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Chapter 4

Comparative Anatomy of Primates

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SYNOPSIS

Primate comparative anatomy is a field of research that has profoundly interested scientists since several centuries ago, particularly due to its implications to the knowledge of the origin, biology, and/or evolution of our own species, *Homo sapiens*. In this chapter we provide a short summary of the comparative anatomy of humans and other primates that is based on a collaborative work of three experts in the field. A different author has written each of the sections. The first section focuses on osteology (bones and cartilages), the second on myology (muscles and tendons), and the third on external and internal organs. Within each section the information will be presented within an evolutionary context and often includes brief historical and/or functional considerations.

OSTEOLOGY

Introduction

The skeletal configuration of primates has often been related to arboreal and perhaps "visual predation" adaptations (Cartmill, 1972, 1974; see the chapter by Martin in this volume). For instance, the unguiculate (the state of possessing flattened nails) and opposable digits relate to a clear (though not unique or ubiquitous) grasping ability and the presence of a well-defined clavicle in primates that adds solidity to the shoulder in ways that are advantageous for arboreal stability all seem to argue for a life in the trees that more or less defines the order. Likewise, the orbital modifications—not only the bony encircling, but also a general reorganization to move the eyes forward for improved binocular vision—could have evolved to allow visual hunting, perhaps on terminal branches in trees. In short, though there is great diversity in the skeletal adaptations within the order, the primate skull and skeleton typically seem to have evolved for arboreality (Hill, 1972).

The Strepsirrhine Skeleton

There is almost as much skeletal diversity among the extant galagos, lemurs, and lorises (modern members of the suborder Strepsirrhini; see Figure 1) as there is in the whole order. If you 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 diminutive mouse lemurs (*Microcebus*)—as small as 30 g, the smallest of all living primates—to the ~6 kg indri (*Indri*). While this largest of living lemurs is not particularly impressive in size relative to hominoids and some monkeys,

FIGURE 1 Scheme showing the main primate clades and their phylogenetic relationships. (See color plate section).

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 that have given them the moniker the "koala lemurs" (*Megaladipis*). As strange as this taxon was, another extinct lineage (including *Babakotia* and *Paleopropithecus*) had distinct adaptations for underbranch suspension that has given them the name "sloth lemurs" (Mittermeier et al., 2006).

The living strepsirrhines 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; and (4) the "vertical clinging and leaping" lemurs (e.g., the indri, *Indri*, and sifakas, *Propithecus*). Almost all of the living strepsirrhines fall more or less within one of these categories with one amazing exception: the aye-aye (*Daubentonia*). This truly unique animal has a suite of morphology unlike any other primate: as the largest of all nocturnal primates, it has huge ears that it uses in combination with exceptionally long fingers to echolocate wood-boring insects in a feeding method known as "tap foraging." Once it locates an airspace beneath the surface of the wood, it uses its ever-growing incisors (also unique among primates and almost all other mammalian orders) to gouge into those cavities, and then it inserts its long, thin, and highly flexible middle finger into the hole to probe and fish out grubs. This, along with its impressive long and bushy tail, vestigial premolars and molars, inguinal mammaries (breast located in the groin) and highly cryptic behavior, clearly makes this sole member of its own family a truly mysterious primate (Mittermeier et al., 2006). It is arguably one of the strangest of all mammals.

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
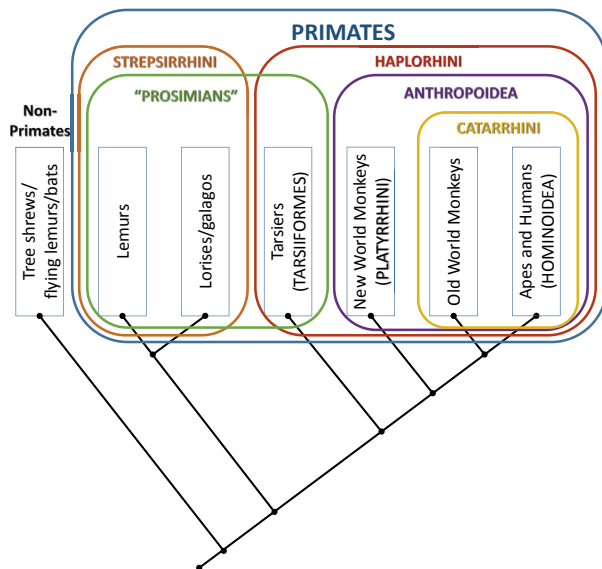
second toe. The truly defining feature of the group—the wet "rhinarium," essentially a continuity between the upper lip and nose that allows improved use of the vomeronasal organ—is a predominantly soft-tissue feature. However, the strepsirrhine emphasis on olfaction does highly influence the shape of 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 (Hill, 1953; Fleagle, 1999).

