

# The phylogenetic system of primates—character evolution in the light of a consolidated tree

Holger Herlyn<sup>1</sup>

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**Abstract** Molecular analyses of the last decades helped solving the major open questions on the external and internal phylogenetic relationships of primates. The present review uses these data for the inference of character evolution along the branches of the primate tree. Altogether, more than 200 evolutionary changes in hard and soft tissue anatomy/morphology, behavior, physiology, and protein constitution are presented in the context of their functional relevance and adaptive value. The compilation focuses on primates as a whole and on the higher-ranked primate subtaxa with living representatives: Strepsirhini: Lorisiformes, Galagidae, Lorisidae, Lemuriformes; Haplorhini: Tarsioidae, Anthropeoidea, Platyrrhini, Atelidae + Cebidae, Atelidae, Cebidae, Aotinae, Callithrichinae, Cebinae, Pitheciidae, Pithecinae, Catarrhini, Cercopithecoidea, Cercopithecinae, Colobinae, Colobini, and Hominoidea. Within Hominoidea character evolution is traced down to more peripheral branches: Hylobatidae, Hominidae, *Pongo*, Homininae, *Gorilla*, *Pan* + *Homo*, *Pan*, and modern humans. Character states in extinct representatives of Plesiadapiformes, Omomyoidea, Propithecidae, Hominini, etc. are always taken into account; they are presented in detail whenever character-state distribution in living species is ambiguous or misleading. The taxonomic sample and the characters included combine to a phylogenetic system that illustrates primate evolution and diversity. The data presented additionally provide a detailed picture of the evolutionary steps and trends involved in hominization. Reflections on the frequently

underestimated role of polymorphisms in phylogenetic analyses complete the survey.

**Keywords** Primates · Character evolution · Phylogeny · Anatomy · Morphology · Physiology · Behavior · Evolutionary novelties · Apomorphies

## Introduction

With the progress of molecular techniques, the major open questions on the phylogenetic relations of Primates could be solved in the last few decades. Especially, insertions into the nuclear genome, fixed in some ancestral population and passed on to all descent lineages, proved to be very informative in this respect. Analyses of these and other kinds of rare genomic changes (e.g., Lebedev et al. 2000; Schmitz et al. 2001; Abdel-Halim et al. 2003; Roos et al. 2004; Xing et al. 2005; Janecka et al. 2007; Kriegs et al. 2007; Osterholz et al. 2009), but also mitochondrial and large-scale sequence data (e.g., Chatterjee et al. 2009; Perelman et al. 2011), enzyme expression (Pollock and Mullin 1987), immunodiffusion, and DNA-DNA hybridization (Sibley and Ahlquist 1987; for a summary, see Martin 1990) yielded consistent trees regarding higher-level primate relations and the internal hominoid branching pattern. Thus, we now dispose of a consolidated tree that can be used as a backbone for tracking the evolution of anatomical and behavioral characters. At the same time, many of the relevant primatological and anthropological standard works at least partially present characters without an assessment of which is the evolutionary new (derived, apomorphic, autapomorphic) and which is the evolutionary old (ancestral, plesiomorphic, “primitive”) state. On the other hand, consequent cladistic reflections seem to be comparably rare amongst the primatological and

✉ Holger Herlyn  
herlyn@uni-mainz.de

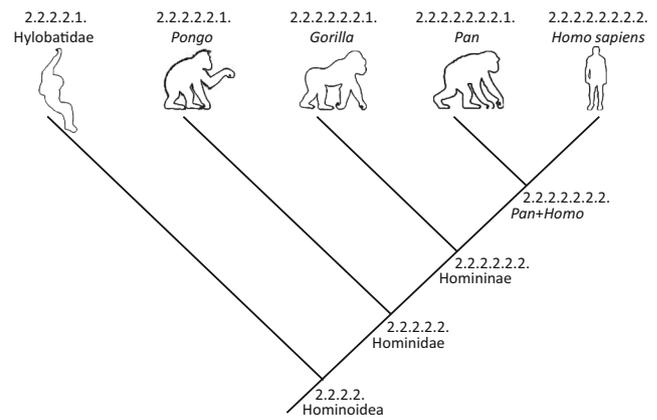
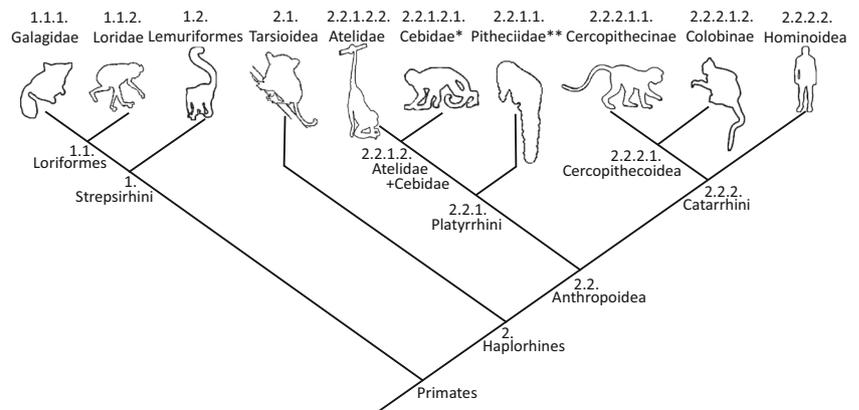
<sup>1</sup> Institute of Anthropology, University of Mainz, Mainz, Germany

anthropological surveys (e.g., Groves 1988; Martin 1990; Diogo and Wood 2012). Still, others leave few pages to primates so that solely a very limited selection of characters is included (e.g., Lecomte and Le Guyader 2006; Schmidt 2010). Moreover, most phylogenetic analyses of primates seem to focus on either hard (e.g., Wible and Covert 1987; Swindler 2002) or soft tissue data (e.g., Gibbs et al. 2002; Diogo and Wood 2012), whereas less studies put stronger emphasis on an integrative approach (e.g., Williams et al. 2010). Last but not least, the most comprehensive phylogenetic analysis merging extensive hard and soft tissue data that I am aware of already dates back 20 years (Shoshani et al. 1996).

The present review aims at providing an updated and comprehensive scenario of hard and soft tissue character evolution in primates in the light of a consolidated phylogeny (Figs. 1 and 2). Molecular, behavioral, and physiological aspects will also be considered. Thereby, I will primarily focus on primates as a whole and on higher-level primate taxa. I will delineate character evolution down to the level of more peripheral branches for Hominoidea (apes and humans). In order to carve out evolutionary changes (evolutionary novelties, derived character states, apomorphies, also autapomorphies or synapomorphies) that emerged in the primate stem lineage, I will additionally take into account plesiomorphic character states (plesiomorphies) in the closer phylogenetic relatives of primates, i.e., flying lemurs (Dermoptera), treeshrews (Scandentia), and rodents (Rodentia, part of Glires) (e.g., Springer et al. 2004; Godinot 2007; Janecka et al. 2007; see also Shoshani et al. 1996; Diogo and Wood 2012). The accent will be put on crown taxa, whereby a crown taxon encompasses the last common ancestor (LCA) of a group of living (extant) species plus all living and extinct descendants of this LCA (Wible and Covert 1987). Solely for the sake of simplicity, I will use Primates, Strepsirhini, etc., when I actually refer to crown-Primates, crown-Strepsirhini, etc. Character states in extinct representatives have always been taken into account but will only be presented in detail when their distribution in living species is either ambiguous, thus hindering the

**Fig. 1** Phylogenetic tree of the higher-ranking (crown) taxa included in the present survey. Numbers refer to sections in the main text that provide general data on the respective primate taxa and evolutionary novelties supporting their monophyly.

\*The chapter on Cebidae contains apomorphies of Aotinae, Callithrichinae, and Cebinae.  
\*\*The chapter for Pitheciidae provides a potential apomorphy of Pitheciinae



**Fig. 2** Phylogenetic tree of the hominoid taxa considered in the present review. Numbers refer to sections in the main text that give general information on the respective taxa and evolutionary novelties in support of their monophyly. Note that all supra-specific taxa are crown groups

inference of a single most parsimonious scenario or contrariwise misleading, thus suggesting a single most parsimonious scenario that does not hold in light of the fossil record. Also, for reasons of simplicity, I will not always stress that a character state refers to the condition in adults.

The taxon sample and the characters included combine to a phylogenetic system that illustrates primate evolution and diversity under special consideration of the steps and trends in hominization. The phylogenetic system of primates is organized as an encaptic system of sister group relationships and does without traditional ranks such as order, family, etc. (Hennig 1966). Furthermore, whenever traditional classification suggests several (redundant) ranks for a single group of (living) species, preference will be given to the taxon name that has the same suffix as the established name of the sister group. Thus, I will prefer the pair Tarsioidae-Anthropeoidea over the alternatives Tarsiiformes-Anthropeoidea and Tarsiidae-Anthropeoidea. Finally, I apologize to all whose contributions could not be included for reasons of space limitation. For additional contributions, I refer to the literature given in Dagosto (1988), Martin (1990), Beard (1993), Shoshani et al. (1996), Diogo and Wood (2012), and Fleagle (2013).

## Primates

The taxon Primates includes >475 living species (Rylands and Mittermeier 2014), besides many extinct representatives (Silcox et al. 2007; Begun 2007). However, any species number must be preliminary considering the continuous discovery and distinction of new species (e.g., Pickering et al. 2011; Rasoloarison et al. 2013). It has further to be considered that survival of diverse primate species in the wilderness is uncertain due to human activities such as habitat destruction, predation, live capture (e.g., Jurmain et al. 2008), and use in traditional medicine (e.g., Nekaris and Starr 2015).

The LCA of all extant primates lived perhaps 65 mya (Silcox et al. 2007), perhaps 76 mya, ago (estimate: timetree.org; Hedges et al. 2015) and almost certainly was provided with more plesiomorphies than apomorphies. One of the evolutionary old character states was the presence of a sublingua, i.e., a callous, some say leaf-like, structure beneath the tongue that lacks muscles and glands (Schmidt 2010). A functional vomeronasal organ represents another plesiomorphy in the primate ground pattern (Smith et al. 2011) and possibly a tapetum lucidum, too (Martin 1990; Fleagle 2013). Other character states in the primate ground pattern are of unclear phylogenetic significance. Dermatoglyphics, epidermal ridges (fingerprints) with frictional and tactile properties on the ventral (palmar, plantar) surface of hand and foot, belong to this group of characters. They are present in primates (Cartmill 1992) and treeshrews (Lemelin 2000), while they are absent in the third subtaxon of Euarchonta, flying lemurs (Lemelin 2000), and in rodents (Tsugane and Yasuda 1995). This character distribution does not allow for the inference of a single most parsimonious scenario—at least not in the light of the Primatomorpha hypothesis that suggests a sister group relationship of primates and flying lemurs (Janecka et al. 2007), a view that is, however, critically seen by others (e.g., Godinot 2007). Irrespectively of this and other unsettled issues, ample apomorphies support primate monophyly:

