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Evolution and Phylogeny of Amniotes

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Definition

Amniotes (Amniota) form a monophyletic group that encompasses the last common ancestor of living mammals and reptiles, and all descendents of that ancestor. They are characterised by the possession of an amniote egg (or at least amniotic membranes in live-bearers) that contains the essentials for embryo development, but is protected by a leathery or calcareous outer shell. This key innovation enabled tetrapods to reproduce on land. Amniotes had larger brains and sense organs, better feeding systems, more mobile necks, and stronger limbs than their predecessors. As a result, amniotes rapidly came to dominate the terrestrial environment, and subsequently colonised the air and recolonised the water.

The classification used in this essay is cladistic and recognises only monophyletic groups (see *Phylogeny of Vertebrates* for a fuller explanation). Ages in millions of years before the present (Ma BP) are based on the most recent geological timescale [1] and the earliest records of occurrence, but should be understood to carry error bars.

Characteristics

The first amniotes are recognised from the Carboniferous period (c. 320 Ma BP) based on skeletal characters (e.g. two sacral ribs, ankle structure), because until the development of calcareous shells, eggs were rarely fossilised. These early fossil amniotes were already split between two major clades, Synapsida and Sauropsida (Fig. 1). The latter is almost equivalent to Reptilia, and

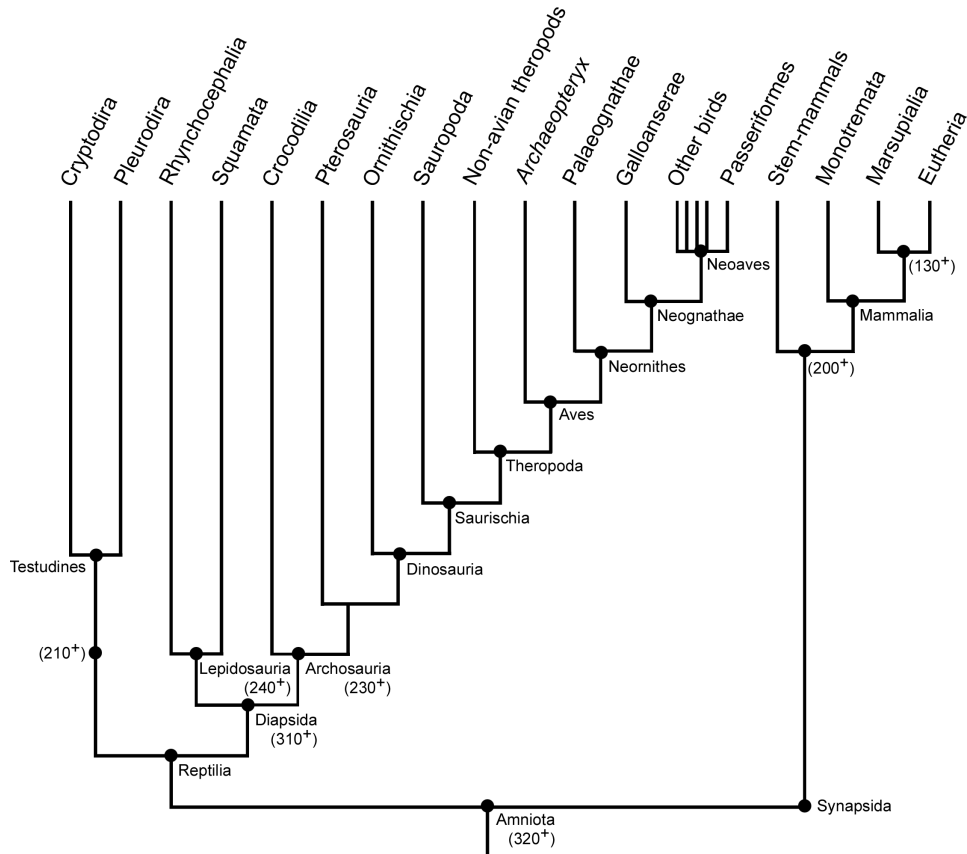
this is used in subsequent discussion. However, under its cladistic definition, Reptilia is the monophyletic group that encompasses the last common ancestor of living lizards and snakes, crocodiles, birds and turtles, and all (but only) the descendents of that last common ancestor. In the past, and even in some recent literature, reptile was used in a paraphyletic sense equivalent to basal amniote (e.g. in the inaccurate term “mammal-like reptile” for early synapsids). Modern reptiles have a long independent evolutionary history and should not be used simplistically as morphological surrogates for the ancestral mammalian condition. For decades, understanding of mammalian ear evolution was obfuscated by attempts to derive the mammalian condition from that of a lizard. Only with the acceptance that the lizard and mammalian eardrums were not phylogenetically homologous (i.e. were not present in the last common ancestor of the two lineages, c. 320 Ma BP), was the problem resolved [2].