The Tarsiiform Skeleton

The small number of species of this group that is found in the islands off of Southeast Asia are 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: the tarsiers have very long ankle bones, giving them enormous leverage for leaping. They also have very sharp teeth for consuming soft animals. 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. 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 (Hill, 1955; Fleagle, 1999).

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).

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 total 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 nonprehensile 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 (Hill, 1957, 1960, 1962; Fleagle, 1999).

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 to 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 (Hill, 1966, 1970, 1974; Fleagle, 1999).

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) (Hill, 1974), 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) and (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). Human adaptations are of such interest that whole courses and indeed whole academic disciplines are devoted to the subject, and thus it is clearly beyond the scope of this chapter to discuss those adaptations in detail (Fleagle, 1999).

MYOLOGY

Introduction

The comparative myology of primates has interested researchers for centuries. This fascination can be observed in Tyson's (1699) illustration that shows the muscles of a chimpanzee (probably a bonobo, *Pan paniscus*) standing in a biped position, as if it were a modern human. Extant primates are characterized by various myological synapomorphies, which are shared, derived features (Diogo and Abdala, 2010; Diogo and Wood, 2012b), 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 (e.g., biceps brachii not inserting onto the ulna and the differentiated opponens digiti minimi) are found in a few other mammals, including nonarboreal taxa such as rats. Below we will list the various groups of head and neck and appendicular muscles found in primates and briefly discuss their evolution within primates.

General Notes on the Evolution of the Primate Muscles

A list of the number of head, neck, pectoral, and forelimb muscles present in representative genera from all major primate groups is shown in Table 1. Diogo and Wood (2012a) have pointed out that the taxa that appear in more derived positions within the primate tree, for instance, humans, are also generally more derived morphologically in the sense that there is a higher number of unambiguous evolutionary steps (concerning these groups of muscles) from the base of the tree to those taxa. For example, ringtail lemurs (*Lemur*) are one of the least morphologically derived primates in the tree and have accumulated only 25 myological changes since the base of the primate tree, while *Homo* has 75 accumulated steps ("number of steps," or NS = 75). Previous studies have shown that the transition rate of mitochondrial DNA has also been extremely low in *Lemur* (e.g., Hasegawa et al., 1990). However, there are exceptions to this generalization. For example, there are more accumulated steps leading to *Saimiri* (NS = 46) than to the Old World monkeys *Cercopithecus* and *Colobus* (44); to *Callithrix* (51) than to *Cercopithecus* and *Colobus* (44) and to *Macaca* and *Papio* (49); and to *Hylobates* (72) than to *Pongo* (59), *Gorilla* (64), and *Pan* (70) (see Glossary). The unique evolutionary history of hylobatids (see Glossary) is reflected in a peculiar mix of plesiomorphic ("ancestral") and derived anatomical structures. Hylobatids are an example of mosaic evolution for although their head and neck muscles (partial NS = 26) are anatomically less derived than those of hominids (partial NS *Pongo* = 28, *Gorilla* = 28, *Pan* = 32, *Homo* = 33) and various monkeys (partial NS *Saimiri* = 27, *Callithrix* = 30, *Macaca* = 28, *Papio* = 27) their pectoral and upper limb muscles are more derived (partial NS = 46) than those of any other taxon, including modern humans (partial NS = 42). The highly specialized pectoral and upper limb musculature of hylobatids is most likely related to their peculiar brachiating lifestyle (e.g., Andrews and Groves, 1976; Michilsens et al., 2009).

Bakewell et al. (2007, p. 7492) suggest that their molecular studies show that "in sharp contrast to common belief, there were more adaptive genetic changes during chimp evolution than during human evolution," that is, their finding "suggests more unidentified phenotypic adaptations in chimps than in humans." However, the results of Diogo and Wood's (2012b) parsimony and Bayesian analyses indicate that, at least regarding the gross morphology of the head and neck and pectoral and upper limb muscles, since the *Pan*/*Homo* split humans have evolved faster than chimpanzees (c. 2.3 times faster according to the lengths of the branches leading to modern humans and to chimpanzees in their most parsimonious tree, that is, the primate evolutionary tree obtained from their cladistic–phylogenetic analysis). In turn, since the *Gorilla*/Hominini split, gorillas have only accumulated two unambiguous muscular apomorphies (derived features), while there are respectively 8 (4+4) and 13 (4+9) unambiguous apomorphies leading to extant chimpanzees and to modern humans.

