

1 General Introduction

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Colobinae, which includes more than 70 species grouped into 10 genera distributed throughout Asia and Africa, show a wide range of ecological and social traits. The colobines are generally forest-living and arboreal, which can make research on this often-elusive group difficult. Despite these challenges, our understanding of colobine behaviour, ecology and morphology has increased a great deal over the decades since the first research review on this primate subfamily was published by Davies and Oates (1994). While new research has demonstrated the incredible variation of colobine natural history, and the adaptability of this group, some colobine populations have declined and are now critically endangered. *The Colobines* brings together experts from around the world in an innovative volume that summarizes the current knowledge on colobine populations. It highlights areas where knowledge is lacking and stresses the importance of this information for conservation. The book is an edited volume with 22 chapters that examine the biological, ecological and societal traits of colobines.

The first section of the book overviews the taxonomy and phylogeny of extant and fossil colobines. The number of species has increased from the 24 that were recognized in the late 1960s to 80 at the present time, due to the elevation of various subspecies to the species level and additions of entirely new species, such as the black snub-nosed monkey (*Rhinopithecus strykeri*) discovered in north-eastern Myanmar in 2010 or the Popa langur (*Trachypithecus popa*) from central Myanmar in 2020 (Chapters 2 and 4). Recent developments in molecular genetics also contribute to expanded taxonomic and phylogenetic classifications. New species have been discovered not only in extant colobines but also in fossil colobines, with the greatest increase in the colobine fossil record in the Late Miocene of Africa (Chapter 3) since the previous 1994 review (Davies and Oates 1994).

The book's second part focuses on colobine anatomy and physiology. Chapter 5 discusses recent studies on the effect of food variability and food physical properties on dental function, especially in Asian colobines. The distinct digestive features of colobines (i.e. foregut fermentation) differ from other primate groups (i.e. hindgut fermentation). There are new developments in our understanding of colobine digestion, including a 'rumination' strategy in proboscis monkeys (*Nasalis larvatus*), the first documented among primate species (Chapter 6). Although there has not been much progress in terms of clarifying their anatomical and physiological attributes, there has been a dramatic increase in the number of colobus species whose diet and nutrient intake have been studied, as well as numerous advances in colobus

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nutrition research (Chapter 8). Notably, technological innovations in genetic analysis (e.g. next-generation sequencing) now allow us to collect detailed genetic information on gastrointestinal microbiota genomes (Chapter 7), which were not described in the previous colobine review in 1994.

The third section documents and summarizes the ecology and behaviour (distribution, habitat, climate, diet, activity patterns, range use, predation, social system and reproduction) of all colobine lineages (Chapters 9–15). Colobines have traditionally been believed to live without food competition or social stratification within or between groups; however, this presumption was largely based on the notion that these species exploit ubiquitous food sources, such as leaves. Recent studies have reported high levels of fruit and/or seed consumption in response to variation in local environmental conditions and have revealed that even leaves vary in their quality and distribution. Many colobines are subject to scramble and contest competition for food; thus, previous assumptions about food competition and its effects on social relationships in folivores are incorrect for most colobine populations. This indicates that an update of how colobines fit into socioecological models is necessary (Chapters 16 and 17). In addition, recent colobine socioecological studies have provided new findings on the complex spatio-temporal social dynamics (i.e. multi-level societies) seen in some species, such as snub-nosed monkeys (*Rhinopithecus* spp.), which were not discussed in the first colobine review (Chapter 18). Based on this accumulated information, competition for food resources, predation, disease and factors affecting population dynamics have been reviewed (Chapter 19).

The final section of the book discusses the fact that an increasing number of colobine species face extinction both in Asia (Chapter 20) and in Africa (Chapter 21) mainly through forest loss and hunting. The detailed information provided on colobine conservation may help prioritize and focus future conservation initiatives.

The aim of this work is to deliver a comprehensive overview of the current research on colobine populations, highlight areas where our knowledge is still lacking and present the current status of colobine populations, emphasizing their conservation importance and exploring the nature of threats to their future survival. We hope that this book will become a ‘go-to’ resource for primate researchers and students and believe that it will provide a departure point from which biological, ecological and societal studies and future conservation efforts can spring. *The Colobines* sets the stage for a new wave of research on colobines in areas where our understanding is just beginning.

