

PERSPECTIVES

Molecular systematics and conservation of the langurs and leaf monkeys of South Asia

K. PRAVEEN KARANTH*

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

Numerous morphology-based classification schemes have been proposed for langurs and leaf monkeys of South Asia but there is very little agreement between them. An incorrect classification scheme when used as a basis for biogeographic studies can support erroneous hypotheses. Further, lack of taxonomic resolution will also confound conservation efforts, given that conservation biologists use traditional morphology-based-classification schemes to prioritize species for conservation. Here, I have revisited recent molecular phylogenetic studies done on langurs and leaf monkeys of South Asia. Results from these studies are in turn used to derive a rational and scientific basis for prioritizing species for conservation. Molecular data support the classification of langurs of the Indian subcontinent—Hanuman, Nilgiri and purple-faced langurs—in the genus *Semnopithecus*, whereas Phayre's leaf monkey along with other Southeast Asian leaf monkeys form another distinct clade (*Trachypithecus*). The phylogenetic position of capped and golden langurs remains unresolved. Molecular data suggest that they are closely related to each other but this group might have evolved through past hybridization between *Semnopithecus* and *Trachypithecus*. Additionally, genetic data also support the splitting of the so-called Hanuman langurs into at least three species. The scores for taxonomic uniqueness of langurs and leaf monkeys of South Asia were revised using this molecular phylogeny-based classification. According to the revised scores, Phayre's leaf monkey and golden langur are priority species for conservation followed by capped and Nilgiri langurs.

*E-mail: karanth@ces.iisc.ernet.in.

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Introduction

Langurs belong to a large group of Old World monkeys called the colobines (subfamily Colobinae) and are distributed in tropical Asia. The colobines are unique among primates in that they are predominantly leaf eaters and exhibit foregut fermentation (Chivers and Hladik 1980). It is generally agreed that the colobines consist of two groups, or clades—the African colobus monkeys and the Asian langur and leaf monkeys (Oates *et al.* 1994; Morales *et al.* 1999; Disotell 2000). Asian colobines have been divided into five or six species groups depending on the author (Napier and Napier 1985; Oates *et al.* 1994; Groves 2001; Brandon-Jones *et al.* 2004). According to the most recent classifications (Groves 2001; Brandon-Jones *et al.* 2004), the Asian colobines consist of five species groups. These include langurs (*Semnopithecus*), leaf monkeys (*Trachypithecus*), surili (*Presbytis*), snub-nosed monkeys (*Rhinopithecus* and *Pygathrix*), proboscis monkey (*Nasalis*), and pig-tailed monkey (*Simias*). In South Asia, colobines are represented by two genera: *Semnopithecus* and *Trachypithecus*.

Traditionally, at least six species of langurs and leaf monkeys have been described from South Asia (table 1). These species include the langurs found in Indian subcontinent—Hanuman langur, Nilgiri langur, and purple-faced langur; the langurs found in the northeast states of India, in Bhutan, and in Bangladesh (northeast)—golden langur and capped langur; and Phayre's leaf monkey that is distributed predominantly in mainland Southeast (SE) Asia but its distribution also extends to the state of Tripura in the northeast (Karanth *et al.* 2008).

Among the langurs found in the Indian subcontinent, the Hanuman langur is the most widely distributed, and its distribution includes much of India and parts of Nepal, Bhutan, Pakistan, Bangladesh and Sri Lanka (Karanth *et al.* 2010).

Keywords. taxonomic uniqueness; hybridization; phylogeny; Hanuman langur; *Semnopithecus*; *Trachypithecus*.

Table 1. Classification of the langurs and leaf monkeys of Asia.