It is, however, important to stress that in this case having a higher number of character state changes in a branch does not mean having a higher number of muscles. For example,

TABLE 1 Table Summarizing the Total Number of Mandibular, Hyoid (Not Including the Small Facial, Extrinsic Muscles of the Ear), Branchial, Hypobranchial, Pectoral, Arm, Forearm, and Hand Muscles in Adults of Primate Genera

	Lemur	Propithecus	Loris	Nycticebus	Tarsius	Pithecia	Aotus	Saimiri	Callithrix	Colobus	Cercopithecus	Papio	Macaca	Hylobates	Pongo	Gorilla	Pan	Homo
Mandibular muscles	8	8	8	8	8	8	8	8	8	7–8	7–8	8	8	8	7	8	8	8
Hyoid muscles (not extrinsic ear)	25	24	24–26	26	24	22	23	21	22	24–25	26–27	25–26	26	26	26	26	26	27
Branchial muscles	14–16	14–16	15–17	14–17	16–17	14–16	14–16	15–16	14–16	13–14	16	14–15	16	17	14–15	15–16	15	16
Hypo-branchial muscles	12	12	12–15	12–15	12	12–13	11–12	12	13	12	12	13	13	13	12–13	13	13	13
Pectoral muscles	17	15–16	16	16	17	15	16	16	17	16	17	17	17	14	15	14	14	14
Arm muscles	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4
Forearm muscles	19	19	18	18	19	19	19	19	19	19	19	19	19	19	18	18	19	20
Hand muscles	30	30	30	34	32–36	22	22	22	21	27	27	27	27	27	20	20	26	21
Total number of muscles	130–132	127–130	128–135	133–139	133–138	117–120	118–121	118–119	119–121	123–126	129–131	128–130	131	129	117–119	119–120	126	123

The taxonomic groups in which the genera seen in this table are included are given in the Glossary.
Modified from Diogo and Wood (2012a).

some of the nine apomorphies of modern humans listed by Diogo and Wood (2012a) involve the loss of muscles (e.g., absence of levator claviculae; absence of dorsoepitrochlearis). In fact, as shown in Table 1, chimpanzees, along with most other extant primates, have more muscles than modern humans. The data provided in that table therefore contradict the *scala naturae* idea that there is a "progress" toward a greater "complexity" of modern humans, at least with regard to the number of muscles and muscle bundles. In the next paragraphs, we briefly summarize and discuss the information provided in Table 1 and compiled from Diogo and Wood's (2012a) studies. We focus on the muscles of the head and neck and pectoral and upper limb muscles and follow the myological nomenclature of Diogo and Abdala (2010). The pectoral and upper limb muscles are divided into five subgroups: pectoral, arm, ventral forearm, dorsal forearm, and hand. Regarding the head and neck muscles, we focus on four main subgroups: (1) Mandibular—these are generally innervated by the Vth cranial nerve, the trigeminal (e.g., the muscles of mastication and one of the middle ear muscles, the tensor tympani); (2) Hyoid—these are usually innervated by the VIIth cranial nerve, the facial (e.g., muscles of facial expression and the other middle ear muscle, the stapedius); (3) Branchial—these are usually innervated by the IXth (glossopharyngeal) and Xth (vagus) cranial nerves and include the majority of the intrinsic laryngeal muscles, although the trapezius and sternocleidomastoideus are mainly innervated by the XIth (accessory) cranial nerve; and (4) Hypobranchial—according to Edgeworth (1935) the muscles in this group are developed from the anterior myotomes of the body and thus they have all migrated into the head (e.g., infrahyoid muscles). Although they retain their main innervation from spinal nerves, they may also be innervated by the XIth and XIIth (hypoglossal) cranial nerves, but they usually do not receive any branches from the Vth, VIIth, IXth, and Xth cranial nerves. We therefore do not discuss the internal and external ocular muscles.

Head and Neck Muscles of Primates

The number of mandibular muscles is essentially constant ($N=8$) within extant primates, including modern humans; an exception is *Pongo*, which lacks the muscle digastricus anterior. With respect to the hyoid muscles, the predicted plesiomorphic condition for the primate clade is four nonfacial hyoid muscles, that is, more than most extant primates, including modern humans ($N=3$). This is because the jugulohyoideus is usually lacking in *Tarsius* and is almost always, if not always, absent in anthropoids. Some phylogenetically derived primates also have more nonfacial hyoid muscles than modern humans (e.g., *Pongo* has four muscles because it has a peculiar muscle stylolaryngeus). However, with respect to the facial muscles, despite

lacking three muscles that were plesiomorphically present in primates (platysma cervicale, sphincter colli profundus, and mandibulo-auricularis), modern humans do have more facial muscles than any other primate studied by us ($N=24$, not including the small extrinsic muscles of the ear). This illustrates the role played by facial muscles in primate and particularly human evolution. Examples of facial muscles that are present in modern humans and missing in most other primates are the risorius and the temporoparietalis.