1. Although this review focuses on anatomical and less on physiological and behavioral data, I start with a molecular evolutionary novelty of primates. Thus, primates are distinguished by having specific interspersed nuclear elements (SINEs) of about 300 bp, named Alu elements. All Alu elements in the nuclear genomes of living primates are regarded as derivatives of a first heterodimer that arose by fusion of two truncated 7SL RNA-derived sequences in the primate stem lineage (Jurka and Zuckerkandl 1991; Quentin 1992; Zietkiewicz et al. 1998; Kriegs et al. 2007). The extent to which new Alu integrations maintain their activity is not fully understood. However, their successful propagation is impressively illustrated by high abundances in primate genomes. For example, the human nuclear genome contains approximately 1 million Alu copies, which equals about 10 % of its size (Price et al. 2004).
2. The third incisor of each lower jaw quadrant underwent complete reduction in the primate stem lineage. Consequently, the primate LCA had a derived dental formula (permanent teeth): two incisors, one canine, three premolars (P2–P4), and three molars per upper and lower jaw quadrant (2.1.3.3/2.1.3.3) (Martin 1990; Swindler 2002; Geissmann 2003; Stringer and Andrews 2005; Fleagle 2013). The closest phylogenetic relatives of primates, treeshrews, and flying lemurs both retained the presumed plesiomorphic state of three incisors in each lower jaw quadrant (Stafford and Szalay 2000; Olson et al. 2004). The presence of a protocone on P3 could be another evolutionary novelty of primates (see “Euprimates” in Dagosto 1988).
3. The inferior surface of the middle ear chamber (tympanic floor, floor of auditory bulla, floor of bulla tympanica) is fully ossified, with the petrosal bone (petrous bone, pars petrosa of temporal bone) being the major element. The tympanic floor is also ossified in the other two taxa of Euarchonta, however, with entotympanic (treeshrews) and ectotympanic (flying lemurs) being the major elements (Shoshani et al. 1996; Bloch et al. 2007).
4. Outgrowths of the petrosal bone form canals that surround the intrabullar portions of the facial nerve and the arteries (MacPhee et al. 1983). Differences in the ontogenesis of the primate canals and likewise structures in treeshrews suggest parallel evolution of the trait in both taxa (for a summary, see Beard 1993).
5. The primate LCA probably possessed a complete or at least virtually complete bony bar encompassing each eye’s rear side (Wible and Covert 1987; Dagosto 1988; Beard 1993; Ravosa et al. 2000; Feldhamer et al. 2014). In support of this view, the distal ends of the frontal and zygomaticum processes involved are more remote of each other in flying lemurs (Stafford and Szalay 2000). Yet, the scenario also implies that the postorbital bar of treeshrews evolved independently. This, again, is not as unlikely as it might appear at the first sight considering that postorbital bars also exist in other mammalian species (Wible and Covert 1987; Beard 1993; Wible 2011). Disregarding the evolutionary scenario, a postorbital bar protects the lateral margins of the eye from deformation through contraction of the temporal muscle, thus increasing the degree of visual acuity during chewing and biting (Ravosa et al. 2000).
6. The primate LCA had orbits with increased frontation and convergence (Wible and Covert 1987; Dagosto 1988; Cartmill 1992; Bloch et al. 2007; Feldhamer et al. 2014) and consequently broadly overlapping vision fields (Martin 1990; Jurmain et al. 2008). One may

discuss to what extent the orbits of the primate LCA were facing forward. However, it seems clear that they were more frontally oriented in the primate LCA than in flying lemurs and treeshrews. The broad overlap of vision fields led to improved stereoscopic vision of the primate LCA that was probably arboreal (Szalay and Drawhorn 1980; Dagosto 1988; Gebo 1988; Stringer and Andrews 2005) and at least occasionally fed on insects (Cartmill 1992; Fleagle 2013), besides angiosperm fruits and flowers (Sussman et al. 2013). Frontation and convergence of the eyes may also have increased acuity by reducing spherical aberration in the periphery of lenses when focusing objects in front. As this beneficial effect is stronger when pupils are widened for capturing faint light, the feature has been invoked in support of a nocturnal LCA of living primates (Heesy 2008). Nocturnality of the primate LCA gained additional support from evolutionary analysis of the short-wave sensitive (S-) opsin (Moritz et al. 2013). Nonetheless, the question for the activity pattern of the primate LCA is far from being settled (see, e.g., Tan et al. 2005; Seiffert et al. 2005; Heesy 2008; Moritz et al. 2013).

7. The great toe (hallux) is divergent and opposable in the vast majority of living primates (Wible and Covert 1987; Gebo 1988; Stringer and Andrews 2005). This condition associates with a deep groove on the calcaneal sustentaculum tali for attachment of the flexor fibularis muscle, which functions as a plantar flexor of the foot and as a flexor of the digits (Szalay and Drawhorn 1980). The entire complex, together with an enlargement of the toe, probably evolved in the primate stem lineage while the plesiomorphic condition of a non-opposable hallux is retained in treeshrews and other non-primates (Napier and Napier 1967; Dagosto 1988). The better prehensile ability of the primate foot is apparently advantageous for grasping branches while moving through trees and bushes. Still, early primates were presumably not only graspers, but also climbers and leapers (Dagosto 1988; Gebo 1988; Bloch and Boyer 2002). The presumably improved leaping ability of the primate LCA resulted from elongation of the tarsal bones and several anatomical changes that increased motion and stability of the upper ankle joint (Dagosto 1988).
8. In primates, the opponens pollicis is usually a distinct muscle while, in non-primate mammals, it is mostly not (Diogo and Wood 2011, 2012). This suggests a shift in the phenotype frequencies for the primate stem lineage toward a higher proportion of individuals with a distinct opponens pollicis muscle. In the human hand, the muscle runs from the flexor retinaculum and the tubercle of the trapezium to metacarpus I. Although it is indeed used for thumb opposition in humans, the muscles' ancestral function was not necessarily true thumb opposition (Napier and Napier 1967; Martin 1990). Considering hand anatomy and thumb opposability in living primates, the LCA of Primates probably had a more hinge-shaped carpometacarpal joint I that essentially confined thumb mobility to abduction and adduction; some degree of thumb rotation might have been possible over metacarpophalangeal joint I, a condition termed pseudo-opposition (Napier and Napier 1967). In the light of this scenario, the "opponens" pollicis might originally have contributed to pseudo-opposition rather than opposition of the thumb.
9. Nails, instead of claws on all digits (hallucal, pollicial, and lateral digits), represent another evolutionary novelty of primates (Napier and Napier 1967; Dagosto 1988; Geissmann 2003) although the issue raised some debates in the past (see, e.g., Wible and Covert 1987). Anyhow, when taking into account evidence from extinct Plesiadapidae and extinct representatives of Euprimates, it becomes quite obvious that the shift from clawed to nailed digits occurred in the stem lineage of crown-Primates, whereby a nail first appeared on the hallux (Dagosto 1988; Bloch et al. 2007). The invention of flattened nails might have increased the grasping and climbing abilities of the primate LCA (Dagosto 1988).
10. Primates have dorsoventrally flattened and medio-laterally widened distal phalanges of digits II–V (Dagosto 1988; Beard 1993; Godinot 1992). There are different alternative states in other mammals, but moderate lateral compression and modestly increased dorsoventral height of the distal phalanges could represent the ancestral condition (summarized in Beard 1993).
11. Primate skin is equipped with tactile corpuscles between the epidermal ridges that lack a surrounding membrane (Meissner's corpuscles) (Napier and Napier 1967). This kind of mechanoreceptors is absent in treeshrews, flying lemurs, and other mammals (Shoshani et al. 1996) and provides primates with enhanced tactile sense (Martin 1990).
12. The cricothyroid muscle whose contraction leads to tension and elongation of the vocal cords is usually differentiated into distinct pars recta and pars obliqua. Other mammalian taxa such as rat, as a rule, display no such clear differentiation of the cricothyroid muscle (Diogo and Wood 2012).
13. In primates, the placenta shows a villous maternal-fetal interdigitation. This evolutionary novelty probably arose from a labyrinthine maternofetal interface. The apomorphic condition might be advantageous in that mothers can sustain longer pregnancies without depleting maternal resources to the point of starvation (Wildman et al. 2006). Either way, the apomorphic villous interdigitation is only one aspect

characterizing the placenta in the primate ground pattern; its confinement to (originally) a single disc and invasion of the fetal chorion by maternal blood vessels seem to represent evolutionary older character states (Wildman et al. 2006).

### 1. Strepsirhini (syn. Strepsirrhini; “moist-nosed” primates)

The taxon’s scientific name refers to the shape of the nostrils which are not just round openings but instead, each, have a cutaneous blind sac (diverticulum nasi) that extends from the dorsal angle of the nostril posteriorly. However, this is a plesiomorphic condition shared with many other mammals that does not support the monophyly of Strepsirhini and neither of “Prosimii” which is a paraphyletic assembly of Strepsirhini and Tarsioida (e.g., Luckett 1976; see also Chatterjee et al. 2009). The same is true for the moist outer surface of the nose (rhinarium) and the medial cleft (philtrum) that anteriorly divides the strepsirhine nose and the upper lip into two halves (Martin 1990; Geissmann 2003; Fleagle 2013). A long and horizontally extending nasolacrimal duct that irrigates the rhinarium is another state belonging to the suite of plesiomorphic character states in the strepsirhine ground pattern (Rossie et al. 2006). The phylogenetic significance of a grooming (toilet) claw on pedal digit II in living strepsirhines and tarsiers aroused much discussion, especially in the light of fossil evidence (e.g., Franzen et al. 2009). Considering the non-parsimonious presence/absence pattern among living primates, I refrain from a definitive phylogenetic assessment. Yet, it must be conceded that the view whereupon grooming claws and other primate “tegulae” evolved secondarily from nails received additional impetus from latest fossil finds (Gebo et al. 2015; see also Dagosto 1988). Besides diverse nuclear insertions (Roos et al. 2004), there are some anatomical changes supporting strepsirhine monophyly:

1. The permanent teeth of the lower jaw form a horizontally oriented (procumbent) toothcomb, whereby the four incisors and two canines involved are pencil-shaped and juxtaposed (e.g., Dagosto 1988; Martin 1990; Rasmussen and Nekaris 1998; Williams et al. 2010; Fleagle 2013; Feldhamer et al. 2014). A toothcomb also exists in the deciduous dentition, although its shape seems to differ from that of the permanent toothcomb (Eaglen 1985). The strepsirhine toothcomb as defined here for the permanent dentition is clearly distinguished from homonymic structures in treeshrews, where it is made up by six more or less loosely arranged incisors (Martin 1990), and flying lemurs, where the toothcomb consists of four pectinate (out of six) incisors (e.g., Feldhamer et al. 2014). The

strepsirhine tooth comb experienced secondary modification in Indriidae (also Indridae) and got fully lost in the aye-aye (*Daubentonia*) (Swindler 2002; Geissmann 2003). The toothcomb is used for grooming of the fur and also as a scoop for ingestion of soft plant food (Martin 1990). Strepsirhines clean their toothcomb with the sublingua (Napier and Napier 1967) whose presence is a plesiomorphic character state of the taxon (see Primates).

2. In tight linkage with the toothcomb, the first (permanent) premolar of each lower jaw quadrant has the shape of a canine (“caniniform” premolar; e.g., Geissmann 2003).
3. In strepsirhines, the placenta is non-invasive, epitheliochorial, and diffuse. The latter attribute refers to the circumstance that the strepsirhine placenta is not anymore confined to a disc, but instead surrounds the fetus. Moreover, the fetal interface is covered by a discrete epithelium (chorialsyncytium) and is not invaded by maternal blood vessels, anymore (Geissmann 2003; Wildman et al. 2006; for a comparison, see Haplorhini). Due to this separation, after birth, the fetal tissue can detach from the uterine wall without taking along maternal layers (non-deciduate) (Napier and Napier 1967). The apomorphic nature of the strepsirhine placenta was proposed earlier (reviewed in Luckett 1976; see also Martin 1990) and gained further support by mapping character states on trees including a representative primate species sample and diverse outgroup representatives (Wildman et al. 2006). Nonetheless, it is worth mentioning that the strepsirhine placenta was long considered to represent an evolutionary older state than its haplorhine counterpart (reviewed in Luckett 1976). Yet, at that time, parsimony analyses of placenta types were hindered by much smaller datasets and widely unresolved phylogenetic relationships of the higher-ranking mammalian taxa.
4. When viewed from posterior, the strepsirhine talus (astragalus)-fibula facet appears more laterally sloping (oblique) in relation to the trochlear facet. The ancestral condition is probably a steep (vertical) facet (Gebo 1988; Shoshani et al. 1996; Williams et al. 2010).
5. The functional axis of intermetacarpal joints and associated dorsal interossei muscles, whose contractions spread the fingers, is digit IV instead of digit III. The latter condition represents the plesiomorphic state as retained in non-strepsirhine primates, treeshrews, and flying lemurs (Diogo and Wood 2012).