	Groves (2001)	Brandon-Jones <i>et al.</i> (2004)	Classification used here
Langurs of South Asia			
Hanuman langur	<i>S. entellus</i>	<i>S. entellus</i>	<i>S. entellus</i>
Nilgiri langur	<i>T. johnii</i>	<i>S. johnii</i>	<i>S. johnii</i>
Purple-faced langur	<i>T. vetulus</i>	<i>S. vetulus</i>	<i>S. vetulus</i>
Langurs of northeast			
Capped langur	<i>T. geei</i>	<i>T. geei</i>	? <i>geei</i>
Golden langur	<i>T. pileatus</i>	<i>T. pileatus</i>	? <i>pileatus</i>
Leaf monkeys of Southeast Asia			
Phayres leaf monkey*	<i>T. phayrei</i>	<i>T. phayrei</i>	<i>T. phayrei</i>
Silvered leaf monkey	<i>T. cristatus</i>	<i>T. cristatus</i>	<i>T. cristatus</i>
Francois' leaf monkey	<i>T. francoisi</i>	<i>T. francoisi</i>	<i>T. francoisi</i>
Dusky leaf monkey	<i>T. obscurus</i>	<i>T. obscurus</i>	<i>T. obscurus</i>

Note: revised classification is based on molecular data. S and T represent genus *Semnopithecus* and *Trachypithecus* respectively. ? Indicates that the *capped-golden* group is not yet assigned to any genus (see text for details). *Species also distributed in India (see text for details).

Nilgiri and purple-faced langurs are restricted to the wetter parts of southwest India and Sri Lanka, respectively.

Numerous morphology-based-classification schemes have been proposed to resolve the generic level taxonomy of langurs and leaf monkeys with very little success (Karanth *et al.* 2008, and references therein). For example, Groves (2001) places the Hanuman langur in the genus *Semnopithecus* and the remaining species in the genus *Trachypithecus* along with other leaf monkeys of SE Asia (table 1), whereas, Brandon-Jones *et al.* (2004) places Hanuman, Nilgiri and purple-faced langurs in *Semnopithecus* and the remaining species in the genus *Trachypithecus*. This incongruence across classification schemes is probably due to lack of adequate morphological variation among species and in some cases due to convergence in morphological characters (Karanth *et al.* 2008). When an incorrect classification scheme is used as the basis for biogeographic studies, it can obfuscate true patterns of distribution and support erroneous scenarios (Karanth 2003). In addition, conservation biologists use traditional morphology-based-classification schemes as the guide to determine the taxonomic uniqueness of a species. Taxonomic uniqueness is one of the important parameters used to rate primate species for conservation action (Oates 1985; Eudey 1987) and has been categorized into three subdivisions: a score of one is assigned to a species that is a member of a large species group (i.e., one of several closely-related species); a score of two is assigned to a very distinct species, or one of a small number of closely-related forms that are clearly distinct from other species; and finally, a score of three is assigned to a member of a monotypic genus (or family) (Oates 1985; Eudey 1987). Based on these scores, conservation resources are often assigned to various species or species groups. The underlying assumption in this

approach is that morphology-based-classification schemes are a reliable index of relationships between various species.

Thus, it is imperative that the taxonomy of these langurs be resolved in a manner that is consistent with their evolutionary relationships. In this regard, recent molecular studies undertaken on the Asian colobines are of much interest. Here, I have revisited these studies and proposed a tentative classification of South Asian langurs and leaf monkeys based on their molecular phylogeny. Additionally, I have compared the scores for taxonomic uniqueness derived from two different classification schemes for langurs of South Asia. The first classification scheme is traditional morphology-based classification (Eudey 1987), and the second is a revised classification based on molecular phylogeny.

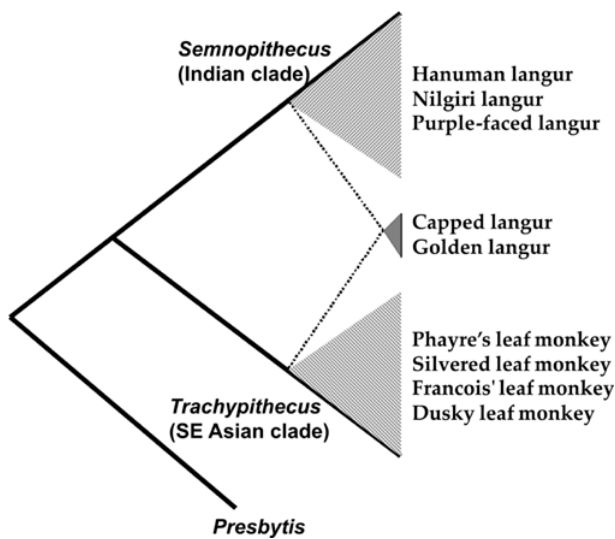
Recent molecular studies on South Asian colobines and their taxonomic implications

