premolar.

The apes has a large lower jaw with large teeth thick enamel particularly molars. This causes the lower jaw to protrude and gives a sloping face. In modern humans the lower jaw is reduced because the teeth are smaller with less enamel. The shorter lower jaw causes the face to be flatter in shape. In apes, the upper jaw teeth arrangement is U shaped whereas in humans the teeth arrangement is bow shaped.

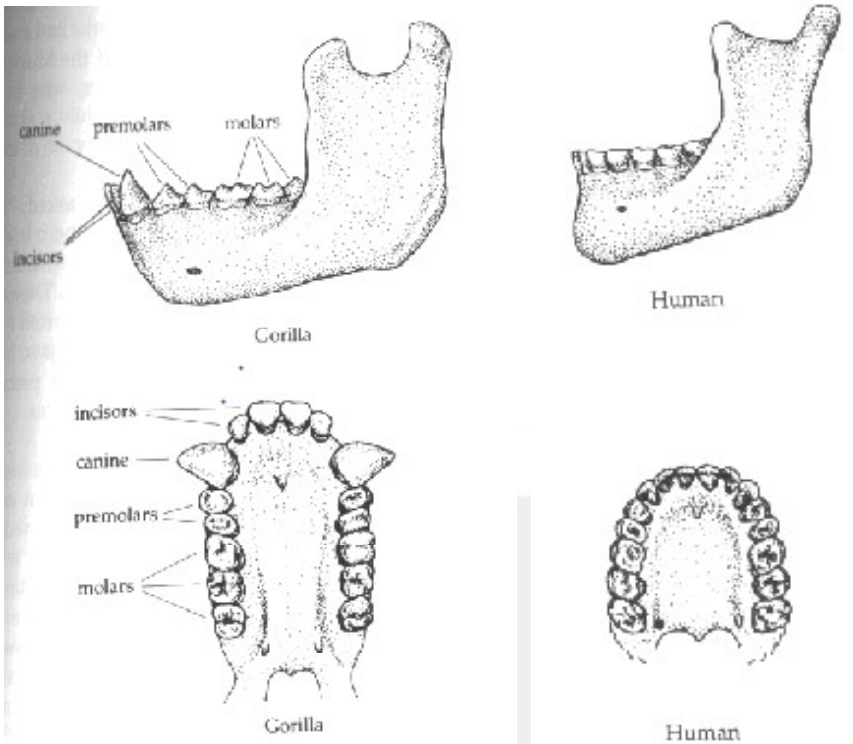

Fig.3: Comparison of Teeth and Jaw Structures of Ape and Human

Source: http://www.talkorigins.org

11.3.3 Backbone

An ape's backbone has a single gentle curve, a human backbone is 'S' shaped. This enables the weight to be carried nearly directly above the hip joints (Apes vs Humans & Skeletal Differences, n.d.).

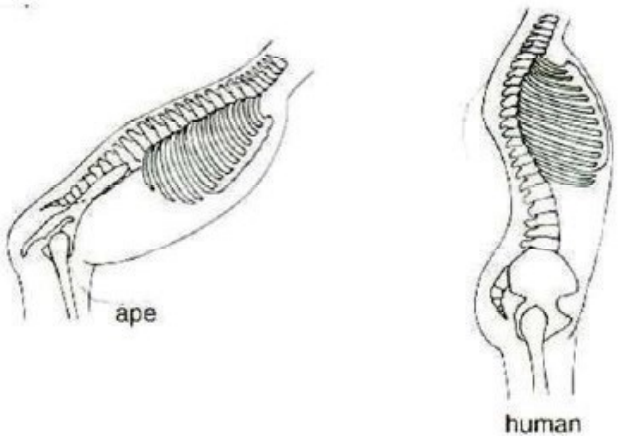

Fig.4: Apes (Left) and Human Backbone (Right)

Source: Jaiswal, 2013

11.3.4 Hip Girdle

In quadrupedal mammals the hip bone is long, but in humans it forms a bowl shaped support for the abdominal organs. It reduced height and brings the sacroiliac joint close to the hip joint (Apes vs Humans & Skeletal Differences, n.d.).

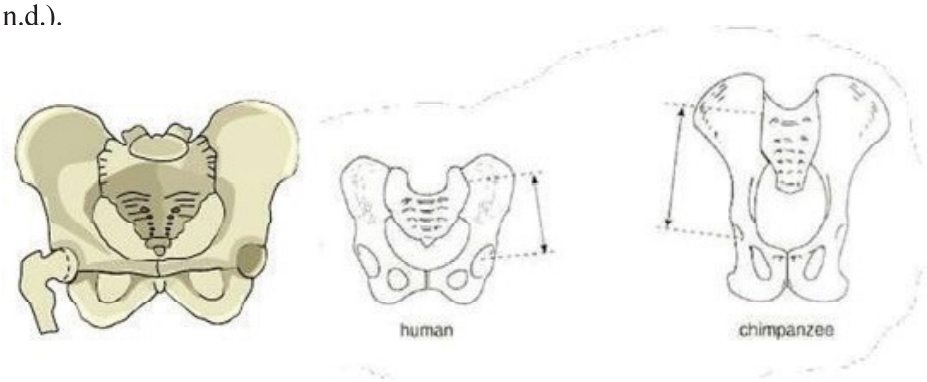

Fig. 5: Hip girdle of Human (Left) and Apes-Chimpanzee (Right)

Source: Jaiswal, 2013

11.3.5 Knee

Unlike apes humans are 'knock-kneed', each knee being almost directly underneath the center of the hip girdle. As a result, when one foot is lifted off the ground, the other is only slightly to one side of the center of gravity and there is little tendency to lose balance. The only way an ape can avoid falling over is to lean to other side. When an ape attempts to walk on two legs it therefore sways from side to side. Humans have a larger 'carrying angle' or better known as the valgus angle. This angle allows the leg to be close to the body's center of gravity (Apes vs Humans & Skeletal Differences, n. d.).