#### 1.1. Lorisiformes (syn. Loriformes; lorises; contains the same living species as Lorisoida/Lorisidea)

The phylogenetic relationships of Lorisiformes were a matter of intense debate (Nekaris and Bearder 2011). Amongst

others, the monophyly of Galagidae and Lorisidae (including pottos and angwantibos) and their relations to lemuriform primates were disputed (Rasmussen and Nekaris 1998). However, three up to six SINE integrations per clade meanwhile have been recognized in support of Lorisidae, Galagidae, and Lorisiformes (Roos et al. 2004). Taking into account the extremely low probability of two or more independent SINE integrations into the very same (ortholog) site of the nuclear genome, it seems justified to conclude the monophyly of the respective taxa. In addition, the SINE-based findings agree with tree topologies inferred from large-scale sequence data (e.g., Perelman et al. 2011; Pecon-Slaterry 2014). Still, it will be a challenge to bring the fossil evidence into line with this phylogenetic backbone (see, e.g., Rasmussen and Nekaris 1998). Another issue that awaits clarification is the phylogenetic significance of the blood supply to the brain in lorisiform primates. In contrast to other primates, the ascending pharyngeal artery is the only derivative of the internal carotid that provides blood to the brain of adult Lorisiformes (Martin 1990; Geissmann 2003; Fleagle 2013). Disregarding the uncertain phylogenetic significance of the latter condition, the monophyly of Lorisiformes is supported by the following character states:

1. The length of digit II of hands and feet is reduced when compared to digits III–V (Geissmann 2003; Schmidt 2010).
2. The retina has only a single type of cones which express middle-wavelength sensitive (green) opsin. This condition presumably results from pseudogenization of the autosomal gene for short-wave opsin and loss of allelic variation at the X-chromosomal locus (Tan et al. 2005). The evolutionary change could reflect relaxation of functional constraint on photopic vision in the lorisiform stem lineage. This, again, might reflect a shift toward a more nocturnal activity, possibly starting from a more cathemeral way of living (see “Primates” section). However, one has to have in mind that the ancestral activity pattern of primates is not yet clarified (see, e.g., Tan et al. 2005; Seiffert et al. 2005; Heesy 2008; Moritz et al. 2013).

### 1.1.1. Galagidae (syn. Galagonidae; galagos, bushbabies; contains the same living species as Galaginae)

These African primates have an agile predatory lifestyle and show only little morphological specialization (Martin 1990; Nekaris and Bearder 2011):

1. The hindlimbs are powerful and elongated relative to the forelimbs (Martin 1990). The longish appearance of the

legs is due to an elongation of the tarsus, especially of the tarsal bones calcaneus and naviculare (tarsifulcrumation). With this evolutionary change, galagids dispose of a strong lever for leaping from a vertical clinging position and for bipedal jumping (Hall-Craggs 1965; Martin 1990). It is worth to be noted that the hindlimbs of galagids do not appear elongated in relation to body length (Hall-Craggs 1965).

2. Increased size of pinnae of the ears may represent another apomorphy of the group. The large and highly mobile pinnae are deployed for prey localization (Napier and Napier 1967). The character seemingly evolved in parallel in the stem lineage of Tarsioidea (see there).

### 1.1.2. Lorisidae (syn. Loridae; loris, angwantibos, and pottos)

The taxon name Lorisidae is alternatively used for galagos, bushbabies, loris, angwantibos, and pottos (Rasmussen and Nekaris 1998; Nekaris and Bearder 2011; Fleagle 2013). I herein follow others and subsume only loris, angwantibos, and pottos under Lorisidae (e.g., Perelman et al. 2011; Pecon-Slaterry 2014). Most of the below apomorphies of these African and Asian primates associate with a stealthy, slow-moving pattern of locomotion that enables stalking of prey such as insects and roosting birds (Walker 1969):

1. Pincer-like prehensile hand and feet: digit II of hand and foot, already shortened in the LCA of Lorisiformes, experienced further size reduction in the stem lineage of Lorisidae while pollex and hallux became stronger (Beddard 1902; Martin 1990). Also, the position of digit I relative to digits III–V underwent a change that allows for a pincer-like grasping, whereby digit I is opposed to digits III–V. Endurance of grasping is possible through retia mirabilia, reticulate complexes of arteries and veins, in arms and legs that increase the exchange rate of metabolites (e.g., Schmidt 2010). With respect to the hands, this kind of grasping obviously differs from true thumb opposition in catarrhine primates. As no thumb rotation is involved and carpometacarpal joint I is still hinge-shaped, the condition is, in fact, a derived form of pseudo-opposition (Napier and Napier 1967).
2. The spine column is elongated due to an elevated number of vertebrae (e.g., Geissmann 2003). The elongated spine column facilitates lateral undulations that increase step size.
3. The tail is reduced to a stump (Martin 1990; Fleagle 2013), probably in adaptation to the stepwise locomotion of the members of Lorisidae through foliage.

4. Mates hang backward on branches during copulation (Dixson 2009). This inverted copulatory posture evolved in parallel in the aye-aye (Lemuriformes).

### 1.2. Lemuriformes (lemurs, herein used inclusively the aye-aye; contains the same living species as Lemuroidea)

Some investigators allocate the aye-aye to an extra rank (Chiromyiformes) and exclusively subsume Lemuridae, Cheirogaleidae, Indriidae, and Lepilemuridae under the taxon name Lemuriformes, thereby appreciating the long independent evolutionary history of the aye-aye (e.g., Groves 2001; Chatterjee et al. 2009; Perelman et al. 2011). I herein follow other authors and include also the aye-aye into Lemuriformes (e.g., Martin 1990; McLain et al. 2012; Fleagle 2013; Pecon-Slattery 2014; Kistler et al. 2015). Irrespective of the alternative taxonomy, there is a common agreement that the highly specialized aye-aye probably represents the sister taxon of all other non-human Malagasy primates. Before humans conquered Madagascar about 1500 or 2000 years ago, the lemur fauna was even more diverse than it is today (e.g., Geissmann 2003; Storch et al. 2013). Those species that went extinct since human arrival were mainly of larger size. Several of the subfossil remains display typical signs of butchering such as sharp cuts near joints, spiral fractures, and percussion striae so that humans could have contributed to their disappearance (Godfrey and Jungers 2003). Either way, phylogenetic analyses of DNA sequence data revealed a nested position of the extinct species, for which ancient DNA was available, inside crown-Lemuriformes. This finding was taken as evidence that the complete lemur diversity arose from a single founder population that once arrived on Madagascar (Karanth et al. 2005; see also Kistler et al. 2015). However, the data rather evidenced that Lemuridae, Cheirogaleidae, Indriidae, Lepilemuridae, and the extinct species included in the study constitute a monophylum. Yet, the data did not finally resolve the question if Madagascar was conquered only once, by an ancestor of Lemuriformes (including the aye-aye), or twice, by an ancestor of the aye-aye and by an ancestor of the remainder Lemuriformes (excluding the aye-aye) (Chatterjee et al. 2009). Whether Madagascar was conquered once or twice by non-human primates, the interplay of climatic shifts and geographic relief fostered a consecutive radiation that led to a still high diversity of lemurs on the Malagasy island (Wilmé et al. 2006). In contrast to the extinct forms, the living lemur species are of moderate to small size and one of their representatives, Madam Berthe's mouse lemur (*Microcebus berthae*), is even said to be the smallest primate of the world (average adult mass ~33 g; Schäffler and Kappeler 2014). Apomorphic traits are not easy to define for Lemuriformes:

such novelties could be strict seasonality of breeding, inward location of a free ectotympanic ring, and the circumstance that blood streaming from the internal carotid to the brain exclusively passes through the stapedia artery (Martin 1990; van Schaik and Kappeler 1993; Fleagle 2013). However, the phylogenetic significance of these traits is not quite clear so that only a single apomorphy remains for Lemuriformes:

1. The first interdigital pad is fused with the thenar pad so that the palmar surface of the hand has only five instead of six pads (Martin 1990).

### 2. Haplorhini (syn. Haplorrhini; “dry-nosed” or “simple-nosed” primates)

The placenta of the haplorhine LCA was probably deciduate (after birth, fetal tissue is stripped off together with the maternal decidua), discoidal (confined to a disc-like contact zone between mother and fetus), and hemochorial (no chorion epithelium between maternal and fetal tissues; fetal chorionic villi are in direct contact with maternal blood) (e.g., Napier and Napier 1967; Lockett 1976; see Strepsirhini for comparison). This condition was long regarded as a derived state (e.g., Lockett 1976; Geissmann 2003; Martin 1990), but in light of a broader dataset and recent insights into mammalian phylogeny, this is rather a plesiomorphy (Wildman et al. 2006). While the phylogenetic significance of different placenta types seems to be settled, some features relating to the ears and eyes are not. In tarsiers and catarrhines, the tympanic bone (ectotympanic) forms a tube-like acoustic meatus (auditory meatus) that is fused to the outer margin of the bulla from which it extends in dorsolateral direction. Three alternative states occur in primates: either the ectotympanic is ring-shaped and lies inside the bulla (lemuriform primates; see there) or it is ring-shaped and attached to the inside wall of the bulla (lorises) or it is ring-shaped (at maximum slightly expanded) and fused to the outer margin of the bulla (New World monkeys) (Napier and Napier 1967; Martin 1990; Fleagle 2013). The situation gets even more complicated when one additionally takes into account converse spatial arrangement and shape of the ectotympanic in treeshrews and flying lemurs (e.g., Shoshani et al. 1996). Despite the confusing character state distribution, an elongated ectotympanic has occasionally been regarded as a catarrhine apomorphy (e.g., Geissmann 2003; Schmidt 2010). In support of this view, some specimens of the likely catarrhine stem line representative *Propliopithecus zeuxis* (formerly *Aegyptopithecus zeuxis*; Propliopithecidae) have been reported to show solely an incipient development of the auditory meatus (Simons et al. 2007). Additional data from other extinct species provide extra support to the view that an elongation of the ectotympanic

occurred on the catarrhine stem line while platyrrhines retained the ancestral annular structure (reviewed in Simons et al. 2007). Still, we cannot be sure about the evolutionary scenario behind the character state distribution in extant and extinct species. The same holds true for the presence/absence of a tapetum lucidum. Such a reflecting layer behind the retina is lacking in the extant members of both sister groups within haplorhines, tarsiers (Tarsioidae), and anthropoids (Anthropoidea) (e.g., Martin 1990). However, if this lack of a tapetum results from reduction in the haplorhine stem lineage (Shoshani et al. 1996; Geissmann 2003) or rather represents an ancestral state is a matter of ongoing debate (Martin 1990; Williams et al. 2010; Moritz et al. 2013). In any case, absence of a tapetum not only coincides with higher visual acuity, but also implies less light sensitivity (e.g., Fleagle 2013). Another unsettled issue refers to the rear side of the eyes, especially to the question if the eyes of the haplorhine LCA rested in solid sockets. In support of such an assumption, tarsiers and anthropoids both possess a postorbital closure (also postorbital plate, postorbital septum) consisting of zygomatic, frontal, and (ali)sphenoid bone. Moreover, all three bones have contact to each other in tarsiers and anthropoids. The zygomaticum-alisphenoid contact is even unique within vertebrates (Kay et al. 1997, 2004). On the other hand, the degree of closure (partial in tarsiers vs. complete in anthropoids) and the detailed construction of the postorbital plate differ between tarsiers and anthropoids (Rassmussen 2007). Lack of a postorbital plate in fossil remains of Omomyoidea further challenges the homology of eye sockets in tarsiers and anthropoids—at least, when regarding the respective omomyoids as stem group representatives of tarsiers (Beard et al. 1991; Rassmussen 2007; Gebo et al. 2000; Storch et al. 2013). However, the omomyoids in question may actually be paraphyletic stem group representatives of (crown-) Haplorhini and a partial closure could have evolved in the haplorhine stem line after the last omomyoid-haplorhine split (Kay et al. 1997, 2004; Seiffert et al. 2005). Irrespective of the true evolutionary history, a posterior closure quite obviously protects the eye from squeezing by the temporal muscle, thus warranting visual acuity while chewing (Fleagle 2013; Shoshani et al. 1996). An excursion to the basocranium completes the list of uncertain apomorphies: tarsiers and anthropoids have an (anterior) accessory chamber in front of the tympanic chamber, which they might have inherited from the haplorhine LCA (Martin 1990; Kay et al. 1997, 2004; Williams et al. 2010; Fleagle 2013). Yet, lack of an accessory chamber in all fossil species (Beard 2004) and, thus, also in omomyoids again hampers a phylogenetic interpretation of the alternative character states. Irrespective of these unclear aspects, there is strong evidence for a sister group relationship of tarsiers and anthropoids from molecular and anatomical data:

1. The mere number of molecular insertions supporting haplorhine monophyly let me once more return to the molecular level: 19 genomic Alu SINE insertions, 22 long interspersed nuclear elements (LINEs), and 63 long terminal repeats (LTRs), all conflict-free markers, corroborate a sister group relationship of tarsiers and anthropoids. This lowers the probability of erroneous acceptance of haplorhine monophyly to  $7.2 \times 10^{-50}$  (Hartig et al. 2013; see also Schmitz et al. 2001).
2. The outer surface of the haplorhine nose is dry (no rhinarium *sensu stricto*), and the upper lip is partially or not split (Martin 1990; Geissmann 2003; Shoshani et al. 1996; Williams et al. 2010; Fleagle 2013). The dry outer appearance associates with a change in the orientation of the aforementioned nasolacrimal duct (see Primates), which drains lacrimal fluid from the medial lid angle of the eye. In haplorhines, the duct is shortened, is vertically oriented, and runs to the nasal cavity (Rossie et al. 2006). The plesiomorphic condition is retained in strepsirhines, where the duct is longer and extends horizontally from the eye to the rhinarium (Rossie et al. 2006; also Williams et al. 2010; Fleagle 2013). Furthermore, the inner surface of the haplorhine nasal cavity is reduced due to a decline in the number of ethmoidal conchae (ethmoturbinalia; Martin 1990; Geissmann 2003; Williams et al. 2010; Fleagle 2013). Despite some variation in the number of ethmoturbinals also within single species (e.g., two to three per side in humans; Grünwald 1917), haplorhines clearly have less ethmoturbinals than strepsirhines (four per side). Finally, haplorhine nostrils are just simple openings without diverticula nasi. The general reorganization of the nose reflects less reliance on olfaction in haplorhines as compared to strepsirhines (Niimura 2012), a circumstance that finds its expression also in a shortening of the snout (Stringer and Andrews 2005). It is worth mentioning that less inner surface of the nasal cavity not only suggests a change in sensory behavior but also should have an effect on thermoregulation and respiration (Fleagle 2013).
3. In haplorhines, blood coming from the internal carotid mainly flows through the promontory branch to the brain and less through the ascending pharyngeal artery (Martin 1990; Kay et al. 1997; Fleagle 2013). This character state is accompanied by a marked reduction or complete absence of the stapedia artery in adult haplorhines (Williams et al. 2010). Notably, persistence of the stapedia artery in humans can evoke symptoms like pulsation (Silbergleit et al. 2000) and ear bleeding (Lefournier et al. 1999).
4. Adult haplorhines cannot synthesize vitamin C (e.g., Williams et al. 2010), probably as a consequence of zero expression of the enzyme mediating the final step in the synthesis of L-ascorbic acid (vitamin C) from glucose, L-

gulonolactone oxidase (GULO, also GLO, LGO) (Pollock and Mullin 1987; Drouin et al. 2011; Yang 2013). Pseudogenization of the coding gene has been documented for several anthropoid species (Drouin et al. 2011; Yang 2013) and can also be assumed for tarsiers: own BLAT search on the UCSC Genome Browser sides (<https://genome.ucsc.edu/>), carried out separately for each of the altogether 11 exons of the GLO gene in *Otolemur garnetti* (ENSOGAT00000025787; genome assembly OtoGar3), against the *Tarsius syrichta* genome (tarSyr2.0.1) yielded only a single hit that appeared meaningful regarding its length and identity with the query sequence (KE944148v1:9318–9416), namely when using exon 6 as a query. The metabolic lesion in the haplorhine stem lineage explains why haplorhines including humans suffer from scurvy when relying on vitamin C-depleted diet (e.g., Pollock and Mullin 1987).

5. The haplorhine retina has apomorphic differentiations in the temporal region close to the optical disc, namely the yellow spot or macula lutea and, therein, a small pit called fovea centralis (e.g., Geissmann 2003; Shoshani et al. 1996). The yellowish appearance of the macula is due to an agglomeration of lutein and zeaxanthin, two carotenoids that protect from short-waved light and oxidants (Martin 1990). The fovea enables high visual acuity through an increased density of light-sensitive cells. While the fovea has more photopic cones than scotopic rods in most diurnal anthropoids, the fovea is rod-dominated in nocturnal tarsiers (Moritz et al. 2014). Disregarding these differences, the mere presence of a retinal topology in tarsiers and anthropoids could be the legacy of a diurnal haplorhine LCA.
6. Haplorhine females usually give birth to only a single infant instead of having multiple offspring as retained in strepsirhines (Martin 1990; Fleagle 2013; Feldhamer et al. 2014). This condition reflects a general evolutionary tendency toward more parental investment in less offspring on the lineage to humans (Jurmain et al. 2013). Notwithstanding this general trend, multiple births also occur in haplorhines and, especially, in Callithrichinae twinning is even the rule rather than the exception (see Platyrrhini, Cebidae, Callithrichinae).

### 2.1. Tarsioidea (tarsiers; contains the same living species as Tarsiiformes and Tarsiidae)

Tarsiers live in the primary rain and secondary forests of the Southern Philippines, Sumatra, Borneo, and Sulawesi (Jablonski 2003). Their diet exclusively consists of animals, especially insects and small vertebrates (Niemitz 1979), that these nocturnal haplorhines locate visually

and auditorily (Napier and Napier 1967). Moreover, tarsiers are distinguished by possession of grooming claws on the second and third toes that possibly evolved secondarily from nails (Dagosto 1988; Gebo et al. 2015). The formerly monogeneric clade has lately been split into three geographically separated genera that differ in sociality, number of mammae and chromosomes, and shape of the tail tuft (Groves and Shekelle 2010). Disregarding these differences, there are ample anatomical character states in support of the clade's monophyly:

1. Tarsiers possess exceptionally augmented eyes, each eye being larger than the brain (e.g., Geissmann 2003; Fleagle 2013). This enlargement apparently compensates for the low light sensitivity of the tarsier eye, a consequence of the lacking tapetum (see Haplorhini). The eyes are involved in the location of the prey during night (Napier and Napier 1967), possibly in terms of a vision-mediated calibration of the auditory orientation (Moritz et al. 2014). Another aspect of the tarsier eye is that they are widely immobile (Niemitz 1979).
2. The aforementioned deficit in eye mobility is more than compensated by an enormous mobility of the head along the axis of the vertebral column (Napier and Napier 1967). Thus, the head can be rotated in each direction for about 180° (e.g., Geissmann 2003; Feldhamer et al. 2014). This circumstance enables tarsiers to focus on prey and/or support on the rear side before leaping from a vertical clinging position (Dagosto et al. 2001).
3. Tarsiers have a derived dental formula reflecting the reduction of one incisor per lower jaw quadrant: 2.1.3.3/1.1.3.3 (permanent dentition; Swindler 2002). Pointed permanent incisors, canines, and premolars that aid in capturing the prey may also belong to the evolutionary novelties of the taxon. If derived or ancestral, the permanent molars have three well-formed cusps that allow for forceful cracking of insect exoskeletons and vertebrate skeletons (Swindler 2002; Jablonski 2003).
4. Elongated feet and long and powerful hindlimbs facilitate the outstanding jumps of these vertical clingers and leapers (Martin 1990; Peters and Preuschoft 1984; Geissmann 2003; Fleagle 2013). The longish appearance of the feet essentially is the consequence of an elongation of two tarsal bones, namely calcaneus and naviculare (Beddard 1902; Peters and Preuschoft 1984; Gebo 1988). This tarsi-fulcrumation obviously evolved in parallel in Galagidae (see there).
5. The lower leg bones, tibia and fibula, are distally fused. This synostosis involves about 60 % of the tibia's length (Rasmussen et al. 1998) and also relates to the increased jumping ability of tarsiers.
6. The tarsier tail is elongated and has cutaneous ridges on its ventral side (Hill 1953; for comparison, see Platyrrhini,

Atelidae). The tail provides support to the body in vertical clinging position by being pressed to the stem or branch (Martin 1990). During jumps, movements of the tail induce and steer rotations along the body axis (Peters and Preuschoft 1984).

7. The carpometacarpal joint I permits only a very limited range of movement (Napier and Napier 1967). The condition associates with an increased mobility of metacarpophalangeal joint I that includes abduction, adduction, and rotation (Napier and Napier 1967; Ankel-Simons 2000; Geissmann 2003). However, the gain of mobility over metacarpophalangeal joint I does not fully compensate for the reduced mobility of carpometacarpal joint I. Consequently, the tarsier thumb has been classified as being non-opposable (Napier and Napier 1967).
8. Male tarsiers do not possess a penile bone, baculum, anymore. The same condition evolved in the human stem lineage (see *Homo sapiens*) and inside the New World monkey clade. Males of the other extant primate species retained a penis bone, as it is also the case for flying lemurs and other mammals (Shoshani et al. 1996; Dixson 2009).

## 2.2. Anthropoidea (syn. Simii, Simiae, Simiiformes; “higher” primates, monkeys and apes)

Some authors regard more anteriorly facing orbits as an evolutionary novelty of Anthropoidea (e.g., Shoshani et al. 1996), a condition that is here postulated for the LCA of Haplorhini (see there). Yet, this is not a contradiction but rather reflects a general tendency for increasing frontation of the orbits from the primate to the anthropoid stem lineage. It seems also to be a common view that an unpaired frontal bone (Shoshani et al. 1996; Jurmain et al. 2008) or at least early obliteration of the frontal suture (median frontal suture, metopic suture) is an apomorphy of anthropoids (Martin 1990; Geissmann 2003). However, medio-frontal suture fusion is a widespread phenomenon in primates and typically happens early in tarsiers, too (Rosenberger and Pagano 2008). Hence, (early) fusion of frontals seems to be less suitable for distinguishing anthropoids from other primates than previously thought (see also Kay et al. 2004). Still, the frequency of early fusion may have increased in the anthropoid stem lineage. There seems to be more agreement with respect to activity pattern and lifestyle: the anthropoid LCA probably was diurnal, arboreal, and primarily insectivorous (Dagosto 1988; Ni et al. 2013). Leaving aside the question for the phylogenetic significance of the latter character states, we can conclude the following evolutionary novelties for Anthropoidea:

1. The anthropoid LCA probably had spatulate (shovel-like) incisors adapted for biting and cutting (e.g., Shoshani et al. 1996). The emergence of spatulate incisors might point to a significant dietary shift with increased emphasis on incisal biting in the anthropoid stem lineage (Martin 1990).
2. The two halves (dentaries) of the lower jaw are fused tightly early in life which gives rise to a single unpaired and continuous mandible (e.g., Kay et al. 2004; Jurmain et al. 2008). This anthropoid feature differs from the ancestral state displayed by strepsirhines, tarsiers, and other mammals whose dentaries are anteriorly midline-joined by connective tissue (symphysis). When present, the symphysis allows some degree of movement between the dentaries during chewing (Fleagle 2013). The functional significance of symphyseal fusion is elusive, but an increased relevance of horizontal chewing movements presumably played a role in the emergence of the trait (Ravosa and Hogue 2004). The specific anthropoid condition associates with a jaw hinge position above the occlusal plane of the cheek teeth (premolars and molars), rather than virtually coinciding with it as in tarsiers and strepsirhines. Symphyseal fusion evolved in parallel inside Lemuriformes as demonstrated by fossil remains from Madagascar (Martin 1990).
3. Female anthropoids have an unpaired uterus (uterus simplex) instead of a bicornuate one (uterus bicornus) as in strepsirhines and tarsiers (Luckett 1976; Martin 1990; Shoshani et al. 1996; see also Luckett 1980). Furthermore, anthropoid females only have one pair instead of multiple pairs of teats as shown by non-anthropoid primates and other mammals (e.g., Schmidt 2010). Both anthropoid character states probably evolved in the context of a condition inherited from the haplorhine LCA: single infant births as a rule (see Haplorhini).
4. Anthropoid primates do not possess a sublingua (Hofer 1977) although a fold of the mucous membrane called plica fimbriata might represent a vestigial sublingua (Napier and Napier 1967). As strepsirhines (Schmidt 2010; Wilson and Hanlon 2010) and tarsiers share the presence of a sublingua with diverse other mammals (Hofer 1977), reduction of a sublingua seems to be an evolutionary novelty of anthropoids.
5. Virtually complete (total) closure of the postorbital plate (Napier and Napier 1967; Martin 1990; Shoshani et al. 1996). The remaining openings let the blood vessels and optical nerve traverse. The ancestral condition might be a partial closure as present in tarsiers (for a discussion, see Haplorhini).
6. Several evolutionary changes suggest a decreased use of the feet for vertical climbing and their increased use for above-branch quadrupedalism (Gebo 1988): short and less robust hallux, long metatarsals with broad proximal ends, and small peroneal tubercle of first metatarsus (Gebo 1988; Shoshani et al. 1996).