Results from three recent papers on molecular phylogeny of the langurs and leaf monkeys of South Asia (Karanth 2008; Karanth *et al.* 2008; Osterholz *et al.* 2008) are summarized and discussed here. These studies have used a range of different kinds of markers and have been successful in resolving higher order relationships between species. The following conclusions can be made based on these molecular studies, the results of which are summarized in table 2 and figure 1. First, the langurs of Indian subcontinent, Hanuman, Nilgiri, and purple-faced langurs are closely related and should therefore be classified in the same genus. This scenario is supported by four molecular markers and two retroposon insertions. Second, the leaf monkeys of SE Asia along with Phayre's leaf monkey form another distinct clade. This clade is also supported by multiple markers (table 2).

Table 2. Molecular markers used to assign langurs and leaf monkeys to *Semnopithecus* (S) and *Trachypithecus* (T).

		Molecular markers					
		mt1	mt2	Y	nuL	nuP	RP
Indian clade (<i>Semnopithecus</i>)							
Hanuman langur	<i>S. entellus</i>	S	S	S	S	S	S
Nilgiri langur	<i>S. johnii</i>	S	S	S	S	S	S
Purple-faced langur	<i>S. vetulus</i>	S	S	S	S	S	S
Capped-golden lineage							
Capped langur	? <i>geei</i>	S	T	T	T	x	x
Golden langur	? <i>pileatus</i>	S	T	–	T	x	–
SE Asian clade (<i>Trachypithecus</i>)							
Phayre's leaf monkey	<i>T. phayrei</i>	T	T	T	T	T	–
Silvered leaf monkey	<i>T. cristatus</i>	T	T	T	T	T	T
Francois' leaf monkey	<i>T. francoisi</i>	T	T	T	T	x	T
Dusky leaf monkey	<i>T. obscurus</i>	T	T	T	T	T	T

Markers: mt, mitochondrial cytochrome b (mt1=Karanth *et al.* 2008, Osterholz *et al.* 2008; mt2= Wangchuk *et al.* 2008); Y, Y-chromosomal SRY (Osterholz *et al.* 2008); nuL, nuclear lysozyme (Karanth *et al.* 2008); nuP, nuclear protamine 1 (Karanth *et al.* 2008); RP, retroposon integration (Osterholz *et al.* 2008); 'x', marker did not resolve the phylogenetic position of the species; –, data not available.

**Figure 1.** Consensus phylogeny of langurs and leaf monkeys of Asia based on molecular data (see text for details).

As per Brandon-Jones *et al.* (2004) and Osterholz *et al.* (2008), members of the Indian clade have been placed in the genus *Semnopithecus* whereas those in SE Asian clade in the genus *Trachypithecus* (table 2 and figure 1). These two clades occupy different regions of Asia. The Indian clade (*Semnopithecus*) is confined to the Indian subcontinent, whereas the SE Asian clade (*Trachypithecus*) is restricted to SE Asia. Thus, the revised classification is also consistent with the biogeography of langurs and leaf monkeys of Asia. Third, the evolutionary relationship of capped and golden langurs with respect to the other langurs and leaf monkeys remains unresolved, due to conflicting results between the nuclear *Lzm*

