

The Phyletic Position and Systematics of the Douc Langurs of Southeast Asia

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In recent years, two major questions concerning the phyletic relationships and systematic position of the douc langurs have arisen. These concern, firstly, the taxonomic level at which the doucs as a group should be distinguished and, secondly, the number of taxa of doucs that should be recognized. It has recently been demonstrated on the basis of an exhaustive phylogenetic analysis that the doucs are generically distinct from the snub-nosed langurs and that they should be referred to as species of *Pygathrix* and *Rhinopithecus*, respectively [Jablonski and Peng, *Folia Primatologica* 60:36–55, 1993]. The present investigation was directed toward testing this conclusion using an expanded data set and a different method of character coding, and toward addressing the question as to the number of species or subspecies of doucs that should be recognized. A wide variety of data from large samples of doucs ($n = 38$), snub-nosed langurs ($n = 53$), and an outgroup (macaques; $n = 191$) were assembled, coded, and analyzed using an interactive computerized program for phylogenetic analysis. The specimens of *Pygathrix* examined included skeletal specimens, skins, and, when possible, living animals representing the three recognized taxa of doucs, *nemaeus nigripes*, and *moi*. The data base for the study comprised 178 characters, including measurements of skeletal specimens (98 characters), qualitative (presence or absence) morphological features (36 characters), characteristics of the pelage (39 characters), and 5 miscellaneous characters.

The conclusions of the study were that 1) as a group, the taxa of *Pygathrix* preserved a larger number of primitive features for the *Pygathrix-Rhinopithecus* clade than did the taxa of *Rhinopithecus*; 2) the taxa of *Pygathrix* were less different from one another than are the species of *Rhinopithecus* were from one another; 3) the subspecies *Pygathrix nemaeus moi* Kloss, 1926 be synonymized with *Pygathrix nemaeus nigripes*, as suggested by Napier [Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles. Part III Family Cercopithecidae, Sub-Family Colobinae. London, 1985]; 4) the extant doucs were best recognized as two subspecies, *P. nemaeus nemaeus* for the red-shanked douc and *P. nemaeus nigripes* for the black-shanked douc; and 5) the phylogeny of the

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doucs and snub-nosed langurs proposed by Jablonski and Peng [op cit., 1993] was found to be robust. © 1995 Wiley-Liss, Inc.

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INTRODUCTION

The phylogeny and systematics of the so-called odd-nosed colobine monkeys of Asia have been subjects of debate for most of this century. For the last 20 years many workers have followed the scheme proposed by Groves [1970; Thorington & Groves, 1970] in his comprehensive review of the taxonomy of the Colobinae. According to this scheme, the odd-nosed forms were relegated to two genera with two subgenera each: *Nasalis* E. Geoffroy, 1812 comprising the proboscis monkey *Nasalis (Nasalis)* and the simakobu or pig-tailed leaf monkey *Nasalis (Simias)*; and *Pygathrix* E. Geoffroy, 1812 accommodating the doucs *Pygathrix (Pygathrix)* and snub-nosed langurs *Pygathrix (Rhinopithecus)*. While Groves's classification has been followed by some [e.g., Napier, 1985; Vogel and Winkler, 1990], it has not been universally accepted, and many workers have chosen, for various reasons, to retain some or all of the four original generic rankings for these animals.

In this work the phylogeny and systematic position of the douc langurs were considered. Specifically, the present study was undertaken with the aim of shedding light on the major question that exists concerning the classification of the doucs, that of the number of taxa that can be accommodated in *Pygathrix* and the taxonomic level at which they should be recognized.

Most primatologists recognize that the doucs and snub-nosed langurs are more closely related to each other than they are to any other colobine, but opinions have differed as to how this relationship can be best expressed. The species of doucs and snub-nosed langurs occupy non-overlapping ranges from near the east bank of the Mekong River of central and southwest China south into Indochina, through to southern-most Vietnam. They form an adaptive array, from the doucs in the tropical rain forest habitats of Laos, Vietnam, and Cambodia east of the Mekong River to Biet's snub-nosed langur (also known as the Yunnan snub-nosed langur or Yunnan golden monkey) in high altitude coniferous forests at the eastern edge of the Tibetan Plateau [Jablonski, 1990].

The taxonomy of the douc langurs has a long and relatively complex history. The douc was first named *Simia nemeaus* by Linnaeus in 1771, but was included in *Cercopithecus* by Erxleben in 1777. It was named *Pygathrix nemeaus* by E. Geoffroy in 1812, but was shifted to *Lasiopyga nemeaus* by Desmarest in 1820 and later to *Semnopithecus* by F. Cuvier in 1825 [Forbes, 1896]. Some of the confusion over the naming of the douc was settled by Pocock [1935] who confronted the taxonomic difficulty by dividing *Semnopithecus* into *Pygathrix* Geoffroy, 1812 (*nemeaus*); *Presbytis* Eschscholtz, 1821 (*aygula* [= *comata*]); and *Semnopithecus* Desmarest, 1822 (*entellus*).

The major controversies over the classification of the doucs have centered around two issues: whether the snub-nosed langurs should be united with the doucs at the generic level, and how many species or subspecies of doucs there are. It appears that Groves's [1970] consolidation of the taxonomy of the doucs and snub-nosed langurs derived from his concern that the classification of the Asian colobines, and in particular that of the odd-nosed forms, was "very top-heavy." Recently, Jablonski and Peng [1993] showed that the generic distinction of the doucs and snub-nosed langurs was clearly warranted on the basis of a large suite

of characters of the skeleton, dentition, gut, and pelage that could be traced to the relatively long, independent evolutionary trajectories of the two groups.