7. In anthropoids, the chorda tympani, a branch of the fascialis nerve, traverses the middle ear mainly above (epitensoric) instead of mainly below (hypotensoric) the tensor tympani muscle as in non-primate taxa and most non-anthropoid primates (Diogo and Wood 2012).
8. A potential apomorphy of anthropoids is that ovarian hormones have much less rigid effects upon female receptivity than in non-anthropoid primates (“loss of oestrus”; Dixson 2009). Consequently, receptivity, though often maximal around the time of ovulation, is not tightly restricted to a specific period in anthropoids (Martin 1990).

### 2.2.1. Platyrrhini (New World monkeys, “broad-nosed” monkeys)

Color vision has a fascinating genetic background in most members of the clade (Jacobs et al. 1996; Surridge et al. 2003): short-wave (blue-)opsin is encoded by an autosomal gene; allelic variants of a X-chromosomal gene code for opsins with absorption maxima in the middle (green)- and long-wave (red) range. Consequently, hemizygous males and females that are homozygous for the X-chromosomal gene have dichromatic color vision. Yet, X-chromosomally heterozygous females are provided with the—for primate relations—full suite of three opsins and thus are trichromats. This allelic form of trichromacy is widespread in platyrrhines and differs from routine trichromacy in the platyrrhine howler monkeys (*Alouatta*; see Atelidae) and Catarrhini (see there). Although trichromacy should be beneficial for the distinction of ripe fruits against a green background, the detailed advantage of trichromats over dichromats is not fully understood (for a summary of the hypotheses, see Surridge et al. 2003). The same is true for the question of how the platyrrhine ancestor entered the New World (see, e.g., Jurmain et al. 2008). While platyrrhine monophyly is demonstrated by manifold molecular insertions (Zischler 2007), only few anatomical changes can be postulated for the platyrrhine stem lineage—and these are rather subtle:

1. Unique to platyrrhines, zygomaticum and parietale have contact to each other. The plesiomorphic condition is a contact of frontale and (ali-)sphenoid as shown by non-platyrrhine primates and other mammals (Shoshani et al. 1996; Fleagle 2013).
2. The ectotympanic lies outside the bulla. It is large and horseshoe-shaped and forms the thick-walled opening of the external acoustic (auditory) meatus. The plesiomorphic condition is unclear since the shape of the ectotympanic varies across the other primate taxa (see, e.g., Martin 1990; Shoshani et al. 1996).

3. Most platyrrhines have a peculiar, strong fascial connection between axillary arch muscle and the subscapular fascia and/or the scapula. When such connection exists in single individuals of non-platyrrhine primates, it is not as strong as in platyrrhines (Diogo and Wood 2012).

#### 2.2.1.1. Pitheciidae (titi monkeys, sakis, uakaris; contains the same living species as Pithecoidea)

I am not aware of any anatomical evolutionary change of the group. Slight procumbency of the lower incisors in *Cacajao*, *Pithecia*, and *Chiropotes* (Napier and Napier 1967; Swindler 2002; Fleagle 2013) could point to an evolutionary novelty of the subtaxon Pitheciinae.

#### 2.2.1.2. Atelidae + Cebidae

The group has occasionally been referred to as Ceboidea (Fleagle 2013). All atelid and some cebid species use the tail for grasping (e.g., Fleagle 2013; Storch et al. 2013). This character distribution could be taken as evidence for the presence of a grasping tail in the LCA of Atelidae and Cebidae. However, tail myology and also the details of tail use differ between both taxa so that the behavioral similarities probably reflect parallel evolution (Lemelin 1995).

##### 2.2.1.2.1. Cebidae (capuchins, squirrel and owl monkeys, Goeldi’s monkey, marmosets, and tamarins)

I am not aware of any anatomical apomorphic character state in support of Cebidae as a whole but monophyly of some of its subtaxa is substantiated by several evolutionary changes relating to anatomy, morphology, behavior, physiology, and life history. Thus, owl or night monkeys (Aotinae; occasionally subsumed under Aotidae) are distinguished by secondary nocturnality, enlarged orbits, and monochromacy (e.g., Martin 1990). The majority of owl monkey specimens seem to lack a fovea, but it is rod-dominated when present (Moritz et al. 2014). Also monophyletic marmosets (Callithrichinae; occasionally referred to as Callithrichidae) are characterized by secondarily clawed digits (except for the hallux), procumbent (lower) incisors (used for skinning the bark from trees; exudates are then ingested), loss of third molars, non-opposable thumb due to an immobile carpometacarpal joint I, and widespread reduction of a distinct opponens pollicis muscle (Napier and Napier 1967; Martin 1990; Diogo and Wood 2011, 2012). Callithrichinae show further a general tendency for multiple offspring (typically twins) and

secondary dwarfing (Martin 1990). In line with the latter aspect, Callithrichinae includes the smallest species amongst living anthropoids, i.e., the pygmy marmoset (*Cebuella pygmaea*) with female and male weights of about 110 and 122 g, respectively (Lindenfors 2002). Members of the monophyletic subtaxon Cebinae (capuchin monkeys) are known for frequent bipedal posture and locomotion and also for stone tool use and social learning (Otoni and Izar 2008). Improved learning ability in capuchin monkeys seems to associate with an extra-ordinarily long postmenopause of females relative to other non-human primates (Fleagle 2013).

#### 2.2.1.2.2. Atelidae (howler, wooly and spider monkeys, wooly spider monkey)

The taxon Atelidae contains the largest living platyrrhines with males reaching >9 kg in some species (Lindenfors 2002). Howler monkeys (*Alouatta*) have routine trichromacy so that all individuals (ignoring potential secondary color asthenopia) are equipped with three kinds of retinal cones with differing light sensitivity (Jacobs et al. 1996). Routine trichromacy evolved in parallel in the stem lineage of Catarrhini (see there). Howlers are additionally distinguished by an enlarged hyo-laryngeal complex (larger in males and still increased in females) that serves as a resonating chamber for their calls (Fleagle 2013). The thumb underwent reduction inside Atelidae, a state that was reached independently in the stem lineage of Colobini (see Colobinae) (Napier and Napier 1967).

1. The prehensile tail (e.g., Feldhamer et al. 2014) has distally a ventral bare friction field reminding of the dermatoglyphics of hand and feet.

#### 2.2.2. Catarrhini (“small-nosed” monkeys, Old World simians)

Unfortunately, English and German terminology is not consistent with respect to catarrhines: while the English taxon name Old World monkeys refers to the catarrhine subtaxon Cercopithecoidea, the German taxon name “Altweltaffen” relates to Catarrhini as a whole. Irrespective of this inconsistency in terminology, Catarrhine monophyly is well documented by several anatomical and molecular apomorphies:

1. Catarrhines have two premolars per quadrant (Martin 1990; Swindler 2002; Jurmain et al. 2008; Geissmann 2003; Shoshani et al. 1996; Fleagle 2013) instead of three as retained by tarsiers, most strepsirhines, and most platyrrhines (Shoshani et al. 1996). Reduction of one premolar (per quadrant) also occurred inside lemuriforms and platyrrhines.
2. The anterior-most premolar of the lower jaw quadrants (sectorial premolar, P<sub>3</sub>; Napier and Napier 1967; Geissmann 2003) has a long and narrow crown that hones the upper canine during occlusion (e.g., Shoshani et al. 1996; Swindler 2002). This character state is fully developed in the living Old World monkey species while the reduction of the honing anatomy seems to be an overall trend in hominoids; in humans, for instance, it is absent (e.g., Shoshani et al. 1996).
3. The catarrhine thumb is (truly) opposable (Napier and Napier 1967; Martin 1990; Geissmann 2003; Fleagle 2013). The uniqueness of this trait is the expanded mobility of the thumb which, in addition to the plesiomorphic ability for abduction and adduction, now can be opposed to palm and other digits (Napier and Napier 1967). True opposability of the catarrhine thumb is tightly linked to the apomorphic saddle conformation of carpometacarpal joint I. Movement at the metacarpophalangeal joint I adds to thumb opposability in catarrhines, though to less degree in man (Napier and Napier 1967). The plesiomorphic condition of pseudo-opposability is displayed by most of the non-catarrhine primate species (see Primates).
4. Catarrhine thumb opposability associates with a reorganization at the muscular level: the adductor pollicis muscle underwent further differentiation into transverse and oblique heads. The plesiomorphic condition of only a partial differentiation into oblique and transverse heads is conserved in platyrrhines. Strepsirhines and tarsiers retained an even more ancestral state: their adductor pollicis usually does not display such differentiation (Diogo and Wood 2012).
5. The catarrhine LCA presumably had ischial callosities (see, e.g., Jurmain et al. 2008; Geissmann 2003; Fleagle 2013), i.e., tough, cutaneous pads covering broad and roughened protuberances on the ischial bones of the pelvic girdle, called ischial tuberosities. This complex of character states probably evolved in adaptation to long periods of sitting (Napier and Napier 1967), possibly on branches (Vilensky 1978). Ischial callosities are retained in Old World monkeys, gibbons, and siamang (Napier and Napier 1967; Martin 1990) while they are absent in humans. They are said to be in the process of disappearing in non-human representatives of Hominidae (Vilensky 1978).
6. In catarrhines, the depressor septi nasi, a triangular muscle running from the upper lip to the nasal septum, is usually a distinct muscle (Diogo and Wood 2012). Contraction of the muscle draws the alae of the nose downward, thus constricting the nostrils. This illustrates that the muscles' function is tightly linked to juxtaposed and downward facing nostrils as they are present in catarrhines (Jurmain

et al. 2008; Fleagle 2013). Most authors refrain from an assessment of the phylogenetic significance of the specific catarrhine nostrils. However, when accepting more remote and sideward facing nostrils as a plesiomorphy of platyrrhines (Geissmann 2003) and a distinct depressor septi nasi muscle as an evolutionary novelty of catarrhines (Diogo and Wood 2012), juxtaposed and downward facing nostrils should be an evolutionary novelty of catarrhines.

7. Functionality of the vomeronasal organ got lost in the catarrhine stem lineage (e.g., Schmidt 2010) as evidenced by a reduced number or even absence of functional vomeronasal receptor genes in diverse members of the clade (Halpern 1987; Smith et al. 2011; Nei et al. 2008; see also Hohenbrink et al. 2013). Also, the *TRP2* gene that encodes a channel protein essential for pheromone signal transduction experienced pseudogenization in the catarrhine stem lineage (Zhang and Webb 2003). When present, the organ takes the form of two hollow tubes resting inside a cartilaginous capsule between mouth and nose (Smith et al. 2011); pheromones are then sensed via two foramina just behind the upper incisors (Martin 1990).
8. Catarrhines have routine trichromacy (SurrIDGE et al. 2003; Gilad et al. 2004): As in platyrrhines, short-wave opsin is encoded by an autosomal gene; however, contrary to most platyrrhine species, mid- and long-wave opsins are encoded by separate X-chromosomal genes. This genetic background implies that in catarrhines, all members of a population have trichromacy—as long as individuals, typically males, are not color-blind. Especially in humans, additional gene copies coding for mid-wave opsin may occur in single individuals. The (first) mid-wave opsin and the long-wave opsin quite certainly arose by tandem duplication placing two allelic forms on the same chromosome (SurrIDGE et al. 2003). Trichromacy may confer an advantage in the distinction of ripe fruits against a green background. However, the adaptive value of trichromacy relative to dichromacy is actually not fully understood (for a summary of the hypotheses, see SurrIDGE et al. 2003).