and *SRY* versus mitochondrial *Cyt-b* genes. Moreover, the nuclear *Prm1* as well as retroposon data were also unable to assign these species to either *Trachypithecus* or *Semnopithecus*. The distributional pattern of capped and golden langurs is very interesting. They are distributed in an area that is sandwiched between *Trachypithecus* and *Semnopithecus* in the northeast. These results suggest that the capped-golden group might have evolved due to past hybridization between Indian clade (*Semnopithecus*) and SE Asian clade (*Trachypithecus*) (Karanth *et al.* 2008). Indeed Karanth (2008) based on unusual phylogenetic position of nuclear copies of mitochondrial genes of these two species came to a similar conclusion, thereby lending additional support to the hybridization scenario. This hybridization event was estimated to have occurred around 7.1 to 3.4 million years ago (mya). Nevertheless, *Cyt-b* sequences of capped and golden langurs generated by Wangchuk *et al.* (2008) suggest that these two species are related to *Trachypithecus*. Thus, their work does not support a discord between nuclear and mitochondrial genes. Nevertheless, this result cannot be taken as evidence to reject the hybrid origin hypothesis because hybrids are predicted to harbour alleles from both the parental populations. Therefore, capped and golden langurs carry *Cyt-b* sequences that are similar to those from both *Trachypithecus* and *Semnopithecus*. A comparable scenario might emerge for nuclear markers, wherein capped and golden langurs might harbour nuclear alleles from both *Trachypithecus* and *Semnopithecus*. Clearly for a robust test of this scenario multiple rapidly evolving nuclear markers from more individuals need to be analysed. Until then placing capped and golden langurs in the genus *Trachypithecus*, as suggested by Wangchuk *et al.* (2008), is not warranted.

Although molecular data has not been successful in resolving the phylogenetic position of capped and golden langurs, both nuclear and mitochondrial markers strongly supports their sister relationship with very little divergence between them (Karanth *et al.* 2008). Indeed, Groves (1989) has suggested that the golden langur is merely a well-differentiated offshoot of the capped langur. If the *capped-golden* langur group is indeed the product of past hybridization between members of *Semnopithecus* and *Trachypithecus*, then perhaps these two closely-related species deserve their own genus in recognition of this unusual and unique evolutionary history. Here these two species have been tentatively assigned to a separate lineage termed 'golden-capped lineage', which is currently considered as genetically equidistant from *Semnopithecus* and *Trachypithecus* (figure 1; table 2).

Molecular systematics of the genus *Semnopithecus*

The molecular phylogenetic studies on langurs discussed above suggest that the genus *Semnopithecus* consists of at least three species: Hanuman, Nilgiri and purple-faced langurs. Among these three species, the Hanuman langur (*Semnopithecus entellus*) is one of the most widely distributed and morphologically variable species (Newton 1988) and is distributed throughout much of South Asia. Within the range of distribution of the Hanuman langurs are found the other two species of langurs, each having more restricted distributions. The Nilgiri langur is found in the wet evergreen forests of southwest India, and purple-faced langur is found predominantly in the wet zone of Sri Lanka.

There is much disagreement in the literature regarding the species and subspecies status of various Hanuman langur populations (Karanth *et al.* 2010, and references therein). Hanuman langurs are broadly classified into two major forms based on tail carriage (Roonwal 1984). These are northern type (NT-Hanuman), which has a tail that loops forward towards the head, and the southern type (ST-Hanuman), which has a tail that loops backward away from the head. The NT-Hanuman is distributed north of Tapti and Godavari rivers, while the ST-Hanuman is distributed south of these rivers in southern India and Sri Lanka.

Karanth *et al.* (2010) studied the evolutionary relationship between various Hanuman langur populations sampled from across the range and their relationships with Nilgiri and purple-faced langurs. This work was based on the phylogenetic analyses of mitochondrial *Cyt-b* gene and nuclear *Prm1* genes. Results from this work indicate that the mitochondrial DNA (mtDNA) of the so-called Hanuman langurs is not monophyletic (figure 2). Instead, the mtDNA of the ST-Hanuman from Sri Lanka branches with that of purple-faced langur of Sri Lanka, and the mtDNA of the ST-Hanuman from south India groups with Nilgiri langur to the exclusion of NT-Hanuman. Thus, the mtDNA of the genus *Semnopithecus* (Hanuman, Nilgiri, and purple-faced langur species complex) has at least three divergent clades (figure 2). These include the north Indian clade (NT-Hanuman), south Indian clade (ST-Hanuman from South India and Nilgiri langur), and Sri Lankan clade (ST-Hanuman from Sri Lanka and purple-faced langur). The individuals of the north Indian clade are separated from the south Indian clade by