2 Taxonomic Classification of Colobine Monkeys

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Introduction

Colobine or leaf-eating monkeys are a species-rich group of Old World primates with extant species mainly found in the tropical belt of Africa and throughout most of South and Southeast Asia. Today, 10 genera, 80 species and 125 taxa (species and subspecies) are recognized (following Mittermeier et al. 2013; Rowe & Myers 2016; Roos et al. 2020; for a full list of colobine taxa, see ESM, Appendix 2.1). However, the classification of colobine monkeys has changed considerably over the decades, mainly concerning the number of taxa recognized (genera, species), but also concerning the genus, species group and species affiliation of certain taxa. The number of genera has increased from 6 recognized in 1976 to 10 in 2013/2016. Part of this is due to a recent emphasis on the use of time since divergence to differentiate taxa above the species level, as opposed to the traditional method of using morphological differentiation. The number of species has increased even more drastically; from 24 recognized in 1967 (Napier and Napier 1967) to 80 in 2020 (Mittermeier et al. 2013; Rowe & Myers 2016; Roos et al. 2020). This is partially due to the description of new species, e.g. *Rhinopithecus strykeri* or *Trachypithecus popa*, but mainly due to the elevation of various subspecies to species level as a result of adopting the Phylogenetic Species Concept (PSC; Cracraft 1983; for a detailed discussion about species concepts, their pros and cons and their applicability, see Groves 2012; Groves et al. 2017) and by applying molecular genetics. Comprehensive genetic data from colobines, however, are still rare and exist only for a few taxa, but available information provides nonetheless important insights into colobine phylogeny (see Chapter 4) and for instance, led to the taxonomic reassignment of several taxa; e.g. Nilgiri and purple-faced langurs are today recognized as species of *Semnopithecus* instead of *Trachypithecus* (Karanth et al. 2008; Mittermeier et al. 2013; Osterholz et al. 2008; Rowe and Myers 2016; Zhang and Ryder 1998).

In this chapter, I give an overview of the taxonomic classification of colobine monkeys. I follow the taxonomy proposed by Mittermeier et al. (2013) and Rowe and Myers (2016) and discuss taxonomic changes mainly since the seminal work by Napier and Napier (1967) and studies thereafter. Generally, taxonomy is a dynamic science and species delimitations should be regarded as taxonomic hypotheses. The taxonomy of colobines is still under debate and no overall accepted taxonomy is available, which is also reflected by the diverging opinions among the contributors of

This chapter includes Electronic Supplementary Material (ESM) at: www.cambridge.org/colobines

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this book. Part of this debate is due to a lack of ecological, behavioural and genetic data for many colobine species, which has led to classifications largely based on phenotypical differences determined from museum specimens. But an important component is also a general lack of agreement among systematists regarding taxonomic philosophy and how classifications should be generated. The Mittermeier et al. (2013) and Rowe and Myers (2016) classifications generally follow a time-based classification at the genus level and the PSC at the species level, although some exceptions exist where there is a lack of data and/or consensus. Consequently, more work is needed to increase knowledge about colobine diversity and to come to an agreement on taxonomic philosophy towards categorizing this diversity in order to establish a refined and broadly acceptable colobine taxonomy.