The distinction between the red- and black-shanked doucs has long been recognized. The black-legged, southern form was designated *P. nigripes* by Milne Edwards in 1871, but most workers have followed Pocock [1935] in recognizing this form as a subspecies of *P. nemeaus* rather than as a separate species. Pocock [1935] indicated that the pallid face, white lower arms, and rusty rufous lower leg of *P. n. nemeaus* suggested that it was a "partial albino" mutant of *P. n. nigripes*. Brandon-Jones [1984] has maintained Milne Edwards's distinction of the black-shanked douc as the species *P. nigripes*. In addition to the red- and black-shanked forms, however, a third form has been recognized. Kloss [1926] proposed the subspecies *P. nemeaus moi* for a specimen that was distinguished from *nigripes* by a lesser amount of blackness on the brow, hands, and lower abdomen. From his brief description, Kloss [1926] likened *P. nemeaus moi* to *P. nemeaus nigripes* and one is left to conclude that he considered *P. n. moi* more closely related to *P. n. nigripes* than to *P. n. nemeaus*. It is worth noting, however, that the original tags on the paratype series of *P. n. moi* in the Zoological Reference Collection of the National University of Singapore designated the taxon at the species level, as *Pygathrix moi*. Napier [1985] synonymized *moi* with *nigripes*, and placed both taxa in *P. nemeaus nigripes*. This scheme was then followed by Weitzel et al. [1988]. Wirth et al. [1991] recently brought attention back to this problem by raising the question of the status of *moi* and by publishing a color photograph of a female *Pygathrix* with a red collar and brow, white cheeks, cream-colored ears, agouti chest and limbs, and lacking black epaulets. They raised the question whether this female represented a genuine *moi*, a color variation of one of the other doucs, or an entirely new species. Clearly, these questions have stemmed from a suspicion that the respective populations of doucs are reproductively isolated and deserve formal recognition as individual taxonomic entities.

In light of the disagreement that exists in the literature concerning the classification of the doucs, it is clear that an examination of the phyletic relationships within *Pygathrix* and a review of the taxonomy of the animals are warranted. The present study has benefitted from larger and generally more complete samples of all taxa than those sampled by Jablonski and Peng [1993]. For convenience, all the groups of doucs are referred to as subspecies of *Pygathrix nemeaus* throughout the text until the Discussion.

METHODS

In order that the phyletic position of the doucs could be assessed using as many criteria as possible, a comparative data base was established that included morphometric data gathered from skeletal specimens, information on qualitative (presence-absence) morphological characteristics of the skeleton and viscera, details of the pelage and skin color, and information on other aspects of soft-tissue anatomy and karyology. The total sample of doucs comprised 38 skeletal specimens representing all putative subspecies, *Pygathrix nemeaus nemeaus*, *P. n. nigripes*, and *P. n. moi*. When possible, the skins of the relevant skeletal specimens were also considered in order that details of the pelage could be recorded. Details concerning the number and provenance of the skeletal specimens examined is given in Table I. The localities from whence the specimens originated are plotted in Figure 1. Relevant information concerning features of visceral anatomy and diploid chromosome number was gleaned from the literature [Napier, 1985; Peng et al., 1988; Ye et al., 1985]. Living red-shanked doucs were observed at Howletts Zoo in order to clarify details of pelage coloration, which are subject to changes due to preser-

TABLE I. List of Skeletal Specimens Examined in This Study*

Taxon	No.		Sources
	Males	Females	
<i>Pygathrix nemaeus nemaeus</i>	8	5	BM(NH); FMNH; MNHN; NMNH
<i>Pygathrix nemaeus nigripes</i>	11	7	BM(NH); FMNH; MNHN; NMNH
<i>Pygathrix nemaeus moi</i>	4	3	BM(NH) ^a ; NUS
<i>Rhinopithecus (Presbytiscus) avunculus</i>	2	2	BM(NH)
<i>Rhinopithecus (Rhinopithecus) roxellana</i>	8	17	AMNH BM(NH) FMNH MNHN NMNH ROM
<i>Rhinopithecus (Rhinopithecus) brelichi</i>	3	1	KIZ
<i>Rhinopithecus (Rhinopithecus) bieti</i>	9	11	KIZ; MNHN
<i>Macaca sinica</i>	10	5	BM(NH); FMNH; NMNH; RCS
<i>Macaca mulatta</i>	25	23	AMNH; BM(NH); FMNH; KIZ; NMNH; ZRC
<i>Macaca nemestrina</i>	17	18	AMNH; BM(NH); FMNH; NMNH; ZRC
<i>Macaca fuscata</i>	7	7	BM(NH); NMNH; UZI
<i>Macaca fascicularis</i>	43	36	AMNH; BM(NH); FMNH; KIZ; NMNH; RCS; ZRC

*The following abbreviations denote institutions where specimens were examined: AMNH = American Museum of Natural History, New York; BM(NH) = British Museum (Natural History), London; FMNH = Field Museum of Natural History, Chicago; KIZ = Kunming Institute of Zoology; MNHN = Museum National d'Histoire Naturelle, Paris; NMNH = National Museum of Natural History, Washington, DC; NUS = National University of Singapore; ZRC = Zoological Reference Collection; RCS = Royal College of Surgeons, London; ROM = Royal Ontario Museum, Toronto; and UZI = Universität Zürich-Irchel.

^aIt should be noted that the sample of *P. n. moi* from this museum was based on identifications from original skin tags and does not fully agree with the specimens designated as *moi* by Napier [1985].

vation and storage. In addition to the putative species or subspecies of doucs, the present study included samples of the four recognized species of *Rhinopithecus*, *R. (Presbytiscus) avunculus*, *R. (Rhinopithecus) bieti*, *R. (R.) brelichi*, and *R. (R.) roxellana*, as well as those of five species of *Macaca*, *M. sinica*, *M. mulatta*, *M. nemestrina*, *M. fuscata*, and *M. fascicularis*, that together formed the outgroup (Table I). To enable direct comparison with the results of the study by Jablonski and Peng [1993], the ingroup and outgroup taxa examined in the present study were kept the same, but the samples of each taxon were generally larger and had fewer missing values than those considered in the previous study. This was especially true of the postcranial skeleton; in this study only *P. n. moi* and *R. (P.) avunculus* lacked postcrania because none were available in institutional collections.