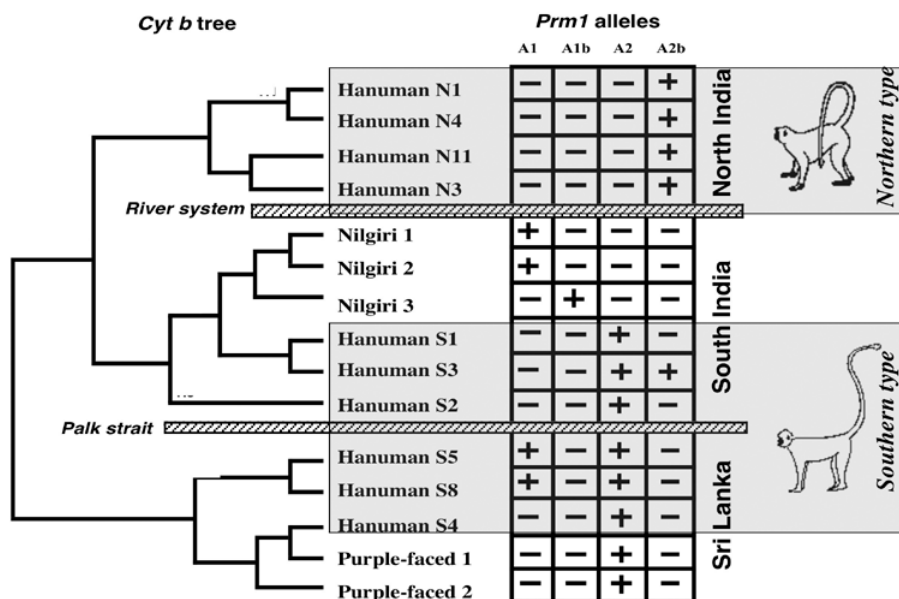


Figure 2. Phylogeny of genus *Semnopithecus* (adapted from Karanth *et al.* 2010). Positive sign indicates the presence of the respective *Prm1* allele.

the Narmada–Tapti river system, and the individuals of the south Indian clade are separated from the Sri Lankan clade by the Palk strait (the shallow sea between south India and Sri Lanka). In the case of nuclear DNA (nDNA) marker, a total of four Prm1 alleles (A1, A1b, A2, and A2b) were found among the three species of langurs (figure 2). Further, the nDNA variation found in Nilgiri and purple-faced langurs is a subset of the variation seen in the Hanuman langurs. This polyphyletic genetic relationship between the Hanuman, Nilgiri, and purple-faced langurs was taken as evidence for a speciation mechanism wherein populations of a Hanuman langur-like ancestral species diverged into Nilgiri langur and purple-faced langur in south India and Sri Lanka, respectively (Karanth *et al.* 2010).

Based on these results, Karanth *et al.* (2010) argue that the so-called Hanuman langurs should be tentatively split into three species such that their taxonomy is consistent with their evolutionary relationships. These species include NT-Hanuman from north India, ST-Hanuman from south India and ST-Hanuman from Sri Lanka (as suggested by Osterholz *et al.* 2008).

Taken together these molecular studies suggest that South Asia has at the least eight colobine species belonging to three different lineages. These include: one species, Phayre's leaf monkey from the *Trachypithecus* lineage; two species, capped and golden langurs from the *capped-golden* lineage; and five species, NT-Hanuman, ST-Hanuman (south India),

ST-Hanuman (Sri Lanka), Nilgiri langur and purple-faced langur from the *Semnopithecus* lineage.

Conservation implications of the revised classification

The goal of conservation biology is to preserve as many species from throughout the phylogeny of a species group, rather than large numbers from one branch. By doing so, one preserves a wider array of species, but it means that one has to know something about the relationships of the organisms involved. Given that the traditional morphology-based classification have not been successful in resolving the evolutionary relationships between the various langurs and leaf monkeys, here I use the revised molecular phylogeny-based classification (table 3) to determine the taxonomic uniqueness of the langurs. Taxonomic uniqueness was determined by Eudey's (1987) categories as a guide to assign scores to these species. These scores are tentative and will have to be revised with accumulation of additional ecological, behavioural, distributional, and genetic data.