Sauropsida

Reptilia *sensu stricto* includes living turtles and tortoises (Testudines), lizards, snakes and tuatara (Lepidosauria), and crocodiles and birds (Archosauria), as well as several important extinct groups such as the plesiosaurs, ichthyosaurs, and dinosaurs. Under this cladistic framework, birds (Aves) do not form a group distinct from reptiles – they are part of the monophyletic Reptilia.

Turtles are first recorded from the Late Triassic period (c. 310 Ma BP), but these fossils are already too highly specialised to shed much light on their immediate ancestry. There is general agreement that turtles are more closely related to lizards, crocodiles and birds than to mammals [3], but the details of that relationship remains unresolved. The traditional view is that turtles are the sister group of the ► *lepidosaurs* and ► *archosaurs* [4]. However, over the last decade increasing numbers of studies have suggested that turtles might be diapsid derivatives, related either to ► *lepidosaurs* [3] or ► *archosaurs* (most molecular analyses, e.g. [5]).

Lepidosauria and Archosauria, with their immediate ancestors, constitute the Diapsida. (The term diapsid refers to the presence of two bony fenestrae in the temporal region of the skull.) Lepidosauria today encompasses two unequal clades – Rhynchocephalia and Squamata. Once a globally widespread group, Rhynchocephalia is now represented by a single surviving genus, *Sphenodon*, restricted to a few islands off the coast of New Zealand. *Sphenodon* has been much misunderstood, regarded as a “living fossil” and sometimes cast into the role of archetypal primitive reptile. Over the last 25 years, our knowledge of extinct Rhynchocephalia has improved considerably. Within Rhynchocephalia, *Sphenodon* is a relatively derived form. Many of the skull characters previously used to



Evolution and Phylogeny of Amniotes. Figure 1 Tree showing relationships amongst major amniote groups. Clade names have been added to appropriate nodes. The numbers at some nodes represent the minimum age estimates (in millions of years) for the last common ancestor of the descendant lineages.

argue for a primitive position are now recognised as secondary specialisations. Nonetheless, compared to lizards, *Sphenodon* does show some apparently primitive features, as well as a low basal metabolic rate and a longevity rivalling that of turtles. The last common lepidosaurian ancestor of squamates and rhynchocephalians lived around 240 Ma BP, and both lineages have undergone evolution in the interim, although squamates diversified more rapidly than other reptiles. This may explain why *Sphenodon* sometimes groups with other reptilian clades in molecular analyses [6].

Squamata is a highly successful clade, with more than 7,000 living species of lizards, amphisbaenians and snakes. There is common agreement that snakes (*Serpentes*) and “worm lizards” (*Amphisbaenia*) each constitute monophyletic groups, but that “lizards” are simply squamates that are neither snakes nor amphisbaenians. For this reason formal names like “*Lacertilia*” should not be used for them. Within squamates, most morphologists recognise four distinct clades, *Iguania* (iguanas, chameleons, agamas), *Gekkota* (geckos and their relatives), *Scincomorpha* (e.g. *Lacerta*, *Scincus*) and *Anguimorpha* (e.g. *Varanus*, *Anguis*), with a

fundamental early split (c. 200 Ma BP) between *Iguania* on one side and all other squamates (= *Scleroglossa*) on the other. Snakes typically group within *Anguimorpha*, but amphisbaenians are more problematic [7]. To complicate matters further, recent molecular analyses have proposed that *Scleroglossa* is not monophyletic and that *Iguania* is nested within it [8].