Colobine Monkeys

Colobine or leaf-eating monkeys constitute the primate subfamily Colobinae. Together with their sister clade, the cheek-pouched monkeys (subfamily Cercopitheciinae), they form the Catarrhini family of Cercopithecidae (Old World monkeys) (Davies and Oates 1994; Groves 2001; Mittermeier et al. 2013; Rowe 1996; Rowe and Myers 2016). African and Asian colobines are traditionally regarded as reciprocally monophyletic clusters (Davies and Oates 1994; Groves 2001; Napier 1970) and sometimes classified as subtribes based on morphology, the African Colobina and the Asian Semnopithecina (Szalay and Delson 1979) or Presbytina (Delson 1975; note: Presbytina has priority), or as tribes based on temporal divergence (Colobini, Presbytini) (Mittermeier et al. 2013; Perelman et al. 2011; Rowe and Myers 2016). However, the reciprocal monophyly of African and Asian colobines was repeatedly questioned. Groves (1989) suggested *Nasalis* (with *Simias* as subgenus) as sister group to all other colobines and classified them as Nasalinae as opposite to Colobinae; both together formed the family of Colobidae. In contrast, Jablonski (1998a) suggested *Procolobus* as sister lineage to all other colobines, while Roos et al. (2011), based on retroposon integrations, found *Colobus* in this position. However, mitochondrial and nuclear sequence data support reciprocal monophyly of African and Asian clades (Finstermeier et al. 2013; Perelman et al. 2011; Pozzi et al. 2014; Roos et al. 2011; Sterner et al. 2006; Springer et al. 2012; Ting et al. 2008; Wang et al. 2012). Here, I recognize African and Asian colobine groups as reciprocal monophyletic clades and classify them as tribes, Colobini and Presbytini, as they separated roughly at the same time, ca. 12 million years ago, as did the two Cercopitheciinae tribes, Papionini and Cercopithecini (Finstermeier et al. 2013; Perelman et al. 2011; Pozzi et al. 2014; Springer et al. 2012).

African Colobines

Following Mittermeier et al. (2013) and Rowe and Myers (2016), African colobines are grouped into three genera with a total of 23 species. The three genera refer to black-and-white colobus (genus *Colobus*), olive colobus (genus *Procolobus*), and red

colobus (genus *Piliocolobus*) (Groves 2001; Mittermeier et al. 2013; Rowe and Myers 2016). However, in the past these three genera were combined into either a single genus (*Colobus*) with three subgenera (Napier and Napier 1967) or into two genera, *Colobus* and *Procolobus*, with either the former (Napier and Napier 1985) or the latter containing *Piliocolobus* as a subgenus (Brandon-Jones 1984a; Davies and Oates 1994; Groves 1989; Grubb et al. 2003; Kuhn 1967; Rowe 1996; Strasser and Delson 1987). Genetic data confirm a sister group relationship between *Procolobus* and *Piliocolobus*, and show that the three major lineages diverged 6–10 million years ago (Finstermeier et al. 2013; Perelman et al. 2011; Pozzi et al. 2014; Roos et al. 2011; Springer et al. 2012; Ting 2008a).

Black-and-white colobus, genus *Colobus*, are distributed across equatorial Africa. In earlier times, only one (*guereza*; e.g. Schwarz 1929) or two species (*guereza*, *polykomos*; e.g. Napier and Napier 1967) were recognized, but nowadays there is consensus that *Colobus* contains (four to) five species (Dandelot 1971; Davies and Oates 1994; Groves 2001; Groves et al. 1993; Mittermeier et al. 2013; Napier and Napier 1994; Oates and Trocco 1983; Rowe 1996; Rowe and Myers 2016). Two of them, the King colobus (*C. polykomos*) and the white-thighed colobus (*C. vellerosus*), are monotypic, while the black colobus (*C. satanas*) contains two subspecies, the Angolan colobus (*C. angolensis*) seven subspecies and the guereza (*C. guereza*) eight subspecies (Mittermeier et al. 2013; Rowe and Myers 2016). It should be noted that the PSC has not been fully applied to this group, and that at least some of the *Colobus* subspecies could be elevated to species status upon re-evaluation of their diversity.

The genus *Procolobus* is monotypic and contains only the olive colobus, *P. verus* (Davies and Oates 1994; Groves 2001; Grubb et al. 2003; Mittermeier et al. 2013; Napier 1985; Napier and Napier 1967, 1994; Rowe 1996; Rowe and Myers 2016). The species has a disjunct distribution in western Africa, but there is no evidence for any subspecific variation (Davies and Oates 1994).