This analysis assumes that capped and golden langurs evolved through hybridization between *Semnopithecus* and *Trachypithecus* clades and therefore should be treated as a distinct lineage. According to molecular phylogeny-based classification there are three major lineages of langurs and leaf monkeys in South Asia, *Semnopithecus*, *capped-golden*

Table 3. Revised score for taxonomic uniqueness of the langurs and leaf monkeys of South Asia.

	Eudey (1987)*	Revised score	IUCN
<i>Semnopithecus</i>			
NT- Hanuman	2**	1	LR
ST- Hanuman (south India)	2**	1	DD
ST- Hanuman (Sri Lanka)	2**	1	DD
Nilgiri langur	2	2	VU
Purple-faced langur	2	2	no
<i>Capped-golden</i>			
Capped langur	1	2	EN
Golden langur	1	3	EN
<i>Trachypithecus</i>			
Phayres leaf monkey	1***	3	no

*Eudey's scores for taxonomic uniqueness are based on Oates *et al.* (1994) classification scheme which is similar to Groves (2001).

**Eudey assigned a score of 2 to Hanuman langur which has now been split into three species.

***Phayre's langur is one of the most common and widely distributed leaf monkey in SE Asia. Therefore on a global scale it is not a unique species and a score of one is appropriate. But a score of three for this species is specific to India (see text for details).

IUCN, the 2000 IUCN Red List of threatened species (<http://www.redlist.org/>); (VU) vulnerable, (LR) lower risk, (EN) endangered, (DD) data deficient, (no) not listed.

lineage and *Trachypithecus* (figure 1). Among these three lineages, the area of distribution of the genus *Trachypithecus* in South Asia is the least (figure 3). Additionally, the genus *Trachypithecus*, when compared with other two lineages, is represented by only one species, Phayre's leaf monkey, in South Asia (table 3). Thus, in South Asia, among the three lineages, the genus *Trachypithecus* represented by Phayre's leaf monkey, is the most phylogenetically unique and distinct lineage. Therefore, from a South Asian or Indian perspective Phayre's leaf monkey deserves highest score of three for taxonomic uniqueness (table 3). It must be noted that from a global perspective Phayre's leaf monkey will not receive such high priority. This is because Phayre's leaf monkey, like the Hanuman langur in the Indian subcontinent, is one of the most widely distributed and common species of leaf monkey in SE Asia. Additionally genus *Trachypithecus*, like the genus *Semnopithecus*, is a widely distributed in SE Asia and consists of over eight species (see Brandon-Jones *et al.* 2004). Therefore, Phayre's leaf monkey is bound to have low score on taxonomic uniqueness when seen on a global scale along with other species of leaf monkeys of SE Asia.

Capped-golden group is the next most unique lineage among the three lineages. This group is distributed in a narrow area between *Trachypithecus* and *Semnopithecus* (figure 3) and probably has a unique evolutionary history (speciation through hybridization). Currently this group consists of only two species (table 3). Therefore these species deserve a minimum score of two for taxonomic uniqueness. Among these two species the golden langur possibly evolved through

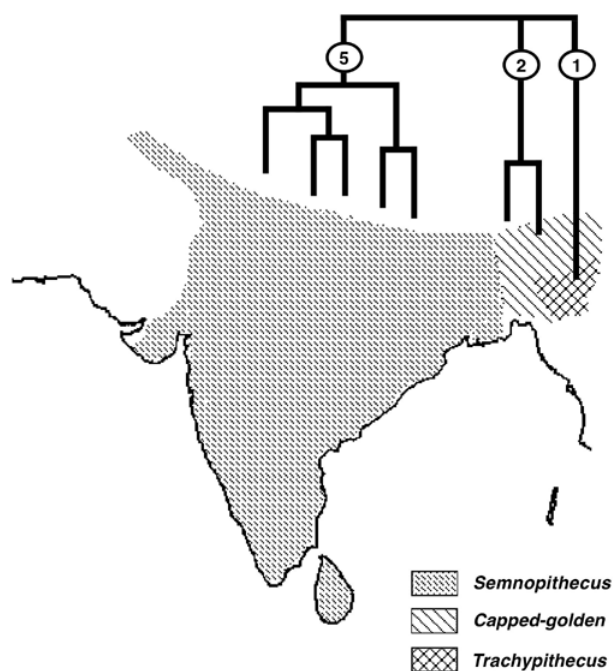


Figure 3. Geographical spread of the three lineages of colobines in South Asia. Numbers indicate the number of species in each lineage.