In order that the results of the phyletic relationships of the doucs could be assessed against a stable, pre-existing phylogeny, the suite of characters employed was identical to that utilized by Jablonski and Peng [1993]. The data base therefore comprised 178 characters (see Appendix A), including 98 morphometric characters (characters 0–96 and 112), 36 qualitative (presence-absence) morphological features (characters 97–111, 114–124, 127, 155, 158, 162, 171, 173, and 175–177), 39 features of the pelage and skin (characters 128–154, 156, 157, 159–161, and 163–169), and 5 miscellaneous features (characters 113, 125, 170, 172, and 174). Computerized phylogenetic analysis of the data matrix was performed using the program Hennig86, version 1.5 [Farris, 1988]. For taxa in which the numbers of

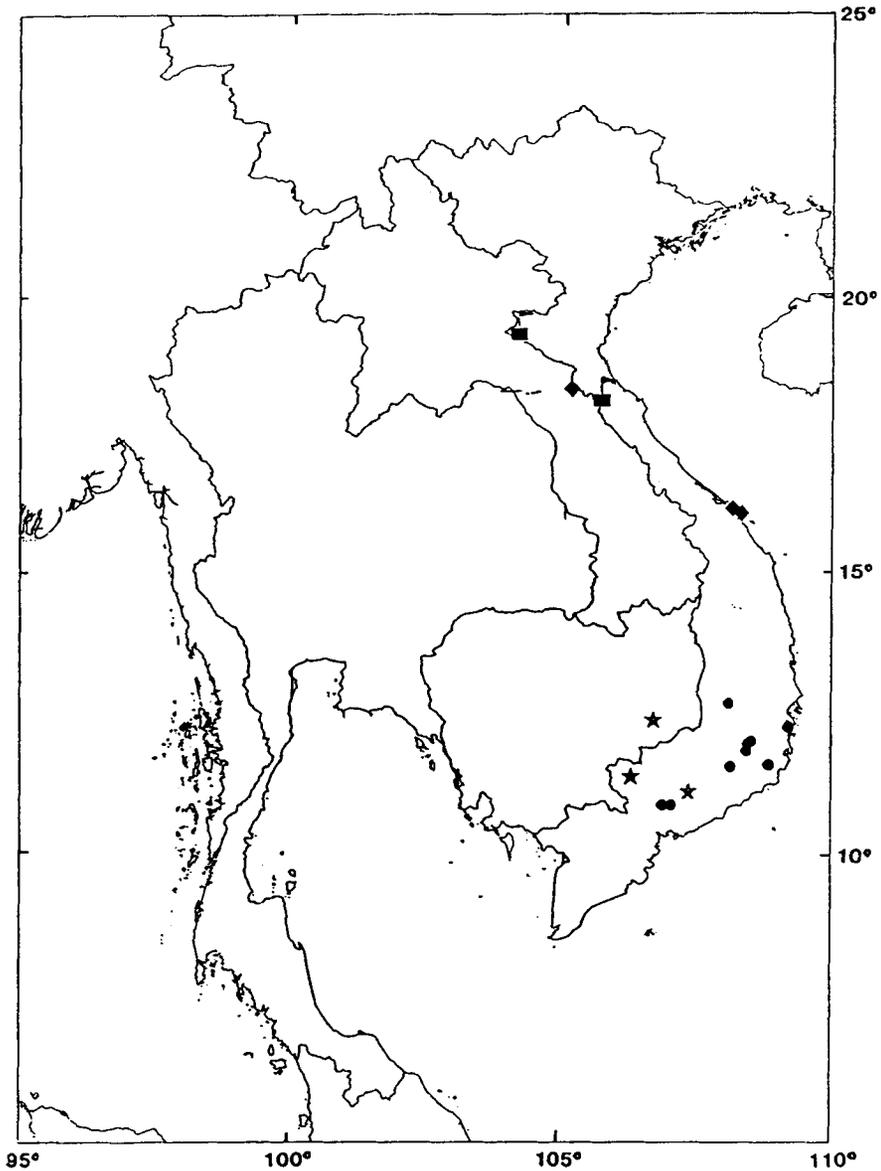


Fig. 1. Localities for samples of douc langurs examined in this study and for other recognized localities. Diamonds designate localities of *Pygathrix nemaeus nemaeus* from whence specimens in this study originated: Ky Son (19°23'N; 104°9'E), V An Cu (16°12'N; 108°8'E), and Mount Sontra (16°7'N; 108°18'E). Flags designate other known localities of *Pygathrix nemaeus nemaeus*: Nape (18°18'N; 105°7'E) and Huong Khe (18°12'N; 105°41'E). Circles designate localities of *Pygathrix nemaeus nigripes* from whence specimens in this study originated: Buon Me Thout (12°45'N; 108°5'E), Bali (12°20'N; 109°12'E), Lang Bian Peak (12°3'N; 108°27'E), Don Duong (11°40'N; 108°50'E), Da Lat (11°55'N; 108°25'E), Di Linh (11°38'N; 108°7'E), Trang Bom (10°57'N; 107°E), and Bien Hoa (10°57'N; 106°15'E). Stars designate other known localities of *Pygathrix nemaeus nigripes*: Senmonerom (12°30'N; 106°40'E), Dinh Quan (11°14'N; 107°20'E), and Nui Ba Den (11°38'N; 106°15'E). Readers are referred to Lippold [1977], Fooden and Feiler [1988] and Nisbett and Ciochon [1993] for further information on the status of the localities from whence doucs have been identified.

males and females were not equal, a geometric correction was made to ensure that the species mean reflected equal numbers of both sexes. This was done in order to avoid biasing the samples toward one end or the other of the size range in these sexually dimorphic species.

In studies where the animals under consideration span a great range of body weight, size adjustment of morphometric variables is often suggested. In this study, size adjustment was not undertaken for three reasons. Firstly, the range of estimated weights of the animals in the ingroup was relatively narrow, with overlapping ranges (Jablonski and Pan, in press). This obviated the need for size-adjustment. Secondly, the range of body weights in the outgroup was larger than in the ingroup, thus preventing the need for the program to extrapolate from the outgroup to the ingroup. And, finally, the smaller species monkeys of the ingroup did not always have the smallest values for morphometric characters, indicating that the size of some features in certain species was affected by factors other than allometry.