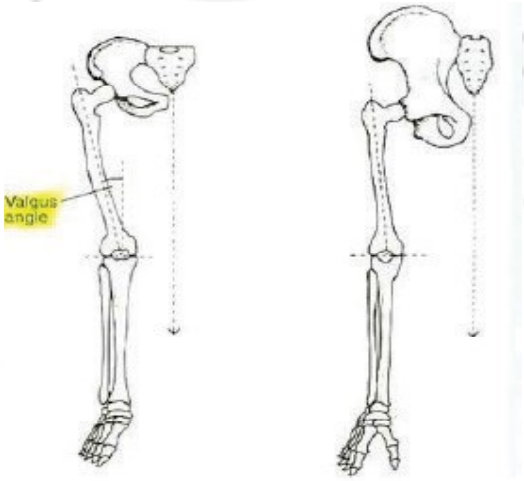

Fig. 6: Knee of Human (Left) and Apes (Right)

Source: Jaiswal, 2013

11.3.6 Foot

The foot in man supports and transmits body weight and acts as a locomotor organ. But in apes the foot is also a grasping organ besides being an organ for locomotion. These differences in function have led to certain structural variations in the feet of man and apes. With regard to the general shape and arrangement of bones, the foot of man resembles that of the apes. The differences are:

- In man the great toe is non-opposable. It is the biggest digit and is in line with the other digits. In the apes the great toe is opposable. It is not well developed and it is not in line with the other digits.
- In man the lateral toes are reduced in size, the fifth one is very small. In the apes the lateral toes are well developed.
- In man either the first or the second digit is the longest, while in the apes the third one is the longest digit.
- In man the dorsal and ventral surface of all digits are in the same way, the ventral surfaces being directed downward. In the apes the ventral surface of the great toe does not face downwards laterally.
- In man the head of the first metatarsal also included in the common transverse metatarsal ligament while in the apes it is not found in that manner.
- In man the metatarsal of all the digits are incorporated in the tissue of the foot. A common covering includes the digits up to the midpoint of the basal phalanx while in the apes the great toe is free from the common covering.
- In man the first metatarsal presents a flattened area at its posterior and to articulate with the flat articular facet of the cuneiform bone. In the apes the articular region of the cuneiform is convex and that of the metatarsal is concave (8 unique comparisons between man and ape, n. d.).

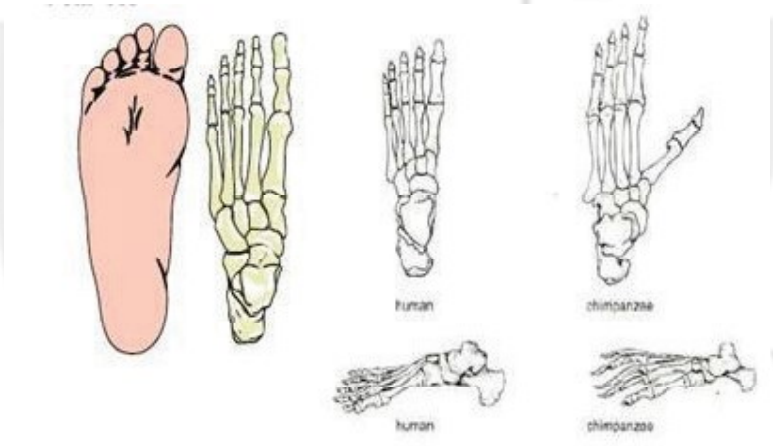

Fig.7: Evolution of Primate Foot

Source: Jaiswal, 2013

11.3.6.1 Comparison of Femur of Man and Gibbon

In general form and arrangement, a femur of man resembles that of a gibbon in the following characters.

The femur of gibbon is long and slender, its shaft is straight and cylindrical showing more or less circular cross section, in man the femur is not so long and is comparatively stout. Its shafts are not perfectly straight but slightly curved and it presents three surfaces and three borders thus the cross-section is not circular.

Upper Extremity

- In gibbon the neck of femur is short, stout and forms a less obtuse angle on the shaft.
- In gibbon the lesser trochanter is placed postero-medially whereas in man it is placed posteriorly.

Shaft

- The linea aspera is faintly developed in the gibbon but in man it is well developed forming a ridge.
- In gibbon the popliteal area is not well marked. The area is convex from side but straight from above to downwards. In man the popliteal area is well marked. It is convex from side to side as well as above downwards.

Lower Extremity

- In gibbon two condyles are almost equal in size while in man the medial condyle is larger than the lateral.
- The medial condyle does not extend below the lateral condyle in the gibbon, but it does so in man.

11.3.7 Hand

The human hand is essential in manipulating objects. The key features are the thumb, which in human differs from that of apes in two important ways:

- It is relatively longer.
- The first metacarpal is connected to the wrist by a saddle joint.
- This enables the thumb to be brought across the hand and touch the tip of any finger.

Another distinctive differences seen in the hand is the phalanges. In humans the phalanges (fingers) are straight, in apes they are curved, allowing the hands to act as hooks during brachiating.

All primates can hold things using a power grip but humans can also use a precision grip for fine manipulative movements (Apes vs Humans & Skeletal Differences, n. d.).

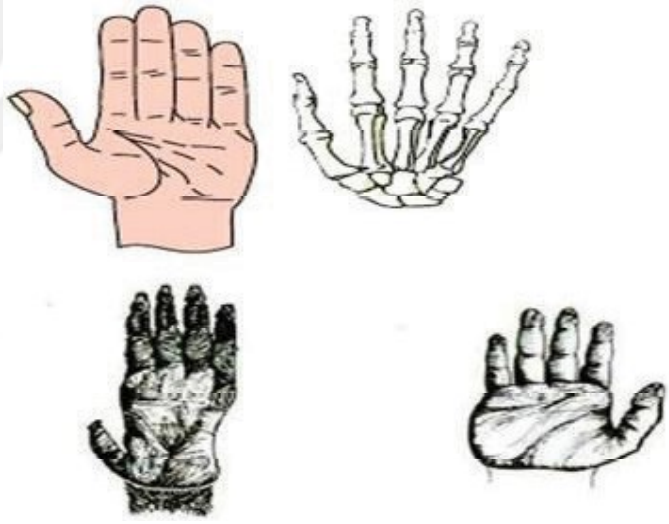

Fig. 8: Evoluation of Primate Hands

Source: Jaiswal, 2013

11.3.8 Chest

The human's chest is flatter from front to back than in apes. This causes the body weight to be concentrated as close to the spine as possible (Apes vs Humans & Skeletal Differences, n. d.).