The earliest definitive archosaurs (*Archosauria*) arose more than 230 Ma BP, but their separation from the ancestors of lepidosaurs occurred before this. Archosaurs were the dominant group throughout the Mesozoic (250–265 myrs), culminating in three major clades – crocodylians, pterosaurs, and the dinosaurs/birds. However, extant birds and crocodylians represent end points of lineages that separated at least 230 Ma BP. Modern crocodiles are amphibious but early forms were small terrestrial reptiles with a parasagittal quadrupedal gait. In contrast, the first dinosaurs were small active bipeds. These diversified into the herbivorous *Ornithischia* (e.g. *Stegosaurus*, *Triceratops*, *Iguanodon*) and the *Saurischia*. The latter group, in turn, split to produce the quadrupedal herbivorous sauropods (e.g. *Diplodocus*, *Brachiosaurus*) and the bipedal,



predominantly carnivorous, theropods (e.g. *Tyrannosaurus*). One group of theropods evolved into a clade of active, small-bodied, large brained raptors (e.g. *Velociraptor*) that were the direct ancestors of birds.

The earliest recorded bird (Aves) is *Archaeopteryx* (c. 140 Ma BP). In many respects this animal was more like its dinosaurian forebears than modern birds (teeth, claws, bony tail), except that it was capable of flight (and had a brain to match). Modern birds seem to have undergone an explosive radiation around 50 Ma BP, and most modern groups (Neornithes) can be traced back to at least that time, or earlier [9]. The most primitive living birds are the ratites (Palaeognathae, e.g. ostriches, emus). Of “higher” birds (Neognathae), the group that encompasses ducks, geese and pheasants (Galloanserae) is thought to be basal [9], with a postulated divergence time of about 90 Ma BP. The remaining birds (Neoaves) fall into a series of groups for which the relationships are poorly resolved, but the large and diverse Passeriformes (e.g. sparrows, blackbirds, robins) is probably the most derived.

Synapsida

Synapsida, the second amniote division, is represented today by the mammals, but includes a wide range of extinct stem taxa. (Synapsida may be defined as incorporating all amniotes more closely related to living mammals than to living reptiles and birds; the term synapsid refers to the presence of one bony fenestra in the temporal region of the skull.) Indeed, the synapsids seem to have undergone the first successful amniote radiation, dominating early terrestrial ecosystems for more than 50 Ma. By 250 Ma BP, some of the most derived synapsids resembled mammals in having a parasagittal stance (that is with the body held upright on limbs that move parallel to the midline of the body, in contrast to the sprawling gait of many small reptiles and amphibians), a differentiated dentition, a hard palate to separate air and food, and bone histology suggestive of at least incipient endothermy. However, the end of the Permian period (c. 250 Ma) was marked by a cataclysmic extinction that destroyed about 80–96% of species, including many lineages of synapsids. In the period that followed, reptiles (and particularly archosaurs) gained the upper hand. Small synapsids survived, perhaps by adopting more nocturnal habits (driving the further evolution of mammalian endothermy, more acute hearing, dark-adapted cone rich retinae, and improved olfaction). A second major extinction at the end of the Cretaceous (65 Ma BP) decimated the reptile lineages and mammals regained control.

Living mammals fall into three major groups – the egg-laying Monotremata, the pouched Marsupialia, and the placentals (Eutheria), and thus Mammalia in the strict sense encompasses the last common ancestor of these three groups and all descendents of that

ancestor. Monotremes (*Platypus*, *Echidnas*) were once more widespread (e.g. South America) but are today restricted to Australia (earliest record c. 110 Ma BP), surviving on a continent that was not colonised by placentals until relatively recently. On the basis of fossil evidence (supported by molecular analyses), marsupials and placentals separated at least 130 Ma BP. Marsupials are today are restricted to Australia except for the American opossums (e.g. *Didelphis*), which probably separated c. 68–72 Ma BP. Placentals are more diverse. Morphological data suggests that the *Xenarthra* (sloths, armadillos, anteaters) are the most basal of living lineages, but several recent molecular studies instead recognise a basal African clade, *Afrotheria*, including elephants, tenrecs, elephant shrews, aardvarks and sirenians [10].

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Evolution and Phylogeny of Vertebrates

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Synonyms

Evolution of vertebrates; Phylogeny

Definition

The phylogeny of a group, in this case back-boned animals (vertebrates), represents the course of evolutionary change undergone by that group over time. It is typically represented in the form of a ► **dichotomous branching tree** in which the vertical axis represents time and the horizontal axis represents closeness of relationship (Fig. 1).