Following geometric correction for unequal numbers of males and females, the morphometric data were additively coded in such a way that the number of increments utilized for coding any particular measurement (character) reflected the amount of variability in the data for that measurement. This was done by adding one-half the standard deviation for the character means to the minimum mean value until the maximum mean value was encountered. In this way a highly variable measurement was coded by a smaller number of increments than a less variable measurement. This approach was suggested by Farris [1966] and Kluge and Farris [1969], who felt that characters should be weighted so that differences reflect the conservativeness of characters; the rationale being that more highly variable (and therefore less conservative) characters should carry less weight in a taxonomic analysis. This method of coding differed from the segmental method employed by Jablonski and Peng [1993] in their analysis of the phyletic relationships of the snub-nosed langurs. Their method, despite reflecting accurately the ordination of the means, did not take character variability into account as effectively as the new method because it used the range instead of the standard deviation. The division of the morphometric data into increments based on the amount of variability in a particular measurement permitted the number of increments to be influenced by the variance structure of each measurement while giving equal weighting to each increment, as is appropriate for continuous characters [Kluge, 1976]. It should be noted here that the topology of the tree produced from this method and that utilizing strictly segmentally coded data were identical, but the latter will not be further discussed.

Qualitative morphological features (characters 97–111, 114–124, 127, 155, 158, 162, 171, 173, and 175–177) were scored as present (1), absent (0), or missing (?). Characters describing pelage or skin coloration (128–154, 156, 157, 159–161, and 163–169) were coded according to a sequence suggested by Hershkovitz [1968] as follows: agouti = 0, black = 1, red/chestnut = 2, dark brown = 3, orange = 4, buff = 5, yellow = 6, gray = 7, cream = 8, and bleached/white = 9. Three features of the pelage that described hypertrichy fields (170, 172, and 174) were coded as follows: short hair = 0, medium-length hair = 1, and long hair = 2. Separation of the male ischial callosities was coded as follows: no separation = 0, narrow separation = 1, and wide separation = 2. Diploid chromosome number (character 125) was scored as 0 for 42 chromosomes and 1 for 44 chromosomes. For all types of characters, missing values were coded as “?”

In choosing characters an attempt was made to reduce the number of uniquely derived characters for any particular species (autapomorphies), which are known

to elevate the consistency index of the cladogram without enhancing its resolution [Kluge, 1989].

Decisions concerning the polarity of characters in the group under study (the ingroup, comprising the doucs and snub-nosed langurs) were made by outgroup analysis. Outgroup analysis avoids arbitrary resolutions of relationships because it is governed strictly by the criterion of maximum parsimony. In outgroup analysis the ancestral states for the ingroup are estimated after consideration of the character states and relationships of outgroups [Maddison et al., 1984]. As mentioned above, five species of macaques formed the outgroup for this study.

For all trees generated, multistate morphometric characters (0–96) were treated as additive, so that a character state progression might appear as 0→1→2→3→4→. . . This assumption means that for any character state to be transformed to another, it must pass through the intervening character states and not be transformed directly into any other. Additive characters are considered the most sensible for treatment of morphometric characters because their nature is ordinal, e.g., a long mandible cannot evolve from a short one without passing through stages of intermediate length. All other characters were treated as non-additive. The phylogenetic tree was calculated using the “implicit enumeration” (i.e. *) option of Hennig86 [Farris, 1988], which finds all trees of minimal length. A list of character transformations for the ingroup was constructed by making an inventory of the possible states of each character at each node and terminal taxon. Neither relationships within the outgroup nor between the ingroup and the outgroup were tallied. In order that hypothetical tree topologies could be compared to the trees produced by the program, the Hennig86 tree editor (“dos equis” or xx option) was employed. This allowed the generated tree to be changed by having branches moved through removal of hypothetical common ancestors to produce hypothetical polytomies. This allowed specific taxa to be paired up with other taxa in order to determine how many extra steps of evolution would be required for their association as sister groups. A further study utilizing a data set with no missing values for the *Pygathrix* taxa was performed to determine whether missing data for *P. n. moi* affected the results.

A complete print-out of the final data matrix is available from the author.

RESULTS

Analysis of the full data matrix produced a single tree with a length of 1,165 steps, a consistency index of 63, and a retention index of 66 (Fig. 2). The number of character transformations between the nodes, and between the terminal taxa and nodes, of the cladogram is given in Table II. A list of the synapomorphies that describe the character transformations enumerated in Table II is provided in Appendix B.

The next shortest two trees were five steps longer and the third closest trees were 10 steps longer. These trees differed from the most parsimonious tree only in the topology of the *Pygathrix* clade. The branch swapping observed appeared to be due mostly to the intermediate position of *P. n. moi* between *P. n. nemaus* and *P. n. nigripes*.

The nature of the synapomorphies that denoted the character transformations listed in Table II are worthy of note. In the transformation from the hypothetical common ancestor of the *Rhinopithecus-Pygathrix* clade (Node 2) to the hypothetical common ancestor of the *Pygathrix* clade (Node 3), the character changes indicated a general diminution of size in both the cranial and postcranial elements. This would suggest that this transformation was accompanied by an overall decrease in body size. That this is simply a size-related phenomenon is belied by increases in

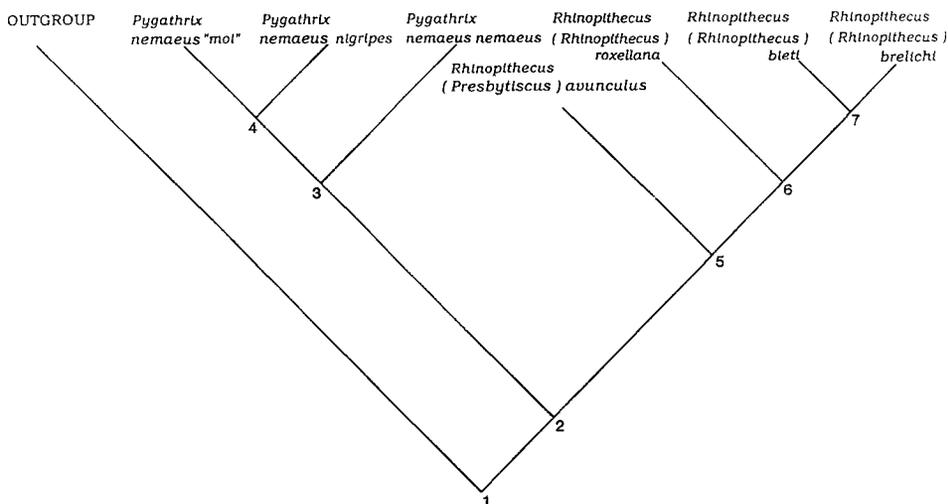


Fig. 2. Cladogram depicting phylogenetic relationships of the douc langurs. Tree length = 1,165 steps; consistency index = 63, retention index = 66. See Table II for the number of character transformations separating the nodes and terminal taxa and Appendix B for a list of the synapomorphies that define each transformation.