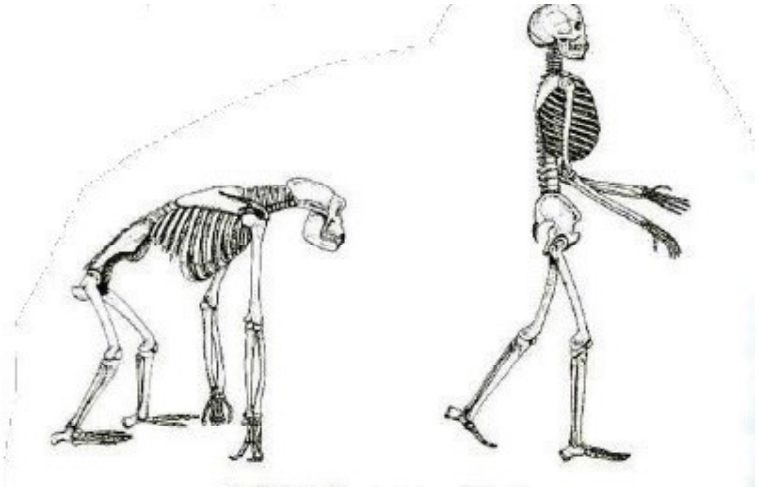

Fig. 9: Gorilla and Human Skeleton

Source: Jaiswal, 2013

11.3.9 Shoulder

Humans have a longer clavicle (collar bone) than apes**.** The scapula (shoulder blade) in humans is positioned on the back, rather than on the sides of the chest as in quadrupeds (Apes vs Humans & Skeletal Differences, n. d.).

11.3.10 Skin

Humans have just as many hair per square cm of skins as a chimpanzee. The difference is humans have very fine and short hair that give the impression of nakedness. Humans' skin does differ to that of apes as we have a greater density of sweat glands (Apes vs Humans & Skeletal Differences, n. d.).

Check Your Progress 2

2) Give a comparative account of teeth and jaw structure of man and ape.

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11.4 SUMMARY OF SIMILARITIES AND DIFFERENCES BETWEEN CHIMPANZEES, AUSTRALOPITHS AND MODERN HUMANS AS A RESULT OF MILLIONS OF YEARS OF EVOLUTION

S.No.	Modern chimpanzees	Australopiths	Modern humans
1	Canines larger and project out from teeth row	Canines slightly larger, but non-projecting	Canines of similar size to other teeth and non-projecting
2	Extended canine size determined by sexual dimorphism	Moderate canine size determined by sexual dimorphism	Minimal canine size determined by sexual dimorphism
3	Thin tooth enamel	Moderate tooth enamel	Thick tooth enamel

4	Dental wear pattern shows grinding action	Dental wear pattern shows crushing action	Dental wear pattern shows crushing action
5	Cranial capacity 400 cc	Cranial capacity 350 - 540 cc	Cranial Capacity > average 1000 cc
6	Foramen magnum opens toward rear of skull	Foramen magnum opens between rear and base of skull	Foramen magnum opens at base of skull
7	Tibiae thin and angled	Tibiae thicker and straighter	Tibiae thick and straight
8	Rib cage broad and extends past vertebral column	Rib cage broad and extends past vertebral column	Rib cage broad and extends past vertebral column
9	Scapulae on the back, shoulder joints oriented to the sides	Scapulae on the back, shoulder joints oriented to the sides	Scapulae on the back, shoulder joints oriented to the sides

11.5 RELATION OF ANATOMY AND POSTURE

The way a species sits, stands or hangs during feeding also influences its anatomy. For example, a siamang's ability to hang by its arms and legs may be more important in enabling it to feed from small branches than as a means of moving from one place to another. Likewise, the structure of a marmosets hand is influenced by the need to hold and process food as well as to grasp a support when moving.

We can relate details of primate anatomy to differences in locomotion and posture and can use the information to reconstruct the behaviour of species known only from fossil. However, we scarcely understand why some species leap, others are arboreal quadrupeds, some swing by their arms and one is a biped.

11.6 HOW ANATOMY IS RELATED TO MOVEMENT

From field studies we can learn the movements of each species and the ecological context in which they are used. Understanding how anatomy is related to movements is complicated by the fact that most primates can move in many ways, most leap at some times and run quadrupedally at others and many occasionally suspend themselves from branches. Anatomy hence reflects a series of compromises and an ability to do many things. Nevertheless differences in the frequencies with which primate species use different types of locomotion are reflected in muscles and bones. For example, two closely related species of larger Presbytis from Malaysia show differences in muscular and skeletal anatomy that are associated with the fact that one leaps about 20 per cent more frequently than the other.

Check Your Progress 3

3) Describe the important feature of skull of Modern Human and Gorilla.

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4) Give the descriptive account of the relation of anatomy and posture of primates.

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11.7 SUMMARY

Evolution can be best described as the process of gradual modification in the living organisms (plants or animals) so as to establish diversity in the world of living beings. Structurally, primates are not easily distinguished as a group chiefly because of the fact that, as an order, we and our close relatives have remained quite generalized and there is a list of those evolutionary trends that tend to set the primates apart from other mammals. A common evolutionary history with similar adaptations to common environment challenges is reflected in the limbs and locomotion, teeth and diet and in the sense, brain and art behaviour of the animals that make up order. There is an evolutionary belief that all humans are derived from apes. Whether this is universally accepted or not, there are some who believe the differences between the two are too significant to prove otherwise.

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11.9 ANSWER/HINTS TO CHECK YOUR PROGRESS

1) Primate behaviour is affected by anatomy and the environment, while the environment affects anatomy and behaviour. Evolutionary history affects all three. For example, behaviour such as locomotion determines where a primate moves and how it is capable of moving its body. Most of these abilities are the result of a long history of adaptation to enhance survival in a given, usually arboreal, environment.

2) The significant differences between teeth and jaw pattern of man and ape include:

   - In humans, teeth are much smaller with reduced enamel thickness. This is probably due to the development of tools as weapons and food

cutters, the size of teeth would be less important. The apes has a large lower jaw with large teeth thick enamel particularly molars. This causes the lower jaw to protrude and gives a sloping face.

- In modern humans the lower jaw is reduced because the teeth are smaller with less enamel. The shorter lower jaw causes the face to be flatter upper jaw shape.
- In apes the upper jaw teeth arrangement is U shaped whereas in humans the teeth arrangement is bow shaped.

3) The important feature of skull of Modern Human and Gorilla are as follows:

   a) Modern human skull: Small mandible with prominent chin, small zygomatic arch, gap through which jaw muscles pass, no saggital crest so reduced jaw muscles, vertical face with no snout/muzzle, no brow ridges and forehead is vertical, large brain size (cranium capacity), enlarged particularly in the frontal and occipital regions, associated with increased reliance on vision and advanced thinking including speech.

   b) Gorilla skull: Large mandible with no real chin, prominent snout/muzzle, massive zygomatic arch - gap through which jaw muscles pass, large sagittal crest- attachment of strong jaw muscles, nuchal crest- attachment of strong neck muscles, receding forehead, large brow ridges, smaller cranium capacity.