#### 2.2.2.1. Cercopithecoidea (Old World monkeys; contains the same living species as Cercopithecidae)

Sexual dimorphism of body weight is a common phenomenon within the group. Notably, high ratios of male to female weights have been found to be inversely related to the rates of sequence evolution of sperm proteins such as PH-20 and ZAN, confirming reduced levels of post-copulatory sexual selection in these species (Herlyn and Zischler 2007; Prothmann et al. 2012). Although cercopithecoidea are

doubtlessly monophyletic, I am aware of only one prominent anatomical evolutionary change supporting this conclusion, while the others are more subtle:

1. Marked bilophodonty of molars: ridges, or lophs, span between the anterior two cusps and the posterior two cusps of the molars (e.g., Napier and Napier 1967; Shoshani et al. 1996; Geissmann 2003). Notably, bilophodonty was acquired independently within lemurs, platyrrhines, and non-primate mammals (Martin 1990; Shoshani et al. 1996).
2. Males have (upper) canines with a long mesial groove that extends onto the root. The plesiomorphic condition is a shorter or absent mesial groove (e.g., Shoshani et al. 1996; Swindler 2002).
3. A very narrow elbow joint with a reduced medial epicondyle and a relatively long olecranon process on the ulna may represent another apomorphy of the clade (Fleagle 2013).

#### 2.2.2.1.1. Cercopithecinae (baboons, macaques, vervet monkeys)

Most species of this taxon live in Africa, but some representatives also occur in Asia. Only the distribution range of the Barbary macaque (*Macaca sylvanus*) includes a very restricted European area, namely Gibraltar (Modolo et al. 2005). As typical for non-human primates, most cercopithecine species live in more or less warm habitats of the tropes and sub-tropes. Nonetheless, some species withstand cold winter seasons in high altitudes (e.g., black snub-nosed monkey, *Rhinopithecus bieti*) and higher latitudes (Japanese macaque, *Macaca fuscata*). A prominent exception from the general predominance of fruits in the cercopithecine diet is the gelada (*Theropithecus gelada*) from the Ethiopian highlands, where grass makes up a major fraction of its diet (e.g., Fleagle 2013). Geladas may also serve as an extreme example of sexual dimorphism of body weight, with male and female weights in the range of about 20 and 12 kg, respectively (Lindenfors 2002). The smallest catarrhine species, the Angolan talapoin monkey (*Miopithecus talapoin*), with males and females reaching up to 2 and 1.6 kg, respectively, also belongs to this taxon (Lindenfors 2002). Finally, it is worth being mentioned that the patas monkey (*Erythrocebus patas*) is said to be the fastest runner among living primates (Geissmann 2003; Fleagle 2013). Cercopithecine monophyly is supported by comparably few evolutionary novelties:

1. Cercopithecines possess cheek pouches (Martin 1990; Geissmann 2003; Fleagle 2013) that are “crammed with food which is then pushed back into the mouth

by hand, chewed and swallowed at leisure” (c.f., Napier and Napier 1967).

2. Females of Cercopithecoinae indicate high fecundity by exaggerated sexual swellings of the perineal skin. How reliable the signal really is is a matter of ongoing debate. Irrespectively, exaggerated sexual swellings probably evolved at least threefold independently within catarrhine primates. In addition, secondary loss of the character state happened at least twice (Nunn 1999).

#### 2.2.2.1.2. Colobinae (leaf-eating monkeys)

Members of the clade live in Africa and Asia. A prominent Asian representative is the proboscis monkey (*Nasalis larvatus*). Males of this species have an enormous, pendulous nose used for thread display and as an accessory vocal organ that seems to be subject to sexual selection through female choice (Napier and Napier 1967). Leaves may constitute more than 90 % of the diet of Colobinae, depending on the species, season, and habitat (Hu 2011). Some of the evolutionary novelties of the group reflect the aforementioned elevated degree of folivory:

1. Leaf-eating monkeys are foregut fermenters with a sacculated stomach reminding that of ruminants (Martin 1990; Shoshani et al. 1996; Geissmann 2003; Fleagle 2013). The anterior two chambers maintain neutral conditions and house symbiotic bacteria that degrade the relatively indigestible cell wall of leaves with the aid of cellulase (Martin 1990; Schmidt 2010). Part of the microflora is then passed on to the posterior two chambers that maintain acid conditions. In these posterior two chambers, digestion of the symbionts takes place whereby leaf-eating monkeys rely on their own, yet modified, enzyme lysozyme (Martin 1990; Messier and Stewart 1997). At least some species additionally possess modified isoforms of RNase 1 that mediate the uptake of nitrogen, also from decomposed symbionts, from the small intestine (Zhang 2006).
2. In Colobinae, the thumb is reduced in length (e.g., Shoshani et al. 1996). The thumb experienced further reduction in the stem lineage of the subtaxon Colobini. Partial and near-complete reduction of the thumb may be seen as adaptations to frequent swinging by arms below branches (Napier and Napier 1967). Thumb reduction also occurred in the stem lineage of Atelidae (see there).

#### 2.2.2.2. Hominoidea (apes and humans)

The geographic distribution and age of fossil remains suggest that hominoids spread from Africa to Eurasia; following extinction in Africa, the continent was later on re-colonized from

Eurasia (Stewart and Disotell 1998). Whether this scenario is true or not (for a discussion, see Stringer and Andrews 2005), the comprehensive hominoid fossil record illustrates extinction as a normal evolutionary process (Begun 2007). However, hominoids also provide an example for the increased risk at extinction of many non-human primate species, through habitat destruction, hunting, and other human activities (e.g., Jurmain et al. 2008; Feldhamer et al. 2014). Throughout primate evolution, there was more or less continuous increase in (relative) brain and, especially, neocortex size on the lineage to humans. Therefore, not only humans, but also other members of the hominoid clade possess increased intellectual properties as illustrated by tool use, self-medication, and self-recognition (e.g., Storch et al. 2013). However, it is less apparent to what extent the hominoid LCA already disposed of these intellectual capabilities, mainly because of ambiguous observations in hylobatids (see, e.g., Heschl and Fuchsichler 2009; Suddendorf and Collier-Baker 2009). The dietary composition of the hominoid LCA can be assessed with higher certainty (e.g., Martin 1990): considering wide prevalence of plant food in hylobatids, orangutans, and gorillas and still high proportion of plants in the diet of chimpanzees and humans (see, e.g., Storch et al. 2013), the hominoid LCA probably had a strong preference for vegetarian food. It is also very likely that the hominoid LCA was capable of facultative bipedality, yet most evolutionary novelties of the clade rather reflect adaptation to suspensory (upright) locomotion and arboreal climbing (e.g., Martin 1990; Fleagle 2013):

1. The chest (thorax) of the hominoid LCA was supposedly wider than it was in the catarrhine LCA (Shoshani et al. 1996; Geissmann 2003; Fleagle 2013).
2. In the hominoid LCA, the vertebral column probably had a more central position than it was the case in the catarrhine LCA (e.g., Schmidt 2010). Furthermore, at least one lumbar vertebra fused with the sacral bone in the hominoid stem lineage. Additionally, the hominoid LCA quite surely had less caudal vertebrae than the catarrhine LCA. The two to four vertebrae retained by living hominoids do not form an externally visible tail, but instead the coccyx (e.g., Geissmann 2003; see also Lovejoy and McCollum 2010).
3. The shoulder joint is shifted from a ventro-lateral to a lateral position (e.g., Jurmain et al. 2008); in close linkage to this positional shift, the clavicle is elongated and the scapula has a dorsal position (Geissmann 2003; Schmidt 2010; Fleagle 2013).
4. The origin of the levator scapulae muscle along the column spine usually does not extend to cervical vertebra 5, anymore. The plesiomorphic state is represented by non-hominoid primates and other mammals: the muscles' origin extends posteriorly to cervical vertebra 6 or even more caudally (Diogo and Wood 2012).

5. The forelimbs underwent elongation relative to hindlimbs (Geissmann 2003; Jurmain et al. 2008; Shoshani et al. 1996; Schmidt 2010; Fleagle 2013).
6. The attachment plane of the deltoid muscle on the anterolateral surface of the central part of the humerus is round instead of flat (Shoshani et al. 1996).
7. The olecranon process of the ulna that forms the outer bump of the elbow is shortened in hominoids relative to non-hominoid primates (e.g., Fleagle 2013).
8. It is a common pattern in hominoids that the flexor digitorum superficialis muscle partially attaches to ulna and radius. The presumed ancestral state is shown by the majority of the non-hominoid specimens investigated: the entire muscle stretches to more proximal sites, especially to the medial epicondyle of the humerus and/or the common flexor tendon attached to this epicondyle and/or the capsule of the elbow joint (Diogo and Wood 2012).
9. In hominoids, the ulna does not articulate with carpal bones anymore. This loss is due to an evolutionary new fibrous meniscus between the respective bones (Fleagle 2013; Schmidt 2010). As a consequence, inward (pronation) and outward rotations of the hand along the longitudinal axis of the lower arm (supination) exclusively occur over the joint connection of radius and carpus. This evolutionary change contributes to the hominoid peculiarity that the wrist permits rotation of about 160° (Sarmiento 1988).
10. The ilium has a broadened ala in hominoids as compared to non-hominoid primates (Geissmann 2003; Fleagle 2013). This broadening apparently provides support to the inner organs during suspensory bipedality. The width of the ala(e) further increases on the lineage to humans.
11. Lateral and medial condyles on the distal femur show a marked asymmetry in hominoids. Most of the living primate species preserved the plesiomorphic state of symmetrical condyles. Slight asymmetry evolved in parallel inside Lemuriformes (Shoshani et al. 1996).
12. In hominoids, the lower molars ( $M_{1-3}$ ) usually have five cusps with specifically arranged grooves (Swindler 2002). This so-called Y-5 or *Dryopithecus* pattern is occasionally regarded as a plesiomorphic state (e.g., Geissmann 2003; Schmidt 2010). However, even if bilophodonty should differ more from the ancestral catarrhine condition, the Y-5 pattern still can be a derived state (Martin 1990; Jurmain et al. 2008), a view that I follow herein. The Y-5 pattern may associate with an evolutionary new expansion of the talonid portion of the molars (see Geissmann 2003).
13. Living hominoids enter puberty with delayed age of 6–7 years instead of 3–5 years (e.g., Shoshani et al. 1996).
14. Vento-ventral copulatory posture has been observed in hominids and hylobatids, besides the common dorso-ventral manner. The expansion of behavior coincides with a reduction of the baculum length. This, again, may be taken as evidence for a shift toward a single-partner mating system in the hominoid stem lineage (Shoshani et al. 1996; Dixon 2009).
15. The pyriform aperture of the skull was widened in the hominoid stem lineage (Shoshani et al. 1996).
16. Character state distribution in living hominoids suggests that the morphological adjustment of premolar  $P_3$  for honing in males should have been less developed in the hominoid than in the catarrhine LCA (Shoshani et al. 1996).
17. Some authors regard the fusion of two carpal bones, centrale and scaphoideum, in advanced age as another evolutionary novelty of hominoids (e.g., Shoshani et al. 1996). However, occurrence of such a fusion in diverse non-hominoid primates seems to impair a phylogenetic interpretation of the character state (see Kivell and Begun 2007).

#### 2.2.2.2.1. Hylobatidae (lesser apes, small apes)

The taxon is composed of the South-East Asian gibbon species and the siamang. Recent molecular investigations led to the distinction and/or recognition of new species and subspecies with partially very low abundances and high extinction risk (e.g., Roos et al. 2007). With currently 16 recognized species, Hylobatidae is the most specifically diverse taxon within Hominoidea (Fleagle 2013). Lesser apes generally display little sexual dimorphism, with males in the range of 5.5 to 12 kg and females weighing about 5.3 to 11 kg (Lindenfors 2002). All species live widely monogamous, although extra-pair mating also occurs (e.g., Palombit 1994; Reichard 1995). Pairs occupy territories and advertise through vocal duets (Dixon 2009). Lesser apes display suspensory locomotion, but preferentially move by (true) ricochetral brachiation through the canopy (Martin 1990). The following evolutionary changes probably evolved in the context of both kinds of locomotion:

1. Lesser apes have extremely long arms which are actually the longest in relation to body size amongst the living primates. Nonetheless, the ratio of forelimbs and hindlimbs (intermembral index) may be smaller in single hylobatid species than in orangutans (Martin 1990; Fleagle 2013).
2. Hook-like hands with curved metacarpals and strong digit flexor muscles along the lower arm (flexor digitorum profundus and flexor digitorum superficialis) may represent additional evolutionary novelties of the clade (see Geissmann 2003; Fleagle 2013).