TABLE II. Number of Character Transformations Separating the Nodes and Terminal Taxa of the Ingroup for the Cladogram Shown in Figure 1

Nodes and/or terminal taxa	No. of character transformations between—
2 to 3	49
3 to <i>P. n. nymphaea</i>	37
3 to 4	30
4 to <i>P. n. moi</i>	14
4 to <i>P. n. nigripes</i>	37
2 to 5	67
5 to <i>R. (P.) avunculus</i>	31
5 to 6	69
6 to <i>R. (R.) roxellana</i>	54
6 to 7	39
7 to <i>R. (R.) bieti</i>	63
7 to <i>R. (R.) brelichi</i>	68

several cranial variables (palatal width, zygomatic height, lower bicanine breadth, and lower incisive alveoli breadth), and by increases in tibial length and in the robusticity indices for the humerus, ulna, femur, and tibia. In the pelage, the members of the *Pygathrix* clade were united by the possession of adornment of the forehead and temple areas and of the upper chest and neck regions, the presence of red-colored shanks at least in the juvenile coat, and a white sacral patch and white tail with short hairs and no terminal tuft. Although agouti is recognized as the primitive condition for the mammalian pelage [Hershkovitz, 1968], the banding pattern of the agouti pelage of *Pygathrix* is not the same as that of the agouti pelage of the *Macaca* outgroup. The modified agouti of the doucs consists of a regular, white and black ticking pattern that is more striking in appearance than

the primitive agouti. It was not possible to include this change within the coding system, but the agouti in many of the color fields of the *Pygathrix* clade should be considered as a synapomorphy and not as a symplesiomorphy.

In the transformation from the hypothetical common ancestor of the *Pygathrix* clade (Node 3) to *P. n. nemaesus*, the only consistent trends observed in the skull were character changes describing an expansion of the upper facial skeleton and a shortening of cranial and muzzle lengths. In the postcranium, diminution in scapular variables and an increase in the brachial index were observed.

In the transformation from the hypothetical common ancestor of the *Pygathrix* clade (Node 3) to the hypothetical common ancestor of *P. n. nigripes* and *P. n. moi* (Node 4), the character changes indicated a further diminution of cranial dimensions and a further slight reduction of postcranial size that reflect a longer, more slender form with longer trunk and limb segments. In the pelage, the transformation was characterized by a loss of complexity in the coat pattern and the presence of black shanks in the adult.

In the transformation from the hypothetical common ancestor of *P. n. nigripes* and *P. n. moi* (Node 4) to *P. n. moi*, the small number of character changes observed reflected slight increases in facial and cranial breadths. The absence of postcrania for the latter group precludes discussion of transformations in the postcranial skeleton. In the pelage, the transformation was accompanied by a lesser amount of blackness in the coloration of the brows, hands and abdomen.

In the transformation from the hypothetical common ancestor of *P. n. nigripes* and *P. n. moi* (Node 4) to *P. n. nigripes*, the character changes in the skull reflected mostly decreases in facial and cranial dimensions, particularly in midparietal width, but also an interesting increase in the robusticity of the mandibular corpus. In the postcranium, increases in scapular dimensions, skeletal trunk length, and in hindlimb long bone lengths were observed, while slight decreases were noted in the diameters of the humeral and femoral heads.

In the transformation from the hypothetical common ancestor of the *Rhinopithecus-Pygathrix* clade (Node 2) to the hypothetical common ancestor of the *Rhinopithecus* clade (Node 5), the character changes described several important trends in the skeleton and integument. The first of these was an increase in calvarial dimensions, namely, in braincase length, cranial width, and midparietal width. The second was an increase in facial breadths that can be traced to an increase in the breadth of the maxilla in *Rhinopithecus* species as compared to *Pygathrix* species (Jablonski, unpublished observations). The third was a change in the shape of the upper facial skeleton involving shortening of the anterior muzzle and the acquisition of a concave (dished-in) facial profile. The second and third changes noted above appear to have influenced the form of the piriform aperture and nasal bones. Fourthly, considerable increases in the size and robusticity of the masticatory apparatus were observed. The major features contributing to this trend were enlarged temporal fossae (and therefore a greater bizygomatic width), and increased mandibular dimensions, in particular, the heights of the mandibular body and symphysis, the thickness of the corpus, and the dimensions of the condyle. In the dentition, *Rhinopithecus* species were united by the presence of more bulbous (puffy) molars and a high frequency of the tuberculum sextum. In the postcranium, the character changes reflected increases in the robusticity and relative sizes of the limb bones and a different scapular form. In the pelage, the members of the *Rhinopithecus* clade were united by the loss of agouti banding in the hairs, an overall darkening of the dorsal surfaces, and in the loss of much of the complexity in the pattern of the coat, notably in the differentiation of the head, chest, shanks, sacral patch, and tail hair.

In the transformation from the hypothetical common ancestor of the *Rhinopithecus* clade (Node 5) to *R. (Presbytiscus) avunculus*, slight reductions in facial breadths and braincase dimensions occurred alongside increases in the ratio of the biorbital breadth to the postorbital constriction, the height of the occiput, and in the ratio of the foramen magnum length to width. The upturned leaf nose was found to be less well developed in *R. (Presbytiscus) avunculus* than in the Chinese members of its clade.