4) The way a species sits, stands or hangs during feeding also influences its anatomy. For example, a siamang's ability to hang by its arms and legs may be more important in enabling it to feed from small branches than as a means of moving from one place to another. Likewise, the structure of a marmosets hand is influenced by the need to hold and process food as well as to grasp a support when moving. We can relate details of primate anatomy to differences in locomotion and posture and can use the information to reconstruct the behaviour of species known only from fossil. However, we scarcely understand why some species leap, others are arboreal quadrupeds, some swing by their arms and one is a biped.

UNIT 12 HOMINIZATION PROCESS*

Contents

Learning Objectives

After going through this unit, you will be able to:

- review the characteristics which distinguish human from their primate ancestors;
- understand the anatomical and cultural changes associated with the process of hominization; and
- study the significance of these changes during evolution of human.

12.0 INTRODUCTION

During Miocene epoch, the global climatic changes lead to the cold environment on the earth which induced open terrestrial biomes and reduction of tropical forest. Over time, the size of tropical forest decreased and broke up into mosaic where patches of forest were interspersed with Savannah Grassland. As forest shrank, the traditional ape food available on trees became scarce. In response to these ecological change primates came down from the trees and inhabited the terrestrial ecosystem (Haviland *et al.,* 2011). They used to spend more time on the ground. This necessitated foraging food on the ground such as seeds, grasses, roots and others. Eventually they became adapted to exposed terrestrial environment. In due course of time evolution lead to biped locomotion, large brain size, tool making behaviour, development of language and culture, which are significant in defining what makes a hominid. These evolutionary processes which lead to the development of human characteristics distinguished from primates are known as hominization. Thus, hominization could be understood as a multidimensional morphogenesis arising from the interplay of ecological, cerebral, socio-cultural and genetic factors. The process of hominization was intensified by the prolonged infancy and childhood which demand affective ties between generation and associated potential for cultural learning (Wulf, 2012). Now, we humans or *Homo sapiens* are a culture-bearing, upright-walking species that lives on the ground and evolved between 100,000 and 200,000 years ago (Encyclopedia Britannica).

In the present unit we will get an overview of the evolutionary changes which lead to the emergence of human features distinguished from primates.

Prof. Satwanti Kapoor, Retired, Department of Anthropology, University of Delhi, Delhi

12.1 BIPEDALISM

Of all extant primates, humans are the only obligate bipeds (Harcourt-Smith and Aiello, 2004). The erect bipedal posture we possess have been evolved from an knuckle-walking ancestor (Richmond *et al*., 2001). Though some of the primates can assume bipedal posture but only for a short duration that is when peering over tall grass or carrying objects in the hands. Chimpanzee and Gorilla are capable of much longer periods of bipedality but when on the ground they are normally quadrupedal and in knuckle walking stance. True bipedalism is represented only by humans (Swindler, 1996). Over the last several million years of evolution, these characteristic have developed independently at different rates. These patterns, in which physiological and behavioural systems evolve at different rates is called mosaic evolution (Jurmain *et al*., 2014).

Bipedalism in humans is the outcome of a large number of adaptive musculo-skeletal traits which completely transformed human lineage. Such adaptive traits have resulted from long term modifications in the vertebral column, the pelvis, the lower limb and the foot.

Check Your Progress

1) What is meant by Hominization?

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2) Define Mosaic Evolution.

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12.1.1 Evidences for Bipedalism

The fundamental distinction between us and our closest relatives is not our language, not our culture, not our technology, but it is that we stand upright, with our lower limbs for support and locomotion and our upper limbs free from those functions", said Richard E. Leakey, a palaeontologist. Paleoanthropologists mark the divergence between apes and hominids with the adaptation of bipedalism five to six million years ago. However, the process of becoming a fully efficient biped took much longer and was not complete until *Homo erectus* at 1.8 million years ago (Friedman, 2006). Hominid footprints preserved in the ash fall of a volcanic eruption some 3.5-3.8 million years ago (during Pliocene period) at Laetoli site in northern Tanzania, represent the earliest evidence of bipedalism in human evolution. These footprints were discovered by Mary Leakey in the late 1970s and are believed to be the imprints of *Australopithecus afarensis*, the earliest known hominid group (evolutionary lineage that also includes our species *Homo sapiens* (Jurmain *et al.,* 2014).

Early researchers hypothesized that brain enlargement was the first hallmark of the hominid lineage setting them apart from the apes. In 1828, embryologist Karl Ernst von Baer wrote, "Upright posture is only the consequence of the higher development of the brain..... all differences between men and other

animals depend upon construction of the brain" (Gould, 1977). However, the discovery of early hominid fossils exhibiting ape-sized brains and bipedally-adapted morphology showed that bipedalism evolved a few million years before brain. In 1924, an anatomist Raymond Dart discovered the skull of Australopithecine fossil, known as the Taung Child, from South Africa. This specimen belonged to the species *Australopithecus africanus.* The brain size was similar to modern apes but the foramen magnum positioned forward indicated that it held its head erect and walked upright. This was demonstrated most impressively by the finding of nearly complete fossilized skeleton of Lucy (female), a member of the species *Australopithecus afarensis* discovered by Donald Johanson, at Hadar, Ethiopia in 1974. The limb and pelvic fossils provided indisputable evidence of bipedality and erect posture. She had the anatomy of a biped, including a broad pelvis and thigh bones that angled in toward the knees, which brings the feet in line with the body's center of gravity and creates stability while walking (Wayman, 2012).

12.1.2 Anatomical Changes

Have you ever noticed the movement of your limbs when you walk? We maintain the balance on one leg when the other leg swings. Both feet are simultaneously on the ground only about 25 per cent of the time and this figure becomes even smaller as speed of the locomotion increases. Thus, maintaining a stable center of balance during upright walking necessitated many drastic structural and functional changes particularly in the limbs and pelvis.

a) ***Shortening and broadening of pelvis and stabilization of weight transmission***

Quadraped have vertically elongated hip bones positioned parallel to each other along the sides of the lower portion of vertebra. In contrast, hominins illium of hip bone became comparatively shorter and broader. Remodelling of pelvis lead to basin shaped structure that support abdominal organs and allows transmission of weight from lower back to hip joint during erect posture (Jurmain, 2012). This increased the distance between thorax and pelvis and freed the lumbar region from within the pelvis. This modification allowed lower back to move for a greater distance than Great Ape (Lovejoy, 2005). The alteration in pelvis also brought the sacrōiliac and hip joints into close proximity, reducing force transmission stress to the ilium (Aiello and Dean, 1990). Modifications of the pelvis *i.e* expanded and anteriorly projecting iliac blade with respect to the ischium repositioned the gluteal musculature. In quadrupeds, it is positioned to the side of hip bone and function to pull the thigh to the side and away from the body while in humans it is positioned behind the hip, which along with hamstrings muscle help to extend and pull thigh to rear during walking or running (Jurmain *et al.,* 2014).