Red colobus monkeys, genus *Piliocolobus*, have a wide, but patchy distribution from Senegal in West Africa across the continent to Zanzibar in the East. The taxonomy of red colobus monkeys is debated and various classifications with different numbers of species and varying taxon assemblies were proposed. While Rahm (1970), followed by Davies and Oates (1994), lumped all taxa in the single species *badius*, Napier (1985) and Napier and Napier (1967, 1994) recognized two species, *kirkii* and *badius*. Delson et al. (1982), Groves (1993) and Rowe (1996) listed four species (*badius*, *pennantii*, *preussi*, *rufomitratatus*), Oates (1986, 1996a) five species (*badius*, *gordonorum*, *kirkii*, *pennantii*, *rufomitratatus*), Dandelot (1971) split red colobus monkeys into eight species (*badius*, *elliotti*, *kirkii*, *pennantii*, *preussi*, *rufomitratatus*, *tholloni*, *waldronae*), and Groves (2001) into nine species (*badius*, *foai*, *gordonorum*, *kirkii*, *pennantii*, *preussi*, *rufomitratatus*, *tephrosceles*, *tholloni*). Recently, a total of 17 taxa, all recognized as monotypic species (Upper Guinea red colobus, *P. badius*; Bouvier's red colobus, *P. bouvieri*; Niger Delta red colobus, *P. epieni*; Foa's red colobus, *P. foai*; Udzungwa red colobus, *P. gordonorum*; Zanzibar red colobus, *P. kirkii*; Lang's red colobus, *P. langi*; Oustalet's red colobus, *P. oustaleti*; Lomami red colobus, *P. parmentieri*; Pennant's red colobus, *P. pennantii*;

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Preuss's red colobus, *P. preussi*; Tana River red colobus, *P. rufomitratu*s; Semliki red colobus, *P. semlikiensis*; Temminck's red colobus, *P. temminckii*; ashy red colobus, *P. tephrosceles*; Tshuapa red colobus, *P. tholloni*; Miss Waldron's red colobus, *P. waldronae*), have been suggested (Mittermeier et al. 2013; Rowe and Myers 2016). The current classification is mainly based on investigations of museum specimens and limited data from the field. Much more work, including ecological, phenotypical, acoustic and genetic studies, is needed to better describe and understand diversity in red colobus monkeys. So far, only a single genetic study on intra-generic diversity in *Piliocolobus* has been published (Ting 2008a), which however, allows first intriguing insights into *Piliocolobus* phylogeny and suggests relatively deep splits among various taxa; the most recent common ancestor of the genus has been dated back to ca. 3 million years (Ting 2008a; see also Chapter 4).

Asian Colobines

Incorporating the recently proposed changes in *Trachypithecus* taxonomy (Roos et al. 2020), Asian colobines contain 57 species in seven genera. However, the classification of Asian colobines is in ongoing debate and needs further clarification. Although Groves (1989) suggested *Nasalis* (with *Simias* as subgenus) as a sister clade to all other colobines, a common ancestry of Asian colobines is generally accepted and confirmed by genetic data (Perelman et al. 2011; Pozzi et al. 2014; Roos et al. 2011; Springer et al. 2012; Sterner et al. 2006; Ting et al. 2008; Wang et al. 1997, 2012; Zhang and Ryder 1998). In most classifications, Asian colobines are divided into two groups, a langur group subsuming the genera *Presbytis*, *Trachypithecus* and *Semnopithecus*, and an odd-nosed monkey group with the genera *Rhinopithecus*, *Pygathrix*, *Nasalis* and *Simias* (Groves 2001; Mittermeier et al. 2013; Rowe 1996; Rowe and Myers 2016). Genetic data clearly confirm the monophyly of the odd-nosed monkey group, but not of the langur group (Finstermeier et al. 2013; Liedigk et al. 2012; Perelman et al. 2011; Pozzi et al. 2014; Roos et al. 2011; Springer et al. 2012; Sterner et al. 2006; Ting et al. 2008; Wang et al. 2012). In fact, mitochondrial and nuclear data revealed contradicting branching patterns among the three langur genera and the odd-nosed monkeys, and have been suggested to be the result of ancient hybridization events among the three langur genera (e.g. Roos et al. 2011; Ting et al. 2008; Wang et al. 2012; see also Chapter 4).