In the transformation from the hypothetical common ancestor of the *Rhinopithecus* clade (Node 5) to the hypothetical common ancestor of the Chinese *Rhinopithecus* species (Node 6), the character changes described an overall increase in skeletal robusticity. In the skull, these were represented by increases in facial breadths, facial heights, molar row lengths, and in the robusticity of the masticatory apparatus. Of great interest is that this transformation also appears to have been accompanied by increases in canine dimensions, and thus may have been related to changes in the animals' social behavior (Jablonski and Pan, in press). Increases in all postcranial dimensions, especially in limb bone diameters, also characterized this transformation. In characters of the integument, the Chinese *Rhinopithecus* species were united by possession of a large upturned leaf nose, colored facial skin, and sexually dimorphic adornments of the pelage, such as capes and lengthened hairs on the withers and tail.

In the transformation from the hypothetical common ancestor of the Chinese *Rhinopithecus* species (Node 6) to *R. (Rhinopithecus) roxellana*, a further increase in facial breadths, cranial widths, and in the robusticity of the masticatory apparatus was observed. Slight reductions in the anterior muzzle and limb bone lengths were also observed and may be seen as related to the adaptation of *R. (Rhinopithecus) roxellana* to conditions of cold and high altitude in central China. In the pelage, this species was distinguished by a silky, brilliant gold or red gold-colored coat that shows darkening in the dorsal midline. The facial skin was pale to brilliant blue and the lips were pink. Although the reasons for the loss of integumentary pigmentation in this species are not known, it may be traceable to changes occurring at the inferred population bottleneck suffered by the species in the Late Pleistocene [Jablonski, 1992].

In the transformation from the hypothetical common ancestor of the Chinese *Rhinopithecus* species (Node 6) to the hypothetical common ancestor of *R. (Rhinopithecus) bieti* and *R. (Rhinopithecus) brelichi* (Node 7), increases in facial breadths, facial heights, and muzzle length were observed, in addition to increases in characters reflecting postcranial robusticity.

In the transformation from the hypothetical common ancestor of *R. (Rhinopithecus) bieti* and *R. (Rhinopithecus) brelichi* (Node 7) to *R. (Rhinopithecus) bieti*, increases in canine dimensions and in a large number of calvarial and cranial variables (in particular, palatal and tooth row dimensions, facial and braincase widths, and muzzle and braincase lengths) were observed. The increased canine dimensions in *R. (Rhinopithecus) bieti* appear to reflect heightened levels of intermale competition (Jablonski and Pan, in press).

In the transformation from the hypothetical common ancestor of *R. (Rhinopithecus) bieti* and *R. (Rhinopithecus) brelichi* (Node 7) to *R. (Rhinopithecus) brelichi*, a slight diminution of dental dimensions and facial breadths was in contrast with strong increases in the size and robusticity of all the mandibular corpus and glenoid fossa variables.

From the figures listed in Table II, further inferences of biological significance can be offered. Firstly, it would appear that all the members of the genus *Pygathrix* showed fewer synapomorphies than did the members of the *Rhinopithecus* group.

Secondly, *R. (Presbytiscus) avunculus* was seen to occupy a position clearly within the *Rhinopithecus* clade, but without the more derived synapomorphies common to the Chinese *Rhinopithecus* clade. The intermediate position of *R. (P.) avunculus* between the hypothetical common ancestor of the *Rhinopithecus*-*Pygathrix* clade (Node 2 of Fig. 1) and the hypothetical common ancestor of the Chinese species of *Rhinopithecus* (Node 6) was clearly shown by its position 67 steps away from the ancestral node and 69 steps away from the node defining the Chinese *Rhinopithecus* clade. It should be noted that when the tree editor was used to "force" *R. (P.) avunculus* to leave the *Rhinopithecus* clade and join the base of the *Pygathrix* clade at Node 2, the tree grew by a further 42 steps. When it was forced to join a polytomy of the Chinese snub-nosed langurs, a further 38 steps of evolution were required, but when the same species was forced to join a *Pygathrix* polytomy, a further 55 steps of evolution were required. Thirdly, the terminal taxa of *Rhinopithecus* were separated from their respective hypothetical common ancestors (at Nodes 5, 6, and 7 of Fig. 1) by larger numbers of character-state transformations than the terminal taxa of *Pygathrix* were separated from their respective hypothetical common ancestors (at Nodes 3 and 4). In this connection it should be noted that when the tree editor was used to collapse the associations of the Chinese *Rhinopithecus* species into a polytomy, many more steps of evolution (32) were required than when the same function was employed to collapse the associations of the *Pygathrix* taxa (10 steps more). Fourthly, *Pygathrix nemaesus moi* was distinguished from the common ancestor of *P. n. moi* and *P. n. nigripes* by relatively few character-state transformations, although numerous missing values for *P. n. moi* prevented a definitive tally being made. When the tree editor was employed to test the pairing of *P. n. moi*, it was found that moving either *P. n. moi* or *P. n. nigripes* to pair with *P. n. nemaesus* required 5 steps but moving *P. n. moi* and *P. n. nigripes* together required 10. Moving away from the shortest tree involved differing patterns of character homoplasies as well as increased amounts of total homoplasy. Moving *P. n. nigripes* to *P. n. nemaesus* involved forming fewer character homoplasies (9) than joining *P. n. nemaesus* to *P. n. moi* (14). *Pygathrix n. nigripes* and *P. n. moi* were clearly united by features of pelage coloration. The results of the present study thus implied that *P. n. moi* occupied an intermediate position between *P. n. nemaesus* and *P. n. nigripes*, although this conclusion may require modification in light of further information on the polarity of pelage coloration in the doucs as discussed below.

When the analysis was redone so that missing values were eliminated from the *Pygathrix* data set, the resulting tree had a length of 887 steps, a consistency index of 59, and a retention index of 66. This tree had the same topology as that of the most parsimonious tree discussed above, and the results of the branch-swapping routines were comparable to those performed on the original tree. The characters that united *P. n. nigripes* and *P. n. moi* were more robust than those uniting *P. n. nemaesus* and *P. n. moi*. As in the original analysis, the *Pygathrix* taxa did not exhibit a consistent pattern of size increase or decrease in the variables.