The fossils of *Australopithecus afarensis* also known as 'Lucy' presents a shift towards the human pelvic condition. This shift facilitated adaptations to the bipedal locomotion including many changes such as a broad sacrum, a widened inter-acetabular distance and pronounced lateral iliac flare (Berge, 1994).

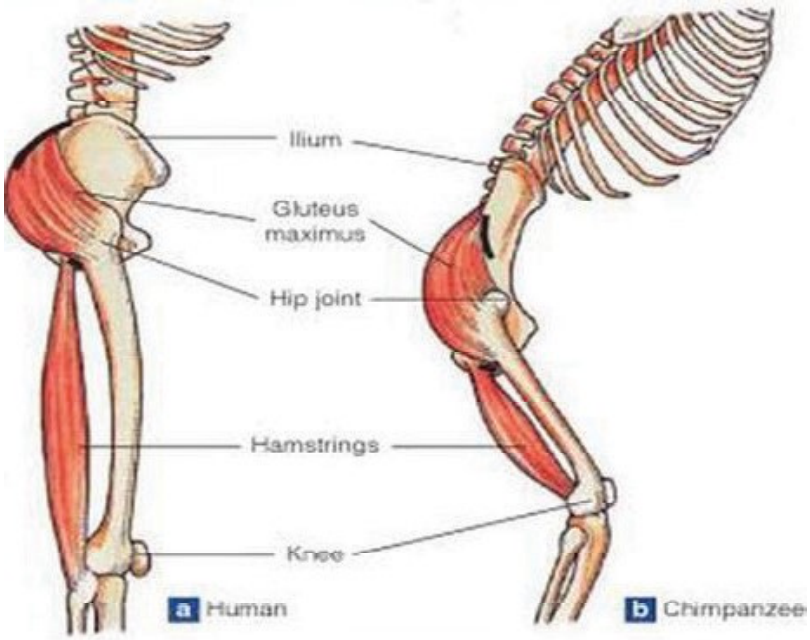

Fig 12.1 : Pelvis bone with the attachment of muscle

Source: Jurmain et al., 2014

Check Your Progress

3) What is considered as the earliest evidence of bipedalism in human evolution?

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4) How did shortening and broadening of pelvis helped in developing upright posture.

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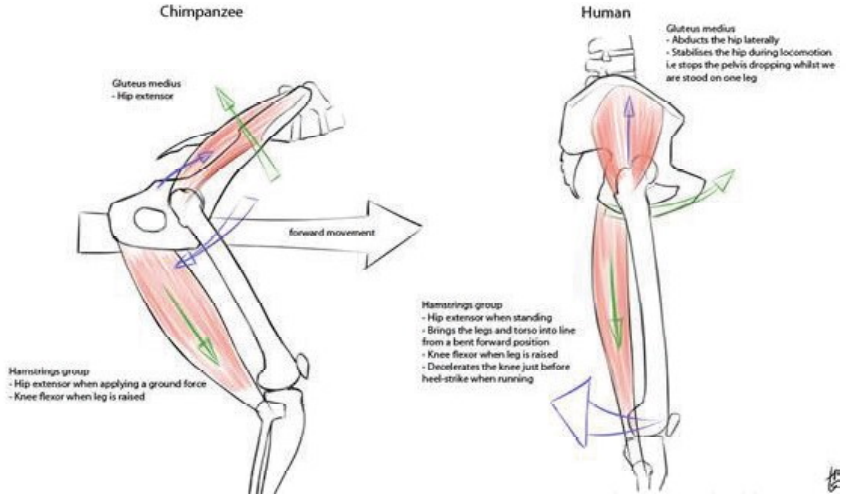
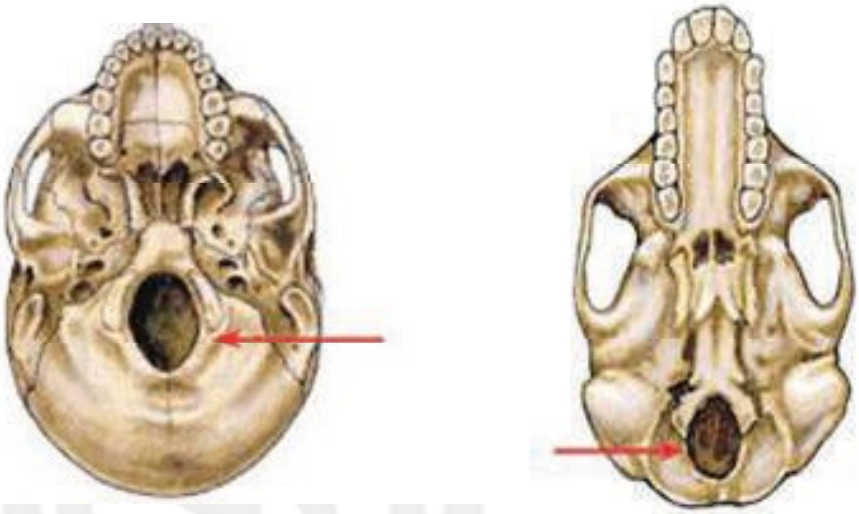


Fig 12.2: Function of limb muscles

Source: http://anthroanatomica_archive.html

b) ***Repositioning of foramen magnum forward, the opening at the base of skull from which spinal cord emerges.***

In comparison to other primates, humans possess foramen magnum in anterior position which is considered as an adaptation for maintaining balance of the head atop the cervical vertebral column. In contrast, Quadrupeds with posteriorly positioned foramen magnum require well-developed musculature and ligaments to bear the weight of head. The unique position of the foramen magnum associated with bipedalism and erect posture, in humans compared with other living orthograde primates, suggest that foramen magnum position may be used to identify bipedal adaptations in fossil hominins (Aiello and Dean, 1990; Berge, 1994; Jurmain, 2012; Jurmain *et al.,* 2014*,* Lovejoy, 2005; Russo and Kirk, 2013).



A) Human B) Chimpanzee

Fig 12.3. Position of foramen magnum

Source: Adapted from Jurmain *et al.,* 2012

c) ***Addition of curves (backward-thoracic, forward-lumbar) in spinal cord to transmit the weight of the upper body to hips in upper in an upright position.***

To maintain the bipedal posture under the effects of gravity, an effective transmission of the upper body weight is required. This transmission is done from the trunk, through the pelvic girdle to the lower limbs. The adaptive change in relation to weight transmission included a posterior concavity of the vertebral column in the lumbar region and convexity in thoracic region. The curvature also helps to absorb the force exerted during walking or running and allows flexion and extension of the trunk (Jamie Kendrick, 2014). Lack of such characteristic flexibility in extant primates restricts their lower back mobility. It also allowed centre of mass to lie centrally and vertically above the hips which consequently balance the body while striding in upright posture. The spinous process of more than half of the vertebrae point caudally. This change in orientation is related to the rearrangement of the muscles of the back which allow erect posture of trunk region (Buttner- Janusch, 1969).