It is predicted that plesiomorphically ("ancestrally"), primates had four, or even five (if both the spinotrapezius and the acromiotrapezius were present as distinct muscles, as is the case in extant taxa such as *Tarsius*), true branchial muscles. Modern humans usually only have three muscles (trapezius, sternocleidomastoideus, and stylopharyngeus) for, as in other hominoids, modern humans usually lack a ceratohyoideus. The number of pharyngeal muscles is relatively constant within extant primates; modern humans have no autapomorphic, unique pharyngeal muscles nor do they lack any muscle that was predicted to be plesiomorphically present in primates. However, modern humans, as well as gorillas, do have more laryngeal muscles ($N=5$) than most other primates (which usually do not have a distinct arytenoideus obliquus). This stresses the importance of vocal communication in primate and human evolution. With a few exceptions, the number of hypobranchial muscles is essentially constant ($N=11$–13) within extant primates, including modern humans. The exceptions mainly concern the presence/absence of the palatoglossus and/or of the omohyoideus, although in some rare cases small muscles derived from the genioglossus may be recognized as distinct structures (e.g., genio-epiglotticus and hyo-epigloticcus in at least some specimens of *Loris*).

Pectoral and Forelimb Muscles of Primates

It is predicted that plesiomorphically, primates probably had 17 pectoral muscles (including a deltoideus acromialis et clavicularis and a deltoideus scapularis, as well as a single rhomboideus—not differentiated into a rhomboideus major and a rhomboideus minor). However, modern humans usually only have 14 pectoral muscles (the rhomboideus occipitalis, levator claviculae, and panniculus carnosus are missing and the deltoideus is not differentiated into a deltoideus acromialis et clavicularis and a deltoideus scapularis, but the rhomboideus minor and the rhomboideus major are differentiated). Extant primates generally have the same number of arm muscles ($N=5$), but because modern humans lack a dorsoepitrochlearis they have only four muscles. Forearm muscles in primates usually number between 18 and 19; two of the 19 muscles that are predicted to be plesiomorphically present in primates may be missing in some groups (e.g., the epitrochleoanconeus is usually absent in hominoids except *Pan* and the anconeus is usually

absent in *Hylobates*). Modern humans, because they usually lack the epitrochleoanconeus but have a flexor pollicis longus and an extensor pollicis brevis, have more forearm muscles than any other primate studied by us (N.B., hylobatids also have a flexor pollicis longus and an extensor pollicis brevis, but they normally lack an anconeus). With respect to the hand muscles, phylogenetically plesiomorphic primates such as strepsirrhines and *Tarsius* usually have more than 30 muscles, but modern humans usually have only 21 muscles. The muscles that are conserved as separate structures in modern humans are those that insert onto the thumb; modern humans also have an additional pollical muscle "volaris primus of Henle" (TDAS-AD *sensu* the present work). The muscles that modern humans have lost relative to phylogenetically plesiomorphic primates (e.g., contrahentes, intermetacarpales, and interossei accessorii) attach to digits 2, 3, 4, and 5. This stresses the role played by thumb movements (produced by hand muscles, but also, importantly, by peculiar muscles such as the flexor pollicis longus and extensor pollicis brevis) in human evolution, probably related to tool manipulation (Diogo et al., 2012).

Variation and Evolutionary History of Primate Muscles, and Comments on the "Scala Naturae"

The muscle groups that show the least variation in number within the primate clade are the mandibular muscles (range 7–8), the arm muscles (range 4–5), and the forearm muscles (range 18–20); then come the pectoral muscles (range 14–17), the branchial and hypobranchial muscles (range 13–17 and 11–15, respectively); the hyoid muscles (range 21–27) and in particular the hand muscles (range 20–36) show the greatest variation in number. With respect to the overall number of muscles in the primate subclades, the New World monkeys are the least variable clade (range 117–121); this is remarkable because the Platyrrhini is the taxonomically more diverse group of extant primates. Then come the Old World monkeys (range 123–131), the hominoids (range 117–126), and the strepsirrhines (range 127–139). Interestingly, the phylogenetically more plesiomorphic groups of living primates (i.e., the strepsirrhines (range 127–139) and tarsiiforms (range 133–138)) are the ones with the greatest number of muscles in total, followed by the Cercopithecinae (range 128–131) and *Hylobates* (129), then by *Pan* (126) and *Colobus* (range 123–126), then by modern humans (123), and lastly by *Gorilla* (range 119–120), *Pongo* (range 117–119), and the New World monkeys (range 117–121 m).

In summary, regarding the evolution of these muscles listed in Table 1 within the order primates, it can be said that there is no simple relationship between muscle number and relative position on the primate evolutionary tree (cladogram). Modern humans have fewer head, neck, pectoral,

and upper limb muscles than most extant primates, including phylogenetically plesiomorphic primates such as strepsirrhines and tarsiiforms, as well as Old World monkeys and chimpanzees. It is remarkable that *Nycticebus* and *Tarsius*, two nonanthropoid genera that include some of the smallest living primates and that are often considered to be anatomically plesiomorphic in comparison to anthropoid primates, have more head, neck, pectoral, and upper limb muscles than any other primate taxon included in Table 1. These data clearly refute the contention (*scala naturae*) that modern humans are the most anatomically complex primate. The only muscle groups for which modern humans have more muscles than most other primates are the muscles of the face, larynx, and forearm. In modern humans the latter include two peculiar muscles that are related to the movements of the thumb; among nonhuman primates extensor pollicis brevis and flexor pollicis longus are only present in hylobatids and as explained above modern humans usually have an additional muscle inserting onto the thumb, the volaris primus of Henle. Therefore, the summary provided here shows that modern humans have fewer muscles than most other living primates, but it is also consistent with the proposal that facial and vocal communication and specialized thumb movements have probably played an important role in human evolution.