The genus-level classification of members of the (probably paraphyletic) langur group was one of the most controversial discussed topics in colobine taxonomy, but seems to be settled now. Today, most authorities recognize three genera, surilis (genus *Presbytis*), lutungs (genus *Trachypithecus*), and Indian langurs (genus *Semnopithecus*) (Brandon-Jones et al. 2004; Davies and Oates 1994; Groves 1989, 2001; Mittermeier et al. 2013; Roos et al. 2014; Rowe 1996; Rowe and Myers 2016), but in the past one to four genera were proposed. While Napier (1985) and Napier and Napier (1967, 1994) combined all taxa of the langur group into the single genus *Presbytis*, Hill (1934) and Pocock (1935, 1939) divided them into four genera (*Presbytis*, *Semnopithecus*, *Trachypithecus*, *Kasi*). Already Reichenbach (1862)

recognized these four groups, but classified them as subgenera of the genus *Semnopithecus*. Alternative classifications suggest two genera, *Presbytis* and *Semnopithecus*, with *Trachypithecus* as subgenus of the latter (Brandon-Jones 1984a, 1995a,b, 1996; Strasser and Delson 1987). Most recent classifications do not accept *Kasi* as a valid genus or subgenus, but Rowe (1996) maintained *Kasi* as a subgenus of *Trachypithecus*. In fact, genetic studies have shown that the two species of *Kasi*, the Nilgiri and purple-faced langur, are paraphyletic and nested within the *Semnopithecus* clade, and consequently should be assigned to this genus (Karanth et al. 2008; Osterholz et al. 2008; Zhang and Ryder 1998).

Compared to the langur group, the genus-level classification of the members of the odd-nosed monkey group was historically less problematic. Generally, it is accepted that the odd-nosed monkeys contain four clearly distinct lineages that are commonly recognized as distinct genera, snub-nosed monkeys (genus *Rhinopithecus*), doucs (genus *Pygathrix*), the proboscis monkey (genus *Nasalis*), and the simakobu (genus *Simias*) (Brandon-Jones et al. 2004; Groves 2001; Jablonski 1998a; Jablonski and Peng 1993; Mittermeier et al. 2013; Napier and Napier 1967, 1994; Rowe and Myers 2016). However, in the past *Rhinopithecus* was classified as a subgenus of *Pygathrix* (Brandon-Jones 1984a, 1996b; Davies and Oates 1994; Delson 1975; Groves 1970, 1989; Napier 1985; Rowe 1996). Likewise, *Simias* was proposed as subgenus of *Nasalis* (Brandon-Jones 1984a, 1996b; Delson 1975; Groves 1970, 1989; Rowe 1996). Genetic data suggest a close phylogenetic relationship between *Nasalis* and *Simias*, and a basal position of *Rhinopithecus* among odd-nosed monkeys (Liedigk et al. 2012; Roos et al. 2011; see also Chapter 4), thus rejecting a monophyletic *Rhinopithecus*-*Pygathrix* clade. Jablonski (1998a) and Jablonski and Peng (1993) further divided *Rhinopithecus* into two subgenera, *Presbyticus* with *R. avunculus* and *Rhinopithecus* subsuming all other snub-nosed monkey taxa, which, however, is not well accepted. Interestingly, *Simias* and *Nasalis* diverged relative recently, just 1–2 million years ago (Liedigk et al. 2012; Roos et al. 2011; see also Chapter 4). This is well in the range of temporal divergences typically found among species and consequently, both genera would need to be combined into a single genus when a time-based classification at the genus level is applied.