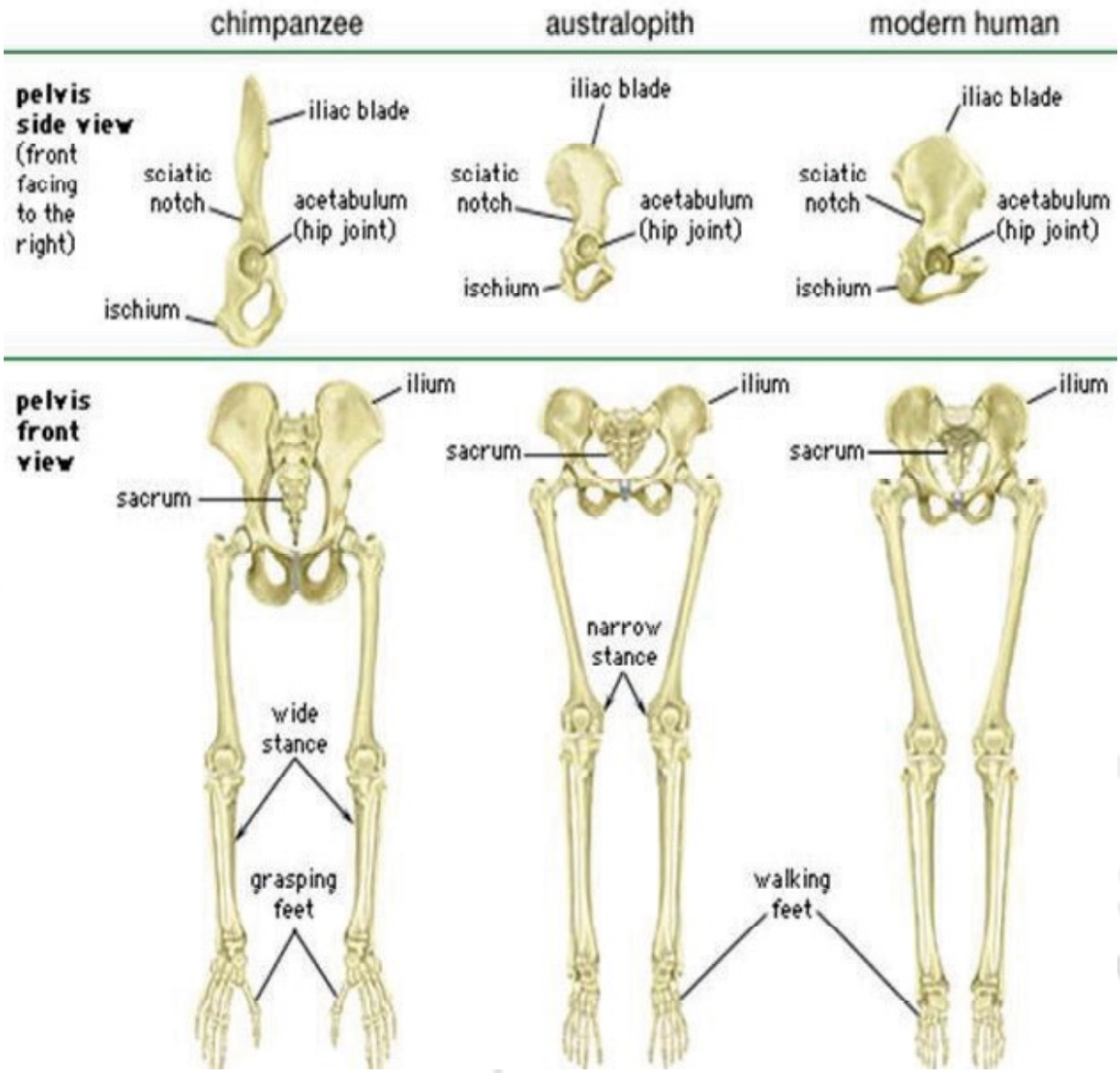
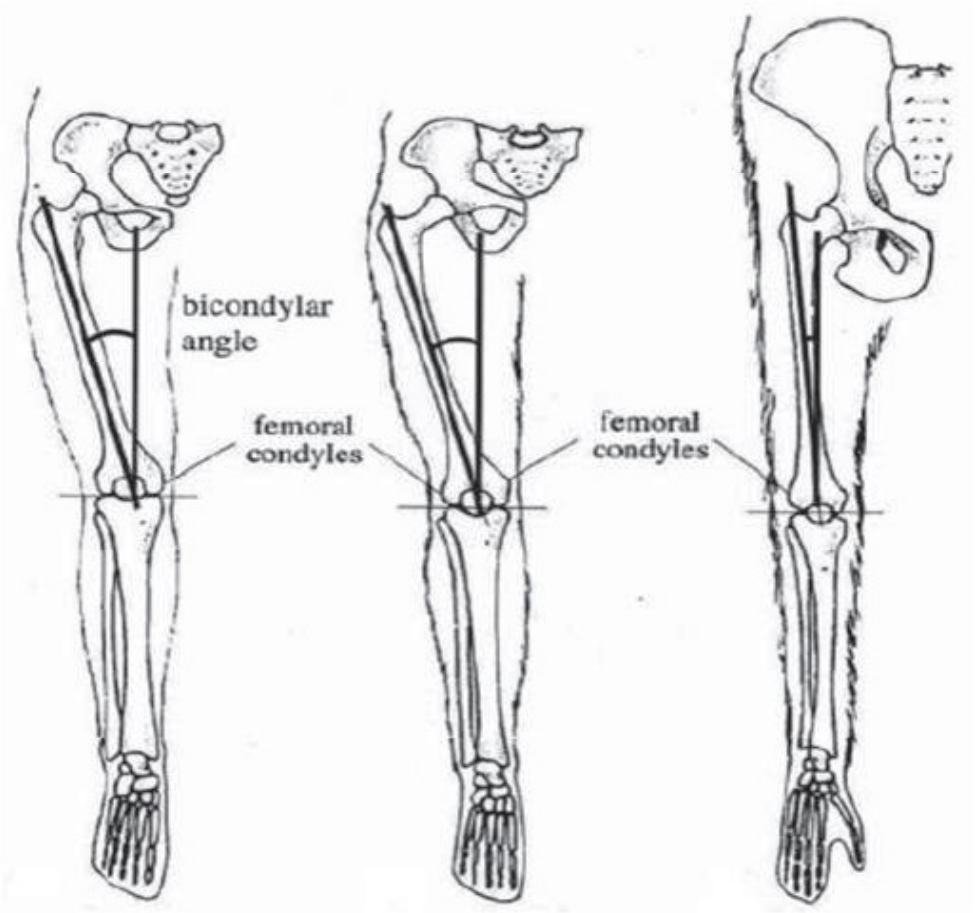