EXTERNAL FEATURES AND INTERNAL ORGANS

Introduction

The constructional morphology framework presents three factors that interact to determine the biological form. These are a *phylogenetic factor*, which is guided by an individual's evolutionary history, a *morphogenetic factor*, which includes both ontogeny and biomechanics, and finally an *adaptive factor*, which acknowledges the role natural selection has on an animal's body plan (Thomas, 1979). As you have read above, there is an incredible variation in the musculoskeletal anatomy among primates. Discussed below is the comparative anatomy of the major organ systems in these mammals. It is important to recognize that although function is often attributed to many of the features described below, there are other factors beyond natural selection that shape the anatomy of a primate.

The internal organs of primates can be relatively conservative in appearance and size. This means that some organs do not deviate from what is expected for an individual's size. Examples of conservative organs are the heart, spleen, liver, and kidneys (Leonard and Robertson, 1992; Aiello and Wheeler, 1995). Some organs do differ in morphology, but on closer examination, these differences most likely are influenced more by phylogenetic or developmental factors, rather than adaptive factors. The lungs are an example of

these differences. Humans typically have three lobes on the right and two lobes on the left (Saladin, 2012). However, despite lobe differences, the segmental architecture of the lung on each side remains the same, and thus functionally equivalent. Other primates, for example, the squirrel monkey (*Saimiri*), the orangutan (*Pongo*), and the gorilla (*Gorilla*) have fewer lobes but the segmental architecture remains the same (Ankel-Simons, 2007). Small differences in morphology, in many instances, do not result in differences in physiology or function.

Below we will highlight the major structural and functional differences of homologous organs and accessory structures across primates, including the nervous system, which includes a discussion on brain size; the visual, auditory, and olfactory systems; the digestive system, which includes comparative lingual anatomy; and lastly the reproductive system.

The Nervous and Sensory Systems

Primates are unique when compared to most other mammals because we have relatively larger brains than expected for our body size (Radinsky, 1972; Fleagle, 2013). Among primates, there is a notable increase in relative brain size between strepsirrhines and haplorhines, and then again between monkeys and hominoids. Measures of relative brain size are hypothesized to be a rough estimate of the intelligence of an animal but, although there is some truth to this hypothesis, the brain cannot be regarded as a single evolutionary or functionally homogeneous entity (Fleagle, 2013). The brain has several different regions, each specialized for a particular function (e.g., occipital lobe = vision). There are gross differences across primates in the relative size of these functional regions that might be masked if brain size alone is examined. For example, if a tarsier (*Tarsius*) and a mouse lemur (*Microcebus*) are compared, both have similar brain sizes and both are similar in size. However, on a closer examination of the functional regions of these animals, the tarsier devotes a larger percentage of the brain to visual processing (Fleagle, 2013).

In primates, the visual system is referenced as one of the most important sensory modalities relative to the other special senses (Le Gros Clark, 1959; Martin, 1990). Although this is true to some degree across primates, this generalization is most fitting for haplorhine primates (Kirk, 2004; Kirk and Kay, 2004). There is remarkable diversity in the visual abilities within haplorhines, but broadly anthropoids are adapted for extremely acute diurnal vision. Visual acuity is the ability to distinguish between two closely spaced visual stimuli (Kirk and Kay, 2004). Comparative studies have pinpointed several features that enhance visual acuity. These are relatively large eyes, an absence of a tapetum lucidum, the presence of short-wavelength filters in the lens and retina that limit chromatic aberration, and the presence

of a central retina with a high photoreceptor density. There are several hypotheses on why these features have evolved in primates, one hypothesis suggesting that this combination of features is well developed in vertebrates that rely on visually directed predators (Ross, 1996).

The ability of primates to discriminate color is unique among mammals (Ahnelt and Kolb, 2000; Arrese et al., 2002; Dominy et al., 2003). Some primates possess three types of retinal cones (Dominy et al., 2003). All anthropoids exhibit at least dichromatic, and in catarrhines trichromatic, color vision (Dominy et al., 2004). Trichromacy in catarrhines is regarded as routine or uniform, meaning both males and females possess three opsins tuned to three key wavelengths: ~430, ~530, and ~560 nm (Jacobs, 1994). Several hypotheses have been proposed for why trichromacy evolved. The visual system of primates may be tuned to stimuli of vital importance, such as food. Some researchers do suggest that routine trichromachy in primates evolved to detect color differences in mature leaves, which are typically green, and immature leaves, which are typically red in color. Immature leaves have fewer toxins and are easier to digest (Dominy and Lucas, 2004). The ability to detect and select red leaves over green may be a foraging adaptation in primates. Other researchers, however, believe that color vision and enhanced visual acuity in catarrhine primates may have evolved to facilitate long-range visual communication and facial recognition. For example, in females of many catarrhine taxa, signal receptive sexual behavior changes with the size, shape, and color of their perianal "sexual" skin (Rowell, 1972). Signaling of this sort can communicate subtle differences in the reproductive state on an individual. Again, the visual system in primates is complex and has long been a topic of interest among scientists. Teasing out differences in the visual system can shed light on the evolution of both the feeding and the social ecology of our order.