Langur Group

Surilis, genus *Presbytis* (*sensu stricto*), occur in the Sundaland region of Southeast Asia with main distributions on Sumatra, Borneo, Java, the Mentawai Islands and the Malay Peninsula. Napier and Napier (1967) divided surilis into five species, *aygula* (= *comata*), *frontata*, *melalophos*, *rubicunda* and *potenziani*, of which the former four were grouped into the *P. aygula* (= *comata*) group, referring to today's genus *Presbytis*, while *potenziani* was assigned to the *P. cristatus* group, which refers to today's genus *Trachypithecus*. Later on, Napier (1985) and Napier and Napier (1994) correctly assigned *potenziani* to what is now referred to as the *P. melalophos* group and recognized, following Groves (1970), a total of seven species, *melalophos*, *frontata*, *rubicunda*, *potenziani*, *comata*, *hosei* and *thomasi*. Davies and Oates

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(1994) and Rowe (1996) followed this classification, but Rowe (1996) in addition separated *femoralis* from *melalophos*. Brandon-Jones (1984a, 1995a, 1996b) recognized also seven species, but he used a different species assembly. He also accepted *frontata*, *potenziani* and *rubicunda* as distinct species, however, he divided the *melalophos* complex into three species, *melalophos*, *femoralis* and *siamensis*, and separated *fredericae* from *comata*, while he followed Napier and Napier (1967) by integrating *thomasi* and *hosei* into *comata*. Although there is now general consensus concerning the distinct species status of *comata*, *hosei*, *frontata*, *thomasi* and *potenziani*, there is ongoing debate about the taxonomy of the *melalophos* complex. Traditionally all taxa were combined into the single species *melalophos* (Chasen 1940; Davies and Oates 1994; Napier 1985; Napier and Napier 1967, 1994), but it was proposed to split them into two (Aimi and Bakar 1992, 1996; Pocock 1935; Rowe 1996; Wilson and Wilson 1977), three (Brandon-Jones 1984a, 1996b; Brandon-Jones et al. 2004), five (Groves 2001), or even eight species (Mittermeier et al. 2013; Roos et al. 2014; Rowe and Myers 2016). Recently, also the two subspecies of *potenziani* and the three subspecies of *hosei* were elevated to species (Mittermeier et al. 2013; Roos et al. 2014; Rowe and Myers 2016). Following the most recent classification (Mittermeier et al. 2013; Roos et al. 2014; Rowe and Myers 2016), the genus *Presbytis* comprises a total of 17 species. Twelve of them, the black-and-white langur (*P. bicolor*), Miller's grizzled langur (*P. canicrus*), white-fronted langur (*P. frontata*), Hose's langur (*P. hosei*), black-crested Sumatran langur (*P. melalophos*), mitred langur (*P. mitrata*), Natuna Islands langur (*P. natunae*), Pagai langur (*P. potenziani*), Sabah grizzled langur (*P. sabana*), Siberut langur (*P. siberu*), black Sumatran langur (*P. sumatrana*), and Thomas's langur (*P. thomasi*), are monotypic, while the cross-marked langur (*P. chrysomelas*) and Javan langur (*P. comata*) contain two subspecies each, the banded langur (*P. femoralis*) three subspecies, the pale-thighed langur (*P. siamensis*) four subspecies, and the maroon langur (*P. rubicunda*) five subspecies. The herein adopted classification of *Presbytis* is highly disputed and should be treated as preliminary, but it reflects best phylogenetic relationships among taxa (Md-Zain 2001; Md-Zain et al. 2008; Meyer et al. 2011; Vun et al. 2011; see also Chapter 4).

With 20 species currently recognized, the genus *Trachypithecus* is the most speciose among all Asian colobines. The genus is widely distributed on the mainland and Sundaland region of Southeast Asia, from Bhutan and Assam in the West, to Vietnam and Southern China in the East, and South to Java. Napier and Napier (1967) classified taxa of today's genus *Trachypithecus* as members of the *Presbytis cristatus* group and recognized a total of seven species, *cristatus*, *francoisi*, *geei*, *pileatus*, *obscurus*, *phayrei* and *potenziani*. One of these species, *potenziani*, was later correctly reallocated to the *P. aygula* (= *comata*) group (i.e. genus *Presbytis*) (Napier 1985; Napier and Napier 1994). Davies and Oates (1994) in principle followed this classification, but included also the two species of the *Presbytis senex* (= *vetulus*) group (Napier 1985; Napier and Napier 1967, 1994), *vetulus* and *johnii*, in *Trachypithecus*, and separated *T. auratus* from *T. cristatus* according to Weitzel and Groves (1985). Rowe (1996) adopted the classification of Davies and Oates (1994), but additionally