DISCUSSION

The adaptive array of *Pygathrix* and *Rhinopithecus* species in China and Southeast Asia is also a phyletic array [Jablonski, 1990; Jablonski & Peng, 1993]. Of these two genera, *Pygathrix* preserves the larger number of primitive features for the *Pygathrix*-*Rhinopithecus* clade and consequently is united by fewer synapomorphies, while the Chinese *Rhinopithecus* species (*R. R. roxellana*, *R. R. brelichii* and *R. R. bieti*) show the larger numbers of derived features for their clade [Jablonski & Peng, 1993]. As discussed by Jablonski and Peng [1993], the many

differences between *Pygathrix* and *Rhinopithecus* reflect the long independent evolutionary histories of the groups and, if taxonomy is to fairly reflect evolutionary history, then the two must be recognized as distinct genera. The fact that *Pygathrix* preserves several features that are primitive for the *Pygathrix-Rhinopithecus* clade is not to say that *Pygathrix* is primitive. The doucs share a number of synapomorphies, including many associated with their locomotor apparatus (Ottaviano and Jablonski, submitted for publication) and gut (Caton, personal communication), that are distinct from those defining the *Rhinopithecus* clade and that indicate that they have acquired many uniquely derived features since they last shared a common ancestor with *Rhinopithecus*. Interestingly, the distinctive pelage of the doucs must be considered primitive for the *Pygathrix-Rhinopithecus* clade. This is because the doucs have retained a coat composed largely of primitive, agouti-banded hairs as opposed to the derived conditions of all hairs with fully saturated pigment seen among *Rhinopithecus* species [Hershkovitz, 1968]. The generic distinction of *Pygathrix* and *Rhinopithecus* established by Jablonski and Peng [1993] was supported by the results of the present study, despite the fact that an expanded data set and different coding procedures were utilized.

The Tonkin snub-nosed langur, *R. (P.) avunculus*, fell almost exactly between the hypothetical common ancestor of the *Pygathrix-Rhinopithecus* clade and the hypothetical common ancestor of the Chinese species of *Rhinopithecus* as demonstrated by the 67 synapomorphies separating Nodes 2 and 5 and the 69 synapomorphies separating Nodes 5 and 6, respectively. This result raised the question as to what rank the species should occupy. Although the results of the present study might be construed to support the separate generic status of the Tonkin snub-nosed langur, the data on the species are still too incomplete to allow this question to be resolved at this time. The results presented here demonstrate its placement securely in the *Rhinopithecus* clade. The tree-editing procedures support the conclusion of a closer relationship of the Tonkin langur to the Chinese species of *Rhinopithecus* than with *Pygathrix* and the continued recognition of the Tonkin species at the subgeneric level within the genus *Rhinopithecus*, as per Jablonski and Peng [1993].

The main question left to be considered in this study was that concerning the number of species or subspecies of *Pygathrix* that warrant recognition. For the purposes of the discussion at this point, the groups of *Pygathrix* are referred to simply as *nemaeus*, *nigripes*, and *moi*. The finding that *nemaeus*, *nigripes*, and *moi* were separated from their respective hypothetical common ancestors by fewer character transformations than the species of *Rhinopithecus* were separated from their respective hypothetical common ancestors clearly suggests that the taxa of *Pygathrix* are less different from one another than the species of *Rhinopithecus* are from one another.

There exist no absolute rules as to how many character transformations define a particular level of the taxonomic hierarchy. In this study, rank has been assigned on the basis of the relative, as opposed to the absolute, number of synapomorphies revealed and, thus, is based solely on internal evidence and argumentation. In order to judge the taxonomic level at which the groups of *Pygathrix* can be recognized, only a relative assessment can be made based on a comparison of the number of character transformations between the hypothetical common ancestors of the recognized species of *Rhinopithecus* (*Rhinopithecus*) (i.e., between Nodes 6 and 7), and between the hypothetical common ancestors of the putative taxa of *Pygathrix* (i.e., between Nodes 3 and 4). This difference amounted to 39 character transformations between the former and 30 between the latter, a difference of 23%. The terminal taxa of *Pygathrix* also diverged from their respective hypothetical com-

mon ancestors by fewer character transformations than did the terminal taxa of *Rhinopithecus* (*Rhinopithecus*), although numerous missing values for *moi* precluded definitive comparison of relative levels of separation. The considerably larger number of steps of evolution necessary to collapse the association of the three Chinese *Rhinopithecus* species into a trichotomy than that required to collapse the association of the *Pygathrix* taxa provided crucial support to this hypothesis.

Together, these findings indicate that while the terminal taxa of *Rhinopithecus* (*Rhinopithecus*) warrant status as separate species the use of the same methods of comparison indicates that the terminal taxa of *Pygathrix* do not. The most appropriate designation for these taxa is that suggested by Napier [1985]: two subspecies of *Pygathrix nemaeus* only, *P. n. nemaeus* and *P. n. nigripes*. Although *moi* can be united with either subspecies, it is closer to *P. n. nigripes* because of the larger number of similarities, particularly the more conservative features of pelage, it shares with that subspecies. Therefore, the taxon designated *moi* is most appropriately recognized as a synonym of *P. n. nigripes*, as suggested by Napier [1985].

The subadult female douc pictured by Wirth et al. [1991] bears a pelage different from that of any of the recognized taxa of *Pygathrix*, including the *moi* variant of *P. n. nigripes*. It is most noticeably different in having uniformly agouti (as opposed to red or black) shanks. The existence of this highly unusual animal only highlights the fact, however, that other, less dramatic color variants are observed in other specimens. For instance, the *moi* male ZD.1908.11.1.2 from the British Museum (Natural History) has some faint agouti on the shanks, as does a *P. n. nigripes* male ZD.1927.12.1.8 from the same museum. Both of these individuals resemble the monkey pictured by Wirth et al. [1991] in their possession of some residual banding on the hairs of their shanks as opposed to displaying the uniformly black hairs more characteristic of *P. n. nigripes*. Examination of the skins designated as *moi* by Kloss shows that his original description [Kloss, 1926] does not adequately represent the variation observed in pelage coloration. Much of the variation in pelage that he highlighted (such as the presence of the black line above the sacral patch) and that has been noted here appears to be due to age-related changes and not to geographical variation. Because of the limitations of sample size, however, pelage variation between individuals of the same chronological ages from different localities could not be assessed.