Olfaction (smell), in contrast to vision, has been greatly reduced in primates. There are two main olfactory systems, the main olfactory system and the vomeronasal system. Primates vary greatly in the size and complexity of these systems. The vomeronasal system is finely tuned to detect sociosexual signals (pheromones) and the main olfactory system is more broadly tuned to detect both ecological and social signals; however, there is evidence for a wide degree of overlap of the two (Garrett and Steiper, 2013). The main olfactory system appears to be relatively well developed across all primates, while the development of the vomeronasal system is variable across the major primate clades. Strepsirrhines maintain a functional vomeronasal system comparable to many nonprimate mammals, while haplorhines exhibit a reorganization or loss of its peripheral sensory organ, the vomeronasal organ (Smith et al., 2007). Platyrrhines and tarsiers have functional vomeronasal organs that have a different distribution of sensory

epithelium compared to other mammals (although research on olfactory marker protein activity indicates that *Saguinus tamarins* has nonfunctional vomeronasal organs), and catarrhine primates have either lost the vomeronasal organ entirely or exhibit nonfunctional vestiges (Kappeler and van Schaik, 2002; Smith et al., 2004, 2005, 2011). The overall reorganization/reduction of the vomeronasal organ in haplorhine primates may have been a consequence of acquiring a complex visual system that was more energetically expensive, and reducing a more finely tuned olfactory system for which the main olfactory system could compensate (Garrett and Steiper, 2013).

The auditory system of primates does not deviate significantly from most other mammals. Primates have "average" hearing. The auditory system is composed of six receptor endorgans that help us detect sound and facilitate movement. Together, these sensory endorgans comprise the "membranous labyrinth" of the inner ear (Purves et al., 2001; Smith et al., 2004). The six receptor endorgans include three semicircular canals, the utricle, the sacculus, and the cochlea. The semicircular canals help with detecting angular acceleration of the head and assist in stabilizing the eyes and head. The utricle and sacculus help detecting linear acceleration of the body and head tilt relative to the plane of gravity. The cochlea detects sounds that are transmitted through the fluid filled canal by the external and middle ear (Kirk and Gosselin-Ildari, 2010). These endorgans are suspended within the petrous temporal bone, and they are difficult to examine without the assistance of high-resolution imagining, such as computed tomography. Primates that are agile and have fast jerky locomotion have significantly larger canals relative to body size than those that are more cautious (Spoor et al., 2007). For example, the gibbon has large semicircular canals for its body size, while slower moving apes like the chimpanzee and gorilla have smaller semicircular canals (Spoor, 2003). In a recent study of 33 primate species Kirk and Gosselin-Ildari (2010) found differences in the length of the cochlea in primates. The dimensions of the cochlea influence hearing abilities in mammals. The basilar membrane length (cochlea) is correlated with both the high- and the low-frequency limits of hearing in mammals with unspecialized cochleae. In primates, as choclear size increases, the range of audible frequencies shifts downward (Kirk and Gosselin-Ildari, 2010). Establishing correlations among skeletal structures (inner ear), soft tissues (cochlear membrane), and function (agility and hearing) has important implications for interpretations of the fossil record (Spoor, 2003).

The Digestive System

The digestive system includes the oral cavity (including the tongue), esophagus, stomach, intestines, and rectum. The tongue is an important structure and the centerpiece of the gustatory system. The function of the gustatory system (taste) is to help determine the chemical contents of foods. Failure to recognize food with a high enough caloric content could mean death, albeit slow, from malnutrition. Obtaining adequate nutrients from food is critical for both males and females. However, food selection (and rejection) may be more important to the reproductive success of females because their reproductive costs are higher than male reproductive costs. As taste is a very important sense involved with food selection and rejection, females may benefit more from greater taste sensitivity than males. In a comparative analysis of primates, taxa with higher reproductive cost (e.g., large brained primates such as *Cebus*, *Gorilla*, *Pan*, and *Homo*) do show a sex-based difference in gustatory anatomy (Alport, 2009; Muchlinsk et al., 2011). The dorsum of the tongue is carpeted with four types of papillae: filiform, fungiform, foliate, and circumvallate. Filiform papillae can be found across the entire tongue and are nongustatory, meaning that they are not capable of transmitting taste information to the brain. Circumvallate, foliate, and fungiform papillae are gustatory and distinct in their location and anatomy (Purves et al., 1997). Circumvallate are located on the posterior aspect of the tongue, whereas foliate are located on the posterolateral aspect of the tongue. Fungiform papillae are located on the anterior two-thirds of the tongue. Fungiform papillae are the first gustatory structure that comes in contact with an ingested chemical (Purves et al., 1997; Buck, 2000). Accordingly, fungiform papillae are critical in food selection and show the most sexual dimorphism. Each papilla contains taste buds that include taste cells. Comparative gustatory research in primates has found that females in some species have a greater number of fungiform papillae, larger fungiform papillae, and a higher density of fungiform papillae than males (Muchlinski et al., 2011). In addition to documented sex-based differences, there is evidence for interspecific variation in fungiform papillae densities among primates who consume sweeter food, like fruit, and those that focus on less sweet food like leaves. Fruit eaters tend to have a higher density of fungiform papillae compared with fruit and insect eaters (Alport, 2009).