Fig. 12.4: Anatomical changes in pelvis

Source: www.encylopediabritinnica.com

d) ***Lengthening of hind limb and large bicondylar angle***

Humans have comparatively longer lower limbs than extant primates which contribute to longer stride length. The femoral bicondylar angle distinguishes bipedal humans from quadrupedal apes as it aligns the body's midline with the distal end of the femur, knee and lower leg. This helped in body's centre of mass to lie directly over the stance leg while walking (Aiello and Dean, 1990). This angle ranges between 8° to 11° in humans while it averages 1°-2° in African apes. A prominent inter-trochanteric line, gluteal tuberosity and a raised linea aspera enhanced attachments for muscles and ligaments in humans that also assisted to maintain upright posture.



a) Modern human **b) Australopithecus** **c) Chimpanzees**

Fig. 12.5. : Femoral- Bicondylar angles

Source: Adapted from Shsefelbine *et al.,* 2002

e) ***Structural changes in foot***

Throughout evolution, primates have retained an arboreal lifestyle, and foot shape characterised by a grasping (opposable) hallux and elongated distal segments. Acquisition of habitual bipedalism involved various anatomical changes (D'Aout and Aerts, 2008):

* A stabilized plantar arch which allows the foot to support body weight,
* loss of hallux (known as big toe in human) opposability and its alignment parallel to other phalanges,
* the proportions of the foot with relatively short phalanges, making it a more effective lever,
* a long and well developed calcaneal tubercle (heel bone) with a long Achilles tendon which impact postural orientation, and
* a talocrural joint (ankle joint) act as synovial hinge joint permitting dorsi-flexion and plantar flexion movement of the foot.

Fig 12.6. : Achilles tendon
Source: www.emedicinehealth.com

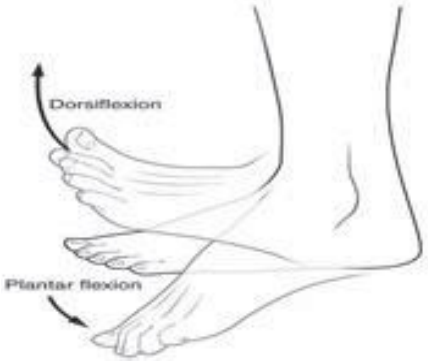


Fig 12.7: Movement of foot
Source: www.wikipedia.com

Bipedalism freed the forearm for use and manufacturing of tools. In bipeds, less portion of body is directly exposed to sun which provides thermo-regulatory advantage and aid in cooling of the body. Moreover, as greater portion of body is away from ground, it prevents warming of body by heat radiation from the ground**.** Bipedal stance provided wider view of the surroundings and early spotting of prey. They became efficient in covering long distance and hunting. Pelvic changes associated with bipedalism resulted in smaller birth canal. Evolutions lead to the birth of an infant at a stage when the head can fit through the birth canal, but induced prolonged growth and dependency periods. This consequently encourage male to guard female with dependant infants and development of affectionate relationship (Jurmain *et al.,* 2012).

Factor	Speculated Influence	Comments
Carrying (objects, tools, weapons, infants)	Upright posture freed the arms to carry various objects (including offspring).	Charles Darwin emphasized this view, particularly relating to tools and weapons; however, evidence of stone tools is found much later in the record than first evidence of bipedalism.
Hunting	Bipedalism allowed carrying of weapons, more accurate throwing of certain weapons, and improved long-distance walking.	Systematic hunting is now thought not to have been practiced until after the origin of bipedal hominins (see Issue, Chapter 12).
Seed and nut gathering	Feeding on seeds and nuts occurred while standing upright.	Model initially drawn from analogy with gelada baboons (see text).
Feeding from bushes	Upright posture provided access to seeds, berries, etc., in lower branches; analogous to adaptation seen in some specialized antelope.	Climbing adaptation already existed as prior ancestral trait in earliest hominins (i.e., bush and tree feeding already was established prior to bipedal adaptation).

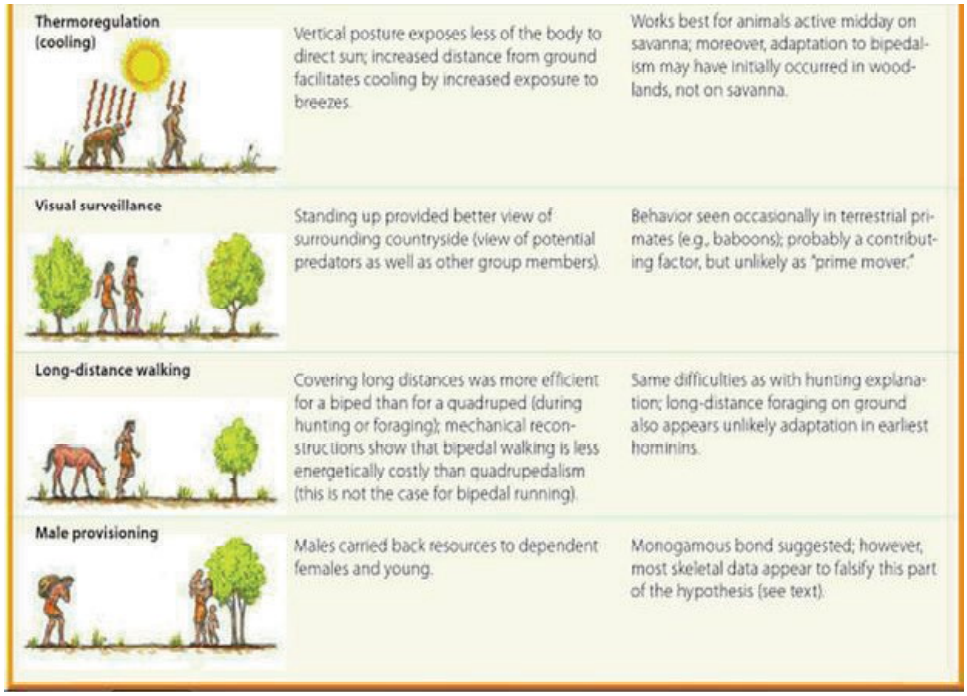


Fig 12.8 : Factors influencing evolution of bipedalism

Source: Adapted from Lewis *et al.,* 2010

12.2 OPPOSABLE THUMB AND MANUAL DEXTERITY

A diminutive thumb with long and curved fingers is typical characteristics of a primate hand (Midlo, 1934). In contrast, the human hand has an opposable thumb combined with fingers that have shortened and straightened. Although apes also share the trait of opposability of thumb but it is only the ability of humans to grip objects firmly in order to manipulate them (Marzke and Marzke, 2000). Human thumb also displays a greater degree of mobility in comparison to other primates which makes it unique and distinctive (Young, 2003).