Characteristics

Underlying Methodology

The framework used here is cladistic. Groups must be monophyletic (including the common ancestor and all its descendants) and are diagnosed on the basis of shared ► **derived characters**. Only monophyletic groups are given formal scientific names. The primitive absence of a derived trait (e.g. the absence of jaws, absence of hair) cannot be used to group organisms. The use of paraphyletic, gradal, groups confuses the discussion of morphological evolution. For example, the old view that reptiles gave rise to mammals (instead of being their ► **sister group**) left many comparative anatomists trying to derive mammalian structures (e.g. the middle ear) directly from those of living reptiles, despite more than 300 million years of independent history.

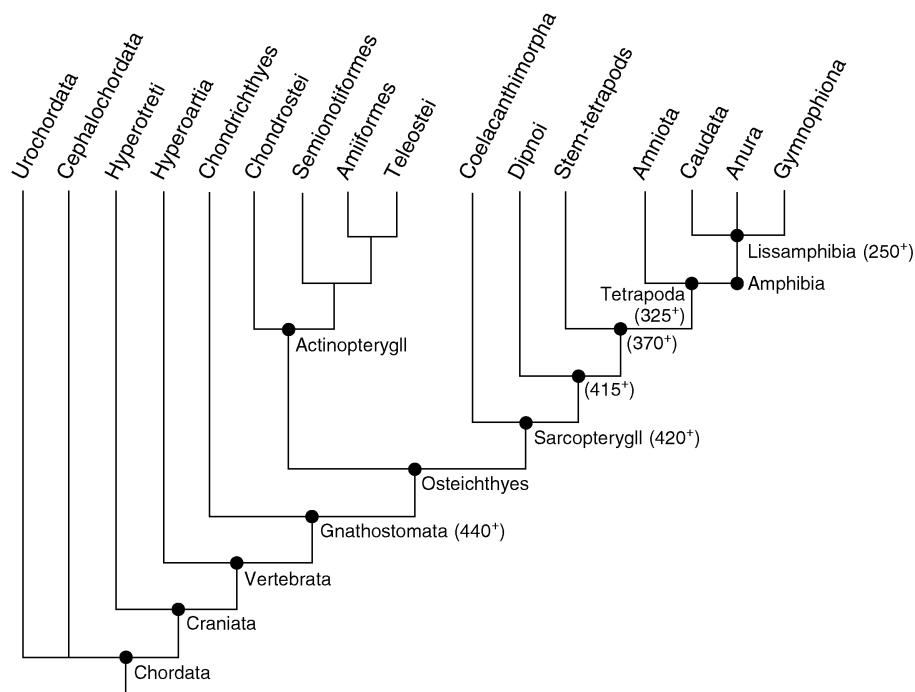
Ages in millions of years before present (Ma BP) are based on the most recent geological timescale [1], but

should be regarded as minimum estimates reflecting the earliest known occurrence of a fossil group or its phylogenetic sister taxon. Given that individual geological strata cannot always be dated with precision, such dates should also be understood to carry error bars.

Vertebrates

Vertebrates (backboned animals) are part of the wider group Chordata (see ► **Phylogeny and Evolution of Chordates**), characterized by the possession of an axial stiffening rod (notochord), a perforated pharynx, a dorsal hollow nerve cord, and a post-anal tail. Chordata has a long fossil record, the earliest known representatives occurring some 570 Ma BP. Today, only two groups of basal chordates survive – the Urochordata (e.g. ► **Ciona**) and the Cephalochordata (e.g. the lancelet, ► **Branchiostoma**). All remaining chordates are craniates (Craniata). The name acknowledges the common possession of an organized head with a brain, well-developed sense organs, cranial nerves, and the beginning of a skull (all linked to the evolution of ectodermal placodes and migratory neural crest).