The digestive system is mainly a hollow muscular tube that can broadly be divided into three: the foregut, midgut, and hindgut. The foregut is the anterior part of the alimentary canal, which includes the pharynx, esophagus, stomach, liver, pancreas, and half of the duodenum. The midgut is the middle section of the alimentary canal, which includes a portion of the duodenum, the ileum, the jejunum, and the first two-thirds of the colon. The hindgut includes the last one-third of the transverse colon, the descending colon, sigmoid colon, rectum, and the upper two-thirds of the anal canal. Each region serves a different function in digestion (Chivers and Hladik, 1980; Hladik et al., 1980a; Hladik, 1981). Many animals are referred to as either foregut or hindgut fermenters. Beyond enzymes, the gut houses

and nurtures a complex microorganism ecosystem. These microorganisms help animals digest foods, particularly cellulose. A symbiotic relationship exists between almost all herbivorous mammals and microbes. The animals provide the food and space for the microbes, and the animals receive, in return, the by-product of fermentation, which includes fatty acids and sugars (Ankel-Simons, 2007). Fermentation is a slow process, and it requires space for it to occur. Animals that rely on fermentation have expanded alimentary canal regions to facilitate digestion.

In primates, foregut fermenters like the Colobidae (e.g., *Colobus* spp., *Presbytis* spp., *Trachypithecus* spp., *Pygathrix nemaeus*, *Nasalis larvatus*) have enlarged saculated stomachs. The advantage of foregut fermentation is that the animals can absorb the by-products of fermentation because digestion of the cellulose occurs prior to entering into the small intestines, which is a region where the majority of nutrient absorption occurs (Fleagle, 2013). There are hindgut fermenters as well; these include members of the genus *Alouatta* and *Indridae*. Hindgut fermentation is facilitated by enlargement of the cecum and colon (Ankel-Simons, 2007). Hindgut fermenting primates tend to be more variable in their diets and focus more on young leaves, flowers, and fruit, than mature leaves (Milton, 1980, 1981). Mountain gorillas are different from other gorillas because they depend more on herbaceous vegetation. Most other gorillas focus primarily on fruit, and then fall back on herbaceous food during periods of food scarcity (Tutin et al., 1991; Nishihara, 1995; Remis, 1997; Rogers et al., 2004). Mountain gorillas are neither foregut nor hindgut fermenters, despite relying primarily on leaves and terrestrial herbaceous vegetation (Rogers et al., 2004). They have a generalized hominoid gut adapted for frugivory (Kay, 1975; Chivers and Hlakik, 1980; Martin et al., 1985), but do have a high number of cellulose-digesting protozoans in their colon (Collet et al., 1984). Thus, although primates may not be specialized for foregut or hindgut fermentation morphologically, they may possess wildly divergent microorganisms that can facilitate cellulose digestion. Faunivores (insect and small vertebrate feeders) are not classified as hindgut fermenters. Many faunivores do have notable enlargement of the cecum relative to other primates. The insect exoskeleton shares structural similarities to that of mature leaves (Chivers and Hladik, 1980). Cecal enlargement in many faunivores (like the tarsiers) slows down digestion by increasing the distance food must travel, and as a result, increases absorption. Beyond an enlarged cecum, all other digestive structures remain relatively simple (Chivers and Hladik, 1980; Ankel-Simons, 2007).

The Reproductive System

All primates have a basic mammalian reproductive system: sperm fertilizes a primary occycte (egg) housed within the female, and the embryo then develops in utero for several months after fertilization. The reproductive organs of both the male and the female are similar to those found among most nonprimate mammals. The male possesses testes, a spermatic cord, seminal vesicles, a prostate, and a urethra. The female has ovaries, fallopian tubes, and a uterus. Humans are no different from most other primates. However, the differences seen in both the external and the internal anatomy of primates is great and is a result of differences in socioecology, a field of biology that examines how social structure (including reproductive strategies) and organization are influenced by an organism's environment. The way females have organized themselves around food (a limiting resource for females) and how males have organized themselves around the females (females are the limiting resource for males) have had a huge influence on the mating behaviors and as a result the reproductive anatomy of primates.