### 2.2.2.2.2. Hominidae (great apes and humans)

The taxon name Hominidae was formerly used for humans and all extinct forms with presumed closer phylogenetic relation to our species than to any other living species. However, the current definition of Hominidae includes orangutans, gorillas, chimpanzees, humans, and the encompassed extinct relatives (see, e.g., Jurmain et al. 2008; Diogo and Wood 2012). Within this broader defined taxon Hominidae, one character (state), which arose in the catarrhine stem lineage, is in the process of disappearance: ischial callosities may be present in about 40 % of the chimpanzees; they are even less frequent in the other two great ape genera and absent in humans (Vilensky 1978). Besides unequivocal molecular evidence (e.g., Lebedev et al. 2000), there are several anatomical traits in support of monophyletic Hominidae:

1. The living great ape species build night and day nests for sleeping and resting, mostly in trees but also on the ground. These nests are usually made of foliated twigs and used for only a single night/day (e.g., Napier and Napier 1967; Fleagle 2013). Although the construction of nests does not belong to the regular human habits, it is very probable that the hominid LCA built nests.
2. Character state distribution in living primates suggests that the hominid LCA had an increased density of eccrine glands over body surface and a reduced hair density on the back. Moreover, it seems to be an evolutionary novelty of hominids that females develop mammarys latest from first pregnancy on (Shoshani et al. 1996).
3. In hominoids, the latissimus dorsi muscle usually extends from the upper arms to the alae of the ilia. In non-hominoid primates, this broadest muscle of the back lacks a pars iliaca and thus does not reach the pelvic girdle (Ruge 1922). The caudal extension of the muscle in living hominids could reflect a more upright orientation of the hominid LCA during quadrupedal locomotion. However, phylogenetic interpretation of the character state should be taken with care as the data available in the twentieth of the previous century were scarce. Moreover, posterior extension of the latissimus dorsi is not postulated for the hominid stem lineage in a more recent phylogenetic analysis of primate muscle traits (Diogo and Wood 2012).
4. A very broad ilium and a robust fibula may represent additional evolutionary novelties of Hominidae (Fleagle 2013). The same is true for the broad articulate surface of the humerus with the ulna (trochlea humeri) (Shoshani et al. 1996). These three character states might again reflect a more upright position of the trunk during quadrupedal walking. Robust fibula and broad articulation of humerus and ulna could additionally be adaptations in the context of increasing body size.
5. Males of the great ape species have paired laryngeal sacs that function as resonance chambers for vocalization and

chest beating (Storch et al. 2013). Although the detailed shape of these structures and their diverticula differs between the great ape species (see, e.g., Dixon 2009), they could have a common origin in the stem lineage of Hominidae. If true, laryngeal sacs got secondarily lost on the human stem lineage.

#### 2.2.2.2.2.1. *Pongo* (orangutans; contains the same living species as Ponginae)

Currently, two living species are distinguished, i.e., the Sumatran (*Pongo abelii*) and the Bornean orangutan (*Pongo pygmaeus*) (e.g., Fleagle 2013). Both species show pronounced sexual dimorphism of cranial morphology and body weight with male and female weights in the range of 80 and 36 kg, respectively (Lindenfors 2002; Banes et al. 2015). Orangutans mainly live in trees where they move by brachiation, climbing, quadrupedal walking on branches, and suspensory locomotion. When on the ground, they preferentially move quadrupedally on inverted, clenched feet and clenched fists (fist-walking) (Napier and Napier 1967; Martin 1990). Most of the evolutionary novelties distinguishing orangutans refer to the male phenotype and to the mating system:

1. Dominant males develop cheek flanges, chin beard, and throat sac as secondary sexual traits (Winkler 1989; Martin 1990). The throat sac provides resonance to the advertising calls of these physiologically and socially mature owners of a territory. The territory overlaps with the smaller home ranges of several females (with immature young) and additionally may show some overlap with other males' territories (e.g., Singleton and van Schaik 2002; Banes et al. 2015). Moreover, there are subdominant males that are similar to females in size and facial morphology and reach sexual maturity typically by the age of 14 years. Although females preferentially mate dominant males, it also occurs that subdominant males sire offspring (e.g., Banes et al. 2015). This two-level system of maturity (bimaturism) and the specific facial morphology of dominant males probably evolved in the stem lineage of the living *Pongo* representatives.
2. In association with a grossly reduced function, the hallux is reduced in size and usually lacks a nail (Napier and Napier 1967). Moreover, the great toe has a backward-shifted position alongside the foot (Storch et al. 2013).
3. The central upper incisors ( $I^1$ ) are greatly enlarged relative to the lateral upper incisors ( $I^2$ ). This condition might have evolved from either somewhat enlarged central upper incisors or from a state of about equally sized upper incisors (Shoshani et al. 1996; Fleagle 2013).

4. Orangutans are further characterized by advanced convergence of the eyes and, as a consequence, also by a narrowed interorbital region (Storch et al. 2013).

#### 2.2.2.2.2. Homininae (African great apes and humans)

The phylogenetic relationships inside the clade were a matter of intense debate but, meanwhile, can be regarded as being settled: humans and chimpanzees are closer related to each other than each of them to gorillas (e.g., Pollock and Mullin 1987; Lebedev et al. 2000; Abdel-Halim et al. 2003). Deviating topologies in analyses of single genes may at least partially reflect incomplete lineage sorting of ancestral polymorphisms (Rogers and Gibbs 2014). The LCA of Homininae quite certainly showed a general preference for terrestrial living and quadrupedality. Thereby, his hands might have touched the ground with the second phalange of digits III and IV (knuckle-walking). In support of this hypothesis, the living representatives of the clade possess specifically shaped proximal carpal bones that enable a stable lock of the distal carpals (conjunct rotation) in knuckle-walking gorillas and chimpanzees (Groves 1988; Shoshani et al. 1996). Moreover, the shape of the distal radius of extinct representatives such as *Australopithecus anamensis* and *Australopithecus afarensis* reminds of extant knuckle-walkers (Richmond and Strait 2000). Yet, when gracile australopithecines that are doubtlessly more closely related to humans than to any other living species (e.g., Storch et al. 2013) were knuckle-walkers, then the LCA of Homininae was certainly, too. According to this scenario, gorillas and chimpanzees retained the trait which got lost on the lineage to humans in the context of emerging bipedalism (see, e.g., Groves 1988; Fleagle 2013). Since this view is not shared by all investigators (see Kivell and Schmitt 2009 and Lovejoy and McCollum 2010), I do not subsume knuckle-walking under the evolutionary novelties of the clade. Nonetheless, the monophyly of Homininae is well documented by several evolutionary novelties:

1. The frenulum of tongue is well developed in gorillas, chimpanzees, and humans while it is absent or poorly developed in other primate species (Groves 1988; Shoshani et al. 1996). Presence of a well-defined frenulum coincides with a muscular tongue that has an active role in chewing (Groves 1988). Another evolutionary novelty of the clade, frontal sinuses (Shoshani et al. 1996), together with the brow ridges, may provide a buttressing mechanism for masticatory action (Groves 1988).

2. Representatives of Homininae have at least on one side of the face a distinct, modern human-like, risorius muscle. Contraction of the muscle, which runs from the fascia covering the parotid gland to the angle of the mouth, produces an “insincere-looking” smile. The muscle might also exist in single hylobatid and orangutan specimens but is usually lacking in these taxa (Diogo and Wood 2012). The increased frequency of the muscle in Homininae could point to a raised importance of gestures in communication. Indeed, gorillas, chimpanzees, and humans share a variety of quite elaborated facial gestures such as frown, smile, nervous lip-tuck, tongue extrusion during concentration, and yawning under stress (Groves 1988).
3. The parotid gland, a salivary gland, is freed from the sternomastoid muscle while it overlies this muscle in other primates (Shoshani et al. 1996).
4. In Homininae, apocrine glands are largely replaced over most of the body surface by eccrine glands (Groves 1988). This character state suggests a generally enhanced relevance of transpiration-mediated thermoregulation in Homininae. Another aspect of the specific thermoregulation in Homininae is that their scalps are more densely haired than the rest of the head and body, thus providing a shield against insolation (Groves 1988).
5. Character state distribution amongst the living representatives suggests that the LCA of Homininae had complex, well-developed axillary organs (Shoshani et al. 1996; Gibbs et al. 2002). Indeed, well-developed axillary organs exist in all representatives of Homininae while they are at best vestigial in orangutans and seemingly absent in other primates (Groves 1988; Shoshani et al. 1996; Gibbs et al. 2002). The stronger development of axillary organs in the stem lineage of Homininae obviously correlated with the loss of a sternal gland (Groves 1988; Gibbs et al. 2002). The postulated change in the suite of glands involved in communication could reflect changes in the social organization in the stem lineage of Homininae (Groves 1988).
6. Dorsal transverse ridges on the metacarpal heads seem to be another novelty of Homininae. According to this scenario, the absence of such ridges in other (living) primates represents the plesiomorphic condition (Shoshani et al. 1996).
7. Adults usually have eight instead nine carpals due to an early centrale-scaphoideum fusion (Shoshani et al. 1996). The resulting reduction in the number of carpal bones has been suggested to have a stabilizing effect during knuckle-walking. However, the functional significance of the trait is actually elusive (Kivell and Begun 2007). Notably, fusion of centrale and scaphoideum also occurs in diverse other primate species (Kivell and Begun 2007). Yet, the evolutionary novelty in Homininae refers to the early timing of the event, rather than to the event as such (Martin 1990; see also Hominoidea).

8. An elongated small intestine could be another evolutionary novelty of Homininae, potentially reflecting a shift in dietary composition (Groves 1988; Shoshani et al. 1996). Such cross-taxa comparisons ideally take into account that the dimensions of the digestive tract can vary within species depending on the diet (Martin et al. 1985).

#### 2.2.2.2.2.1. *Gorilla* (gorillas)

At least two gorilla species thrive through the rain forests of Central and Western Africa: the Western gorilla populations can be subsumed under *Gorilla gorilla* and the Eastern under *Gorilla beringei* (Storch et al. 2013). Gorillas are highly sexually dimorphic, with male and female weights reaching about 175 and 98 kg, respectively (Lindenfors 2002). Single males may even reach 260 kg in wilderness (Storch et al. 2013). The harems of these uni-male breeders usually include a single dominant male, the silverback, and several females plus immature youngsters (Martin 1990). Multi-male groups also have been observed, especially in the mountain gorilla. As far as data were collected for such groups, it was reported that the males were close relatives and that second-ranked males sired offspring as well (Groves 1988; Fleagle 2013). Silverbacks not only display themselves by beating the fists onto the chest, but also impress by their “pungent, choking axillary odour, and powerful and frequent vocalizations” (c.f., Groves 1988). The following potential apomorphies listed below essentially refer to the specific morphology of males:

1. The cranium of silverbacks displays strongly developed sagittal and nuchal crests that provide abutment and lever for the strongly developed temporal and nuchal muscles. The mere presence of such crests is presumably not evolutionary new to gorillas as both traits also occur in male orangutans and chimpanzees (e.g., Geissmann 2003). However, fully developed crests are larger in male gorillas than in males of the other two species—also in relation to the cranium. Thus, at least, the enlargement of sagittal and nuchal crests could be evolutionary new to gorillas. Either presence or the dimension of a pad of fibrous adipose tissue on top of the head of silverbacks might represent another evolutionary novelty of the gorilla clade. Crests and fat pad let the head appear larger which is obviously attractive to females as documented by positive associations of male head contour size and copulation frequency. Remarkably, the specific male features also correlate with higher survival rates of offspring (Breuer et al. 2012).
2. The abdominal head of the pectoralis major muscle usually, at least partially, attaches to the coracoid process of

the scapula in gorillas. This derived feature differs from the ancestral state prevailing in other primates, flying lemurs, etc. where the muscle (including its abdominal head) mainly inserts onto the proximal region of the humerus and not on the coracoid process (Diogo and Wood 2012).