Craniates are divided informally into ► **agnathans** and ► **Gnathostomata**. Agnathans are a gradal concept rather than a valid monophyletic group since they include a range of primitive craniates (mostly now extinct) that lack jaws. Some agnathans (e.g. the



Evolution and Phylogeny of Vertebrates. Figure 1 Tree showing relationships amongst major vertebrate groups. Clade names have been added to appropriate nodes. The numbers at some nodes represent the minimum age estimates (in millions of years) for the last common ancestor of the descendant lineages.

extinct ►[osteostracans](#)) are more closely related to derived vertebrates (gnathostomes) than are others (e.g. lampreys). Today, only two agnathan lineages survive – the primitive hagfish (*Hyperotreti*) and the lampreys (*Hyperoartia*). However, researchers are divided as to whether lampreys are more closely related to hagfish (to form a monophyletic Cyclostomi [2,3]) or to gnathostomes [4]. Under the second hypothesis, lampreys and gnathostomes form the Vertebrata, while hagfish would be considered craniates but not vertebrates. Under the first, Craniata and Vertebrata are synonymous [2]. Fig. 1 illustrates the second hypothesis in order to clarify the conceptual distinction between craniate and vertebrate, but with the recognition that a monophyletic Cyclostomi is more widely accepted amongst neontologists.

Gnathostomes

The evolution of jaws from gill arch (branchial arch) cartilages occurred at least 440 Ma BP. Unlike their predecessors, early gnathostomes were adapted to an active predatory niche, with paired pectoral and pelvic fins and a streamlined body shape. Aquatic fusiform gill-breathing gnathostomes are traditionally, and colloquially, called fish (and were once grouped as Pisces), but “fish” do not form a monophyletic group. A zebrafish is more closely related to a human than either is to a shark. All living “fish” are grouped into one of two major clades – the Chondrichthyes (with a cartilaginous skeleton, like sharks, rays [*Elasmobranchii*] and parrot-fish [*Holocephali*]), and Osteichthyes (with true bone). The monophyletic Osteichthyes includes ALL vertebrates with a bony endoskeleton, ranging from goldfish and lungfish through to dinosaurs, birds and monkeys.

Living osteichthyans are themselves subdivided, based on fin type, into Actinopterygii and Sarcopterygii that separated at least 420 Ma BP. Actinopterygii are the ray-finned fish. As the name suggests, this group encompasses fish in which the fins consist of a fan of delicate rays. The most derived actinopterygians are the teleosts (e.g. zebrafish, cod, tuna), but some members of more ancient stem clades have also survived, including Amiiiformes (the bowfin, ►[Amia](#)), Semionotiformes (gars, e.g., *Lepisosteus*), and Chondrostei (paddlefish, e.g., ►[Polyodon](#), and sturgeons, e.g., ►[Acipenser](#)).

Sarcopterygians

The Sarcopterygii, or lobe-fins, differ from actinopterygians in having a skeletal axis to the pectoral and pelvic appendages. The largest living group of sarcopterygians is comprised, of course, of the tetrapods, but two extant fish groups also fall into this clade – the Coelacanthimorpha or ►[coelacanth](#)s (►[Latimeria](#)) and the Dipnoi or lungfish (►[Lepidosiren](#), ►[Neoceratodus](#), ►[Protopterus](#)). The freshwater lungfish, as the name suggests, have functional lungs, internal nostrils, and a pulmonary

circulation. Both lineages (lungfish and coelacanth) go back more than 415 Ma, but of the two, lungfish are probably the more closely related to tetrapods [but see 5], although not on the tetrapod stem. Paleontological and molecular evidence suggests a rapid diversification of the major sarcopterygian lineages, including the immediate fossil ancestors of tetrapods, within a relatively short space of time around 420–400 Ma BP [5].

Tetrapods

In common parlance, a tetrapod is an animal with four limbs (tetra-pod), but Tetrapoda ►[sensu stricto](#) encompasses the last common ancestor of living amphibians and living amniotes, and all descendants of that ancestor. This definition omits some of the earliest truly limbed vertebrates and these are best termed ►[stem-tetrapods](#). The earliest known stem-tetrapods date from the later part of the Devonian period, around 370 Ma (e.g. ►[Acanthostega](#), ►[Ichthyostega](#), [6]). They were still aquatic, using a combination of lung and gill breathing, like the living Australian lungfish, ►[Neoceratodus](#).