Female primates typically possess two ovaries. These ovaries are connected to the uterus via the fallopian tubes, which are associated with the ovaries via one fimbria. There is considerable variation in the size and length of the fallopian tubes. In most strepsirrhines the fallopian tubes are large relative to the body of the uterus. Additionally, most strepsirrhines and the tarsiers have a uteruses that are bicornuate, or "two horned" (Ankel-Simons, 2007; Fleagle, 2013). This anatomy is most commonly among animals that have twins or have litters (Ankel-Simons, 2007). In contrast, haplorhines tend to have fallopian tubes that are relatively slender and the body of the uterus is not split and is relatively large compared to those observed in strepsirrhines (Fleagle, 2013). This anatomy is most common among animals that generally give birth to one offspring at a time.

One of the most fascinating displays of diversity among female primates is clitoral anatomy. The clitoris is located just anterior to the external urethral orifice and the vagina. In many primates, including humans, the clitoris is hidden under a "hood," which is a double fold of skin and is also the most anterior extension of the labia minora. In contrast, some primates like some Malagasy primates (*Strepsirrhini*: Lemuriformes) and atelines the clitoris is pendulous and larger than their male counterparts penises (Ostner et al., 2002; Drea and Weil, 2008; Fleagle, 2013). Adult males tend to dominate females because of their size and androgen-mediated aggressiveness (Ostner et al., 2002). However, in some primates, particularly the Malagasy strepsirrhines, females clearly dominate males in dyadic agonistic interactions (Tecot et al., 2013). Interestingly, adult female Malagasy strepsirrhines do not exhibit higher androgens than males. The reason behind female masculinization is not completely understood, but is mostly a result of prenatal androgen levels (Ostner et al., 2002). While most lemurs and some New World monkeys present with an enlargement of the clitoris, most Old World monkeys and

hominoids do not; however, most Old World monkeys and hominoids do have enlarged sexual swellings that signal sexual receptivity. As noted above (sensory system section), all primates have a functional main olfactory system, but most catarrhine primates have lost the vomeronasal organ that is responsible for detecting pheromones. Pheromones are excreted hormonal signals. In animals that possess a vomeronasal organ, pheromones can communicate subtle differences in physiology. Researchers have suggested that the loss of the vomeronasal organ in catarrhines is closely correlated with the evolution of the sexual swelling. However, there is a long-standing dispute over whether there is a vomeronasal organ present in adult humans. Embryonic studies do show that developing humans do present with a vomeronasal organ. Recent microscopic studies show that some adult humans, if not most, have retained the vomeronasal organ on at lease one side (Meredith, 2001).

Males match females in genital diversity. Most males, including the apes, have androgen-dependent, keratinized "spines" (some small, and some not so small) along the shaft of the penis. These spines can be simple, like a single-pointed spine observed in the macaque, or more complex. Many strepsirrhines have complicated multispiked spines. Dixson (2012) attributes this variation to mating behavior. Simplified penile morphology tends to be associated with monogamous reproductive strategies in primates, while the more complex morphologies are associated with the more promiscuous strategies. These spines may increase tactile sensitivity of the glans because each spine is associated with tactile mechanoreceptors and is highly innervated. The spine may also help maximize reproductive success (Dixson, 2012). Testes size is also closely linked to androgen levels. In *Mirza coquereli*, and some other Malagasy strepsirrhines, the testes of the male enlarge during the mating season (Fleagle, 2013). The mating system of *M. coquereli* is described as scramble competition polygyny (Kappeler, 1999). Primates that show little mating competition, for example, monogamous (e.g., titi monkey) and single-male multifemale polygynous species (e.g., gorillas), have relatively small testes. Conversely, large testes are observed in primates that are multimale polyandrous where there is a significant amount of male–male competition (e.g., chimpanzees) (Wrangham, 1979; Van Schaik and Van Hooff, 1985; Kappeler and van Schaik, 2002). Interestingly, human male testicular anatomy falls somewhere between polygynous and polyandrous species, but closer to the polyandrous side of the spectrum (Wright, 1994). Interestingly, in many cultures, the correlations between mating systems and anatomy are not as closely linked as in many other primate groups. Based on testicular weight, humans should be polyandrous. Although polyandry is common in Africa (e.g., Northern Nigeria—cohusbands), Europe (e.g., Celtics), Asia (Lahaul-Spiti of the Himalayas), and in areas of the New World, today, monogamy or polygyny are more often the established culturally imposed behavioral norm. However, based on anatomical clues, one could hypothesize that monogamy and polygyny are a more recent phenomenon among humans than many people would like to think (Wright, 1994; see the chapter by Gangestad and Gebe).

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