recognized *delacouri* as a full species. In contrast, Brandon-Jones (1984a, 1995b, 1996b) divided *Trachypithecus* (as subgenus of *Semnopithecus*) into 12 species, *vetulus*, *johnii*, *pileatus geei*, *cristatus*, *auratus*, *obscurus*, *barbei*, *francoisi*, *hatinhensis*, *laotum* and *delacouri*. Compared to other classification, he placed *phayrei* in *obscurus*, and recognized *barbei* as distinct species. Moreover, he separated the *francoisi* subspecies *delacouri*, *hatinhensis* and *laotum* from the nominate form, and reclassified *poliocephalus* as subspecies of the South Indian *johnii*. In 1992, he described a new taxon, *ebenus*, from northern Vietnam as subspecies of the Javan *auratus* (Brandon-Jones 1995b). Roos et al. (2007) subsequently reallocated *ebenus* to the *francoisi* complex and recognized four species within the group, *francoisi*, *poliocephalus* (including *leucocephalus*), *delacouri*, and *laotum* (with *hatinhensis* as subspecies and *ebenus* as synonym of *hatinhensis*). Brandon-Jones et al. (2004) eventually accepted *Trachypithecus* as a full genus and recognized the following nine species: *auratus*, *villosus* (= *cristatus*), *barbei*, *obscurus*, *francoisi* (including *ebenus* and *hatinhensis*), *laotum*, *poliocephalus* (including *leucocephalus*), *geei* and *pileatus*. In contrast, Groves (2001) proposed a classification of *Trachypithecus* into 17 species, arranged in five species groups. According to his arrangement, the *pileatus* group consists of *pileatus*, *geei* and *shortridgei*, the *cristatus* group of *cristatus*, *auratus*, *germaini* and *barbei*, the *obscurus* group of *obscurus* and *phayrei*, the *francoisi* group of *francoisi*, *hatinhensis*, *poliocephalus*, *laotum*, *delacouri* and *ebenus* and the *vetulus* group includes *vetulus* and *johnii*. The taxonomy of Groves (2001) was generally adopted by Mittermeier et al. (2013), Roos et al. (2014) and Rowe and Myers (2016), although with some minor changes. First, the two species of the *vetulus* group were reassigned to *Semnopithecus* (Karanth 2008; Karanth et al. 2008; Osterholz et al. 2008; Wang et al. 2012, 2015; Zhang and Ryder 1998). Second, *barbei* was reallocated to the *obscurus* group (Geissmann et al. 2004). Third, *leucocephalus* was separated from *poliocephalus* on species level (Liu Z et al. 2013a). Fourth, *phayrei crepusculus* was elevated to species level (Liedigk et al. 2009; Roos et al. 2019). Fifth, a new species as described from central Myanmar (*T. popa*) and *phayrei shanicus* was elevated to species level and renamed into *melamera* (Roos et al. 2020). Sixth, within the *T. cristatus* group, *mauritus* and *margarita* were elevated to full species and a new taxon, *selangorensis*, was described (Nadler et al. 2005; Roos et al. 2008). By incorporating these changes, the genus *Trachypithecus* contains four species groups and a total of 22 species: *T. pileatus* group with golden langur (*T. geei*), capped langur (*T. pileatus* with four subspecies) and Shortridge's langur (*T. shortridgei*), *T. cristatus* group with silvered langur (*T. cristatus* with two subspecies), Selangor silvery langur (*T. selangorensis*), East Javan langur (*T. auratus*), West Javan langur (*T. mauritus*), Germain's langur (*T. germaini*) and Annamese langur (*T. margarita*), *T. obscurus* group with dusky langur (*T. obscurus* with seven subspecies), Phayre's langur (*T. phayrei*), Shan States langur (*T. melamera*), Popa langur (*T. popa*), Indochinese grey langur (*T. crepusculus*) and Tenasserim langur (*T. barbei*), and the *T. francoisi* group with the François's langur (*T. francoisi*), white-headed langur (*T. leucocephalus*), Cat Ba langur (*T. poliocephalus*), Delacour's langur (*T. delacouri*), Hatinh langur (*T. hatinhensis*), Laos langur (*T. laotum*) and black langur (*T. ebenus*).