a speciation process wherein peripheral populations of the relatively widely distributed capped langur diverged into a new species. Thus, genetically it might be nested within capped langur (as is the case of Nilgiri langur being nested within southern Hanuman langur). This scenario is supported by low genetic differentiation between capped and golden langurs. Nevertheless, golden langurs deserve a higher score for taxonomic uniqueness than capped langur because they might be adapted to a specific niche as they are highly endemic to a very small area in the northeast. Therefore this species has been assigned a score of three for taxonomic uniqueness. Capped langur, on the other hand, has a much wider distribution and probably better adapted to exploit different habitats. Thus, a score of two would be appropriate for this species.

The genus *Semnopithecus* is the most widely distributed genus (figure 3) and is the least threatened among the three lineages. It consists of at least five species (table 3). Among these five species, the NT-Hanuman, ST-Hanuman (south India), and ST-Hanuman (Sri Lanka) (formerly called as Hanuman langur) are common in their respective regions. These three species are also adapted to a wide range of habitats. Therefore, they have been assigned the lowest score of one for taxonomic uniqueness. Both Nilgiri and purple-faced langurs are genetically nested within ST-Hanuman. But these two species have very restricted distribution and are adapted predominantly to wet evergreen forests. Thus, they deserve a higher score than the Hanuman langurs. Here I have assigned these species a score of two for taxonomic uniqueness.

It is apparent from table 3 that species that were considered important in terms of their taxonomic uniqueness, such as Hanuman langur, on revision of the scores based on molecular phylogeny, now have low score. Additionally, species with low scores (such as golden langur), now have higher scores. Based on taxonomic uniqueness, Phayre's leaf monkey and golden langur are priority species, followed by capped langur and Nilgiri langur. The 2000 IUCN red data list of threatened species (<http://www.redlist.org/>) has assigned different categories for the extent to which these species are threatened. These categories correspond quite well with the taxonomic uniqueness of these species (table 2), with two exceptions, Purple-faced langur and Phayre's langur, which are an important species for Sri Lanka and India, respectively, are not listed. Additionally, capped langur probably should be considered vulnerable rather than endangered. Padmanabhan and Gadgil (2000) prioritized various mammals of India based on their composite conservation value (CCV). CCV is based on various parameters including taxonomic distinctiveness. They too recognize the importance of Phayre's langur giving it a rank of seven among the priority species. Capped langur and golden langur on the other hand are ranked 60 and 124 (Padmanabhan and Gadgil 2000). One of the reasons for the low rank assigned to golden langur might be because the authors used conventional morphology-based classification.

The analysis presented here illustrates the importance of using molecular genetic tools to resolve the systematics of taxonomically problematic species groups. Such molecular phylogeny based-classifications can then be used to derive a rational and scientific basis for prioritization of species for conservation. Additionally, phylogenies can be used to better understand the biogeography of the species group under study. For example, past classification schemes have placed Hanuman langur in the genus *Semnopithecus*, and all the other langurs in the genus *Trachypithecus* (table 1). Therefore, the genus *Trachypithecus*—as defined by these authors—has a highly disjunct distribution (Karanth *et al.* 2008). A number of explanations have been put forward to explain the apparent discontinuity in the distribution of various species in the Indian subcontinent (see Karanth 2003). The molecular data, on the other hand, suggest that the taxonomic schemes that place Hanuman langurs in a genus separate from the other langurs of the Indian subcontinent do not reflect the true evolutionary relationships between these species. These studies support placing purple-faced, Nilgiri and Hanuman langurs in the genus *Semnopithecus*. Thus, the revised classification does not support the discontinuity in the distribution of species in the genus *Trachypithecus* (Karanth *et al.* 2008). Our understanding of the evolution of capped and golden langurs has also been advanced through these molecular studies. We now know that capped and golden langurs are closely related and probably evolved due to past hybridization between *Trachypithecus* and *Semnopithecus*.

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