The main vertebrate colonization of the land appears to have begun during the Carboniferous (c. 340–320 Ma BP), perhaps coinciding with a sharp rise in atmospheric oxygen levels, and the fossil record documenting a gradual radiation of stem-tetrapods into available ►[niches](#). The phylogenetic tree is rather “bushy” at this stage, but two major lineages emerged: amphibians and amniotes. The latter clade includes all truly terrestrial groups (e.g. birds, tortoises, lizards and snakes, mammals) that possess an ►[amniote egg](#) (or a derivative structure such as the placenta). This group is covered in more detail elsewhere (see ►[The Phylogeny and Evolution of Amniota](#)). Amphibia are rather more challenging. Under traditional usage, Amphibia is a paraphyletic group for tetrapods that are not amniotes, but under a cladistic definition, Amphibia encompasses those tetrapods that are more closely related to living amphibians (frogs, salamanders, caecilians) than to amniotes. Unlike amniotes, they still generally require water to reproduce, typically have an aquatic larva, and undergo ►[metamorphosis](#). Paleontologists do not agree as to the ancestry of living forms. For neontologists, this is relatively unimportant except that it impacts on the timing of the divergence between the ancestors of Amphibia and of Amniota. Nonetheless, by any estimate, the last common ancestor of amniotes and amphibians lived more than 325 Ma BP [7].

Modern amphibians comprise of the Lissamphibia: frogs, salamanders and the limbless caecilians. The relationships of the three living clades are not fully resolved. Many workers place frogs (*Salientia*) and salamanders (*Caudata*) as close sister taxa but others argue for separate origins from distinct fossil lineages [7]. Caecilians are even more problematic: they may be the sister group of frogs plus salamanders (most

morphological analyses and some molecular ones), they may be the sister group of salamanders alone, or they may be unrelated [7]. This affects estimated divergence times for the three major groups (325–200 Ma BP). The earliest known fossil stem-frogs are recorded from c. 245 Ma BP, while the equivalent dates for salamanders and caecilians are 170 Ma BP and 190 Ma BP respectively [7,8].

Amongst living frogs, the North American ►*Asca-phus* and New Zealand ►*Leiopelma* represent the oldest and most basal lineages, followed by discoglossids (e.g. ►*Alytes*, *Discoglossus*), and then pipids (e.g. ►*Xenopus*), pelobatids and rhinophrynids. The most diverse and derived frog clade is the Neobatrachia (e.g. ►*Bufo*, *Hyla*, *Rana*). Fossil ascaphids have not been identified with certainty, but discoglossids are recorded with confidence from around 145 Ma BP, basal pipids from 120 Ma BP, and early neobatrachians from at least 80 Ma BP, these dates giving the latest possible divergence times for each lineage [9]. Living salamanders fall into two major groups, Cryptobranchioidea (e.g. ►*Cryptobranchus*, *Hynobius*) and Salamandroidea (e.g. ►*Salamandra*, *Ambystoma*) and, judging from recent fossil finds in China and the USA, these groups had already separated by at least 145 Ma BP. Nonetheless, the position of sirenids (e.g. ►*Siren*) is still uncertain (basal or highly derived, [6]), as are the interrelationships of living families. The fossil record of caecilians is extremely poor and no certain representative of modern families has been recovered from Mesozoic deposits.

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Evolution and Phylogeny of Primates

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Definition

The evolutionary lineage of arboreal placental mammals exhibiting sociality and stereoscopic, color vision as primary adaptations, taxonomically designated as “primates”.

Characteristics

Primates represent a taxonomic order within the class Mammalia. Primates are characterized by a generalized mammalian limb structure including retention of pentadactylism (five digit hands and feet), a tendency toward vertical body posture and extensive head rotation ability. Limb mobility is facilitated by the unfused radius and ulna that maximizes forearm rotation, dorsally located scapulae accommodating free-swinging and suspensory arm motions and ball-and-socket joints of the hip accommodating climbing, quadrupedal and bipedal locomotion. Most primate species have tails (except great apes), with Platyrrhines (New World monkeys) exhibiting prehensile tails able to hold and manipulate objects. Hands and feet display enhanced grasping ability with friction skin on finger and palmer surfaces, sensitive tactile pads at fingertips, flat nails rather than rigid claws and varying degrees of thumb opposability. Eyes are generally enlarged compared to other mammals and enclosed in a complete bony ring with front-facing stereoscopic vision and varying degrees of sensitivity to low light levels. Color vision is also variable, being uniformly trichromatic in Catarrhines—Old World monkeys, great apes, and humans—but variably dichromatic or trichromatic among Platyrrhines [1]. Heterodont dentition (incisors, canines, premolars and molars) and a tooth count reduced from that of primitive mammals are features exhibited by all primates as are complete bony orbits. Reduced prognathism (i.e. projecting muzzle) of the lower face and jaws appears to be associated with a