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Similar to *Presbytis*, the classification of *Trachypithecus* is not fully clarified and needs additional work.

The genus *Semnopithecus* encompasses the langurs of the Indian subcontinent. Most commonly, the genus (or *Presbytis entellus* group) was considered to contain only a single species, the Hanuman langur, *entellus*, with 10–16 subspecies (Brandon-Jones et al. 2004; Davies and Oates 1994; Ellermann and Morrison-Scott 1951; Groves 1989; Napier 1985; Napier and Napier 1967, 1994; Pocock 1928, 1939; Roonwal 1981a; Roonwal and Mohnot 1977; Roonwal et al. 1984; Rowe 1996). However, Hanuman langurs have sometimes been divided into two (either *entellus* and *hypoleucos*; Brandon-Jones 1984a, 1996b, or *entellus* and *priam* Brandon-Jones 2004), four (*entellus*, *schistaceus*, *priam*, *hypoleucos*) (Hill 1939), or seven species (*schistaceus*, *ajax*, *hector*, *entellus*, *hypoleucos*, *dussumieri*, *priam*) (Groves 2001). Moreover, two species, *vetulus* and *johnii*, previously assigned to the genus *Kasi* or *Trachypithecus* have been recently integrated into *Semnopithecus* based on genetic evidence (Karanth 2008; Karanth et al. 2008; Osterholz et al. 2008; Wang et al. 2012, 2015; Zhang and Ryder 1998). In general, the current taxonomy of *Semnopithecus* follows Groves (2001) with the exception that *dussumieri* is not recognized as valid species (Ashalakshmi et al. 2015; Nag et al. 2011) and by including *vetulus* and *johnii*. Accordingly, *Semnopithecus* contains a total of eight species, Bengal sacred langur (*S. entellus*), Chamba sacred langur (*S. ajax*), Terai sacred langur (*S. hector*), Nepal sacred langur (*S. schistaceus*), Malabar sacred langur (*S. hypoleucos* with three subspecies), tufted grey langur (*S. priam* with three species), Nilgiri langur (*S. johnii*), and purple-faced langur (*S. vetulus* with four subspecies). As for the other two langur genera, also for *Semnopithecus* more work, particularly for the northern taxa is required.

Odd-Nosed Monkey Group

Snub-nosed monkeys, genus *Rhinopithecus*, occur only in China, Vietnam and Myanmar, with all species having relatively small geographical distributions (Groves 2001; Mittermeier et al. 2013; Roos et al. 2014; Rowe 1996; Rowe and Myers 2016). Originally, only two species, *avunculus* and *roxellana*, the latter with three subspecies, have been recognized (Ellermann and Morrison-Scott 1951; Napier and Napier 1967, 1994). However, Groves separated first *brelichi* as distinct species (Groves 1970), which was followed by Napier (1985). Later on, Groves (1989) also elevated *bieti* to full species, a classification that is now widely accepted (Brandon-Jones 1984a, 1996b; Brandon-Jones et al. 2004; Davies and Oates 1994; Jablonski 1998a; Jablonski and Peng 1993; Mittermeier et al. 2013; Roos et al. 2007, 2014; Rowe 1996; Rowe and Myers 2016). In contrast, a separation of *avunculus* in its own subgenus *Presbyticus* from its congeners as proposed by Jablonski (1998a) and Jablonski and Peng (1993) has not been adopted and can also not be justified with available genetic data (Liedigk et al. 2012; Roos et al. 2007; Yu et al. 2016; see also Chapter 4). In 2011, a new species of snub-nosed monkey, *strykeri*, was described