Fig. 12.9a: Chimpanzee hand

Fig. 12.9b: Human hand

Source: A model for the hand of the hominid ancestor, Adapted from Napier, 1956

The discovery of fossil hand bones assigned to a 1.8-million-year-old specimen human ancestor Homo habilis at Olduvai Gorge in the early 60s, has put forth a general agreement that the anatomical reconstruction of the hand during human evolution was somehow linked with tool behaviour. This approach is consistent with evidence that early hominid bipedal behaviour would have 'freed the hands' for greater use of tools (Young, 2003).

During the prolonged period of evolution, the hand underwent profound changes that ---adapted it for grasping objects in a manner that allows gripping with strength sufficient to withstand a violent impact and precise control of release. Napier identified them as 'power' and 'precision' grips. In the power grip, the object may be held in a clamp formed by the partly flexed fingers and the palm where counter pressure being applied by the thumb lying more or less in the plane of the palm while in the precision grip, the object may be pinched between the flexor aspects of the fingers and the opposing thumb (Napier, 1956).

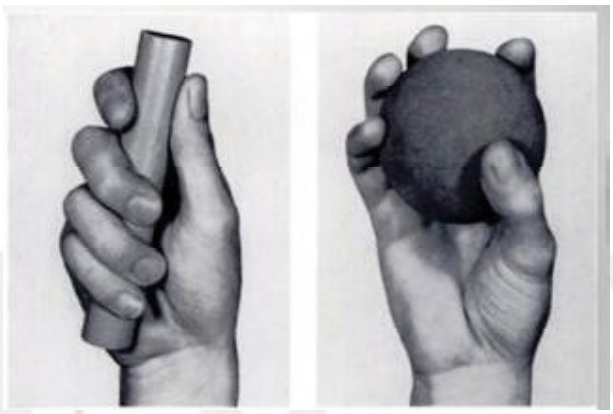


Fig. 12.10 a) : Power grip **Fig. 12.10 b) : Precision grip**

Source: Adapted from Napier, 1956

In Figure 12.10 a), the hand gripping the hammer stone displays the power grip. This grip controls the striking point and absorbs the shock. Core tool is held in a power grip so that it doesn't exit the hand on being stroked.

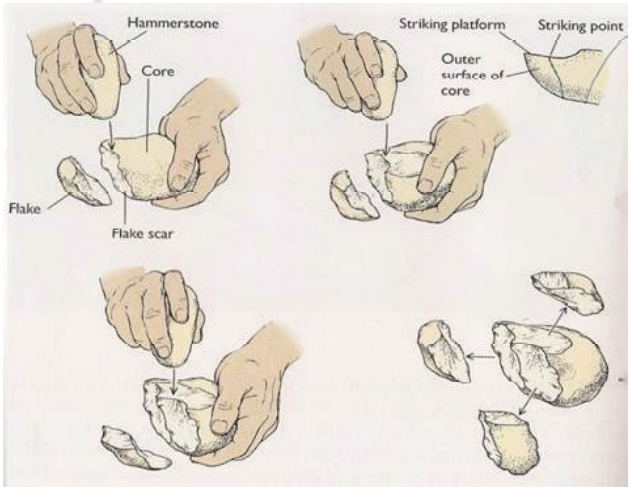


Fig. 12.11: Hand grip during making a tool

Source: http://www.gavilan.edu

When the core or other weapons were used for throwing to strike an enemy they would have needed precision grip. These grips are commonly referred to as the cylinder (power) and ball (precision) grips.

The remodelling of hand not only included anatomical changes in bone and muscles of wrist and finger (metacarpals) but also neurological basis for voluntary control developed. These modifications

a) relieved the stresses which were formed due to opposition of the thumb while manipulating an object and

b) allowed manual dexterity to grip object more firmly or enabled to throw it. Humans also possess flexor pollicis longus muscle which provides strength and control to the movement of thumb (Bade *et al.,* 1993, Marzke and Marzke, 2000).

Check Your Progress

5) What do you understand by power and precision grip?

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6) Write down the neurological changes that supported in remodelling of hand during the hominization.

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12.3 SUMMARY

Artifactual trace of prehistory often provides speculative evidences to paleoanthropologist to understand the hominin adaptation to changing environment and new behaviour adopted. Survival and proliferation of population in the new environment demands not only anatomical or physiological changes but also cultural and genetic transmission of favourable traits and behaviour from generation to generation.

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12.5 ANSWERS/HINTS TO CHECK YOUR PROGRESS

1) During the course of evolution many changes took place which was considered significant in defining what makes a hominid. These include biped locomotion, large brain size, tool making behaviour, development of language and culture. These evolutionary processes which lead to the development of human characteristics distinguished from primates are known as hominization.

2) Mosaic evolution is defined as the patterns in which physiological and behavioural systems evolve at different rates. For further details refer section 12.1

3) Hominid footprints preserved in the ash fall of a volcanic eruption around 3.5-3.8 million years ago (during Pliocene period) at Laetoli site in northern Tanzania represents the earliest evidence of bipedalism in human evolution.

4) Quadraped have vertically elongated hip bones positioned parallel to each other along the sides of the lower portion of vertebra. In contrast, hominins illium of hip bone became comparatively shorter and broader. Remodelling of pelvis lead to basin shaped structure that support abdominal organs and allows transmission of weight from lower back to hip joint during erect posture (Jurmain, 2012). For further details refer section 12.1.2

5) In power grip, the object may be held in a clamp formed by the partly flexed fingers and the palm where counter pressure being applied by the thumb lying more or less in the plane of the palm while in the precision grip, the object may be pinched between the flexor aspects of the fingers and the opposing thumb (Napier, 1956).

6) The neurological modifications that supported in remodelling of hand: (a) Relieving of stress which were formed due to opposition of the thumb while manipulating an object and (b) Enabling of manual dexterity to grip object more firmly or to throw it. For further details refer section 12.2