#### 2.2.2.2.2.2. *Pan* + *Homo*

The clade has occasionally been referred to as Hominina (Abdel-Halim et al. 2003). Others used the term Hominini for the grouping of chimpanzees and humans (e.g., Shoshani et al. 1996; Diogo and Wood 2012). Herein, in analogy to others, I employ the taxon name Hominini for humans and all those extinct representatives with closer phylogenetic relation to our species than to any other living species (e.g., Fleagle 2013; Storch et al. 2013). The LCA of chimpanzees and humans lived about 6.6 mya (e.g., timetree.org) and probably showed the following novelties:

1. Coordinate hunting by several, mostly male, individuals occurs in both chimpanzee species (Groves 1988; Martin 1990; Surbeck and Hohmann 2008; Fleagle 2013; Storch et al. 2013). Since such behavior is well known for humans, it can also be assumed for the LCA of the clade. This behavioral novelty implies a shift from a more vegetarian toward a more omnivorous diet. Killing of congeners belonging to other clans for defending or expanding the own group’s territory (Groves 1988; Martin 1990; Fleagle 2013; Storch et al. 2013) may also have been a behavioral characteristic of the LCA of humans and chimpanzees.
2. The species of the clade are distinguished from other primates by an earlier fusion of the paired to an unpaired premaxillary bone, in which the incisors are lodged. Disregarding individual differences, the period of closure of the premaxillary suture might be summarized best as follows: obliteration regularly begins prior to birth; complete obliteration of the suture at its palatinate side may occasionally postdate completion of permanent dentition (translated from German after Ashley-Montagu 1935 who referred to Remane; see also Shoshani et al. 1996). Closure of the premaxillary suture together with the premaxillary-maxillary fusion gives rise to a continuous upper jaw (Mooney and Siegel 1986).
3. In association with a high rate of sexual activity, the penis when erect is lengthened to over 80 mm while the baculum is shortened in chimpanzees and lost in humans (Groves 1988; Shoshani et al. 1996). Given this character state distribution, it is very likely that the clades’ LCA

possessed a lengthened erect penis and a shortened baculum.

4. As mentioned earlier, there is a general tendency for delayed puberty on the lineage to humans. Thus, it is not surprising that the trend also manifests itself in the stem lineage of humans and chimpanzees: puberty further delayed, reached at >7 years (Groves 1988; Shoshani et al. 1996).
5. The styloglossus muscle which originates from the styloid process and from the stylo-mandibular ligament not only runs anteriorly to the tongue but additionally has a distinct smaller portion that extends antero-inferiorly to the hyoglossus muscle. The absence of such an oblique slip represents the plesiomorphic condition (Diogo and Wood 2012).
6. The obturator groove on the medial surface of the ilio-pubis junction at the proximal or dorsal area of the obturator foramen is deepened and well delineated. The presumably plesiomorphic state of a shallow obturator groove has been retained in gorillas and orangutans (Shoshani et al. 1996).
7. Loss of the dorsalis pollicis muscle, origin of the flexor digitorum brevis muscle from plantar aponeurosis, attachment of the lateral head of the triceps brachii muscle to the lateral intermuscular septum, and origin of the posterior interosseous artery from common interosseous artery may represent additional apomorphies of the *Pan + Homo* clade (Gibbs et al. 2002).

#### 2.2.2.2.2.2.1. *Pan* (chimpanzees)

While the common chimpanzee, *Pan troglodytes*, lives in very variable habitats ranging from rain forests to dry savannahs of Central to Western Africa, the pygmy chimpanzee, *Pan paniscus*, prefers the rain forests of Central Africa (Rogers and Gibbs 2014). The supposedly four subspecies of the common chimpanzee differ considerably in size with male weights in the range of 43 to 60 kg and female weights in the range of 34 to 46 kg (Fleagle 2013). The pygmy chimpanzee or bonobo also shows moderate sexual dimorphism in respect to body weight with males and females weighing approximately 45 and 33 kg, respectively (Lindenfors 2002). Both chimpanzee species live in multilayered societies characterized by varying degrees of spatial and temporal cohesion (Aureli et al. 2008). Remarkably few evolutionary novelties substantiate the monophyly of the clade (Groves 1988):

1. Female chimpanzees signalize receptiveness by exaggerated sexual swellings that are largest around estrous (Groves 1988; Nunn 1999). Since less developed sexual swellings also occur in other primates (Groves 1988;

Fleagle 2013) the “novelty” of the chimpanzee condition is the extent of the swellings rather than their mere presence. Huge sexual swellings evolved at least three times independently in primates (Nunn 1999; see also Colobinae).

2. For hominoid relations, chimpanzee testes are enlarged relative to body weight. This feature reflects high female promiscuity and enhanced sperm competition in chimpanzees as compared to other hominoids (e.g., Harcourt et al. 1981; Shoshani et al. 1996; Dixson 2009).

#### 2.2.2.2.2.2.2. *Homo sapiens* (modern humans, humans of modern aspect, anatomically modern *Homo sapiens*)

All aforementioned statements involving humans actually referred to the anatomically modern *Homo sapiens* (AMHSA). The earliest fossil finds of the AMHSA come from Ethiopia, namely from deposits in the Omo River region that have been estimated to be about 195,000 years old (Jurmain et al. 2008). Other authors regard Ethiopian fossils excavated from about 160,000-year-old deposits at Herto as the oldest definite examples of modern humans (Stringer and Andrews 2005). Irrespective of the detailed timing of the origin, modern humans are highly opportunistic in manifold regards and meanwhile spread over the entire globe (e.g., Fleagle 2013). Moderate sexual dimorphism might reflect a certain incline to polygyny, but monogamous and other mating systems also exist (Fleagle 2013; Feldhamer et al. 2014). It should be noted that the character states summarized below represent apomorphies of the AMHSA in comparison with other living species. Yet, when extinct representatives of Hominini would be included, part of the evolutionary changes would characterize more comprehensive assemblies including our species and at least some of the extinct forms. For reasons of space limitations, the apomorphies of modern humans are summarized in a very compact manner:

1. Cranio-dental traits: The AMHSA has an increased brain case, reduced supra-orbital ridges, jutting instead of fleeing chin, narrow (approaching vertical) angle between mandibular symphysis and rami of mandible, shortened visceral cranium (orthognathy), parabolic and closed dental arch (not u-shape and no diastema, anymore), canines with reduced crown, and molars with very thick enamel. Forward displacement of the foramen magnum under the skull (balanced head in upright position) leads over to the post-cranial peculiarities of our species (combined from Groves 1988; Martin 1990; Shoshani et al. 1996; Geissmann 2003; Jurmain et al. 2008; Schmidt 2010; Fleagle 2013; Storch et al. 2013).

2. The post-cranial skeleton of the AMHSA is characterized by obligate bipedalism with emphasize on running rather than walking, and the anatomical changes involved: full extension of elongated upper and lower leg with the femur and tibia being in alignment (effective striding), shortened pedal phalanges, hallux realigned with other toes and not opposable (final propulsive thrust during striding by the terminal phalanx), transverse arch of the foot supplemented by a longitudinal arch between the heel of the calcaneus and the metatarsal heads (shock absorption), shift of the acetabulum from a more lateral position to under the pelvis (relieves the hip joint in upright position), further broadened ala of the ilium (support of the inner organs in upright position), physiological X- instead of O-position of the knees (stabilizes the body in the one-leg-phase of walking), enlarged gluteus maximus muscle (erection of the trunk relative to the legs), double S-shape of the spine column (shock absorption), inward relocation of the spine column relative to the ribcage (closer alignment of the spine column and line of action), etc. The hands are free with specifically shaped scapho-trapezio-trapezoid joint and carpometacarpal joint I that together entail a highly mobile thumb (extreme opposability). A specifically shaped hyoid bone coincides with the emergence of speech (see below for more changes relating to speech). For whatever reason, the baculum is completely reduced (combined from Napier and Napier 1967; Groves 1988; Arensburg et al. 1989; Martin 1990; Bramble and Lieberman 2004; Tocheri et al. 2005; Harcourt-Smith 2007; Dixson 2009; Fleagle 2013; Storch et al. 2013).
3. Soft tissue: High density of eccrine glands and reduction of a fur (not of hair itself) on the body enable effective transpiration (Groves 1988; Schmidt 2010). This and the anatomical changes relating to biped gait (see above) allow for enduring running at slow speed without getting overheated. Endurance running is perhaps the only physical capability in which humans outcompete every other living terrestrial species (Bramble and Lieberman 2004). Nevertheless, humans are also capable of short fast sprints with up to 45 km/h (Storch et al. 2013). The AMHSA is also distinguished by the largest penis within living primates, and female mammarys are further augmented (Groves 1988; Schmidt 2010). The latter two character states lead to features with some variation in the AMHSA. For instance, humans usually do not have a levator claviculae muscle (Diogo and Wood 2012); nonetheless, the muscle occurs in 2–3 % of the individuals (Rubinstein et al. 1999), albeit sometimes only on one side (Fazliogullari et al. 2010). Human brain size also varies between individuals but is generally increased, absolute (average 1.300 cm<sup>3</sup>) and in relation to body weight, when compared to non-human primates (Martin 1990; Jurmain et al. 2008; Feldhamer et al. 2014). This is especially true with respect to the neocortex (surface area 2430 cm<sup>2</sup>) and the prefrontal association areas (Rapoport 1990). The enlarged brain associates with the elaboration of language and the acquisition of speech, which again coincides with a specifically shaped hyoid (see above) and a downward shifted larynx and epiglottis (Stringer and Andrews 2005). This all stands for generally improved intellectual abilities (e.g., Martin 1990; Storch et al. 2013) that fostered and still foster the cultural “evolution” of our species. Additional evolutionary changes that occurred on the branch to modern humans are included in Diogo and Wood (2012).
4. Life history: The AMHSA is distinguished from other living primates by a change in female life history, namely a markedly longer postmenopause (comp. Cebinae inside Cebidae). With this novelty, grandmothers became an important factor in child care (Hawkes et al. 1998; Storch et al. 2013). Irrespective of the sex, prolongation of senescence and its implication on society seem to be a major cause of the success of our species (Caspari and Lee 2004).
5. Molecular changes: As to be expected, the highly derived phenotype of our species is reflected by manifold changes at the molecular level. For example, humans (AMHSA) are distinguished by a pseudogenized *MYH16* gene. The pseudogenization led to a smaller temporal muscle which, in turn, might have relaxed constraint on the brain case’s function as an abutment for this chewing muscle. This again might have opened the avenue for an enlargement of the brain case, a prerequisite for housing a larger brain (Stedman et al. 2004).

## Conclusions

While the primate tree behind the above phylogenetic system seems to be well established, the one or other aspect relating to an evolutionary change might be refuted by future research. I am aware of this restraint and do not claim to present an ultimate but rather an updated scenario of character evolution in primates. It should also be noted that additional, mostly subtle, apomorphies can be extracted from published data (e.g., Wible and Covert 1987; Dagosto 1988; Shoshani et al. 1996; Gibbs et al. 2002; Diogo and Wood 2011, 2012). Last but not least, the phenomenon polymorphism deserves some more attention. The more specimens are investigated for single species, the more characters turn out to be polymorphic (see “usual,” “mostly,” etc. in the above compilation). These polymorphisms involve soft tissue as demonstrated by the presence/absence of the levator claviculae muscle in humans (see Rubinstein et al. 1999; Fazliogullari et al. 2010; Diogo and Wood 2012) and hard tissue as exemplified by different

numbers of conchae, thoracic, sacral, and caudal vertebrae in gorillas, chimpanzees, and humans (see, e.g., Grünwald 1917; Geissmann 2003; Lovejoy and McCollum 2010). The picture is further complicated by individuals showing alternative character states at a time as it is the case with the one-sided presence of the levator claviculae and risorius muscle in some humans and chimpanzees, respectively (Fazliogullari et al. 2010; Diogo and Wood 2012). Still, other character states may change during development as it is the case with the fusion of the two carpal bones, scaphoideum and centrale, in diverse primate taxa, to name only one example (Kivell and Begun 2007). Physiological and behavioral traits are certainly even more variable between and within individuals. These considerations illustrate that clear-cut transitions from one character state to the other might have occurred less frequently in primate evolution than currently recognized. We might indeed come closer to reality when we accept shifts in phenotype frequency as an extra class of evolutionary novelty besides considering complete displacements of one character state by another. What might appear disturbing at the first sight can hardly be surprising since part of the phenotypic variation will be selectively neutral. In other cases, some character state might be slightly detrimental but will be compensated by advantageous traits of the same individual. In again other cases, disadvantageous character states will only lead to less and not necessarily zero offspring (Harris 2010). Along with comparably short evolutionary timescales, these factors could explain why a row of polymorphisms persisted along diverse internal branches of the primate tree.

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