It is interesting to note that specimens of infant *P. n. nigripes* bear lightish red hairs on the dorsal surfaces of the thigh and leg, and that juveniles of *P. n. nigripes* exhibit a very dark brown with some red on these surfaces whilst blackening from the lateral aspects. This ontogenetic sequence of changes in pelage coloration may be interpreted as either confirming an ancestral position for the red-shanked *P. n. nemaeus* or, alternatively, indicating that the red-shanked form is a more derived descendant of *P. n. nigripes-moi* clade that has retained a juvenile characteristic into adulthood.

The significance of variation in pelage coloration among doucs remains problematical and of questionable taxonomic value. As mentioned above, some of the unusual characteristics of pelage coloration in doucs that have been accorded taxonomic value in the past have been shown to be normal, age-related changes that are unrelated to the animals' geographical origins. It is likely, however, that some genuine geographically based variation in pelage coloration also exists. Biogeographic evidence supports the existence of a post-Pleistocene discontinuity between *nigripes* populations in the tropical/subtropical evergreen seasonal broadleaved forests in southern Vietnam and Cambodia and the more colorful *nemaeus* in the temperate evergreen seasonal broadleaved forests of northern Vietnam and

Laos [Frenzel et al., 1992; NOAA-EPA Global Ecosystems Database Project, 1992]. The existence of a subadult female with agouti limbs from far southern Vietnam illustrated by Wirth et al. [1991] poses further questions. If this animal has maintained its all-agouti limbs into adulthood, it may represent a population that occupies one end of a clinal range of continuous variation in limb pelage coloration among *nigripes* populations. If the loss of agouti is considered irreversible [as per Hershkovitz, 1968], then the specimen pictured by Wirth et al. [1991] must be considered ancestral to all other *Pygathrix*. The ancestral position of the all-agouti doucs would also be supported by the fact that the outgroup is composed of agouti-bearing *Macaca*. Unfortunately, the lack of further information on the all-agouti deme of doucs prevented testing of this variant phylogenetic hypothesis.

If the transformation of pelage coloration in the douc lineage is ultimately shown to follow the sequence from all agouti as the most primitive to black-shanked forms (including moi) as intermediates to red-shanked forms as the most derived, then Nodes 3 and 4 of the cladogram in Figure 1 would have to be exchanged in order to show the ancestral position of the *P. n. nigripes*-moi clade. This is a small change that would not, however, affect the taxonomic conclusions of this study.

In light of the facts that douc populations have been decimated by decades of war and that they continue to suffer extensive losses of habitat, it is unlikely that we will ever be in a position to know the original range of diversity that once existed among these monkeys. The need for further field surveys to document the remaining biodiversity in this unique species is urgent and unquestioned.

CONCLUSIONS

Five major conclusions have emerged from this study:

1. The taxa of *Pygathrix* as a group preserve a larger number of primitive features for the *Pygathrix-Rhinopithecus* clade than do the taxa of *Rhinopithecus*.
2. The taxa of *Pygathrix* are less different from one another than are the species of *Rhinopithecus* from one another.
3. The subspecies *Pygathrix nemaesus moi* Kloss, 1926 should be synonymized with *Pygathrix nemaesus nigripes*, as suggested by Napier [1985].
4. The extant doucs are best recognized as two subspecies, *P. nemaesus nemaesus* for the red-shanked douc and *P. nemaesus nigripes* for the black-shanked douc.
5. The phylogeny of the doucs and snub-nosed langurs proposed by Jablonski and Peng [1993] was found to be robust following testing on a larger sample (with fewer missing values) and utilizing a different method of character coding.

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APPENDIX A: List of Characters Considered in This Study

0. Upper canine buccolingual length
1. Upper canine to upper third molar length
2. Upper first molar to upper third molar length
3. Lower first molar to lower third molar length
4. Upper tooth row length
5. Palatal length
6. Palatal width
7. Upper bicanine breadth
8. Upper bimolar breadth
9. Upper incisive alveoli breadth
10. Postglenoid process to alveolare length
11. Cranial length
12. Braincase length
13. Cranial width
14. Midparietal width
15. Bizygomatic width
16. Postorbital constriction width
17. Temporal fossa length
18. Temporal fossa width
19. Zygomatic arch height
20. Piriform aperture height
21. Piriform aperture width
22. Upper face height
23. Muzzle length
24. Muzzle dorsum length
25. Biorbital width
26. Interorbital width
27. Bimastoid width
28. Occipital height
29. Foramen magnum length
30. Foramen magnum width
31. Basion to alveolare length
32. Glenoid fossa length
33. Glenoid fossa width
34. Lower bicanine breadth
35. Lower bimolar breadth
36. Lower incisive alveoli breadth
37. Mandibular condyle length
38. Mandibular condyle width
39. Mandibular length
40. Mandibular height between the first and second molars
41. Mandibular symphysis length

42. Mandibular corpus width at the first molar
43. Mandibular corpus width at the second molar
44. Scapular length
45. Scapular vertebral border length
46. Scapular glenoid fossa length
47. Scapular glenoid fossa width
48. Humeral head diameter
49. Humeral length
50. Biepicondylar breadth
51. Distal humerus articular surface width
52. Medial epicondyle width
53. Humeral shaft dorsoventral diameter
54. Humeral shaft mediolateral diameter
55. Ulnar length
56. Ulnar length mediolateral diameter
57. Ulnar shaft dorsoventral diameter
58. Radial length
59. Radial neck diameter
60. Carpus length
61. Radial head diameter
62. Skeletal trunk length
63. Acetabular diameter
64. Ischial length
65. Iliac length
66. Pubic length
67. Femoral head diameter
68. Femoral length
69. Femoral shaft dorsoventral diameter
70. Femoral shaft mediolateral diameter
71. Distal femoral breadth
72. Tibial length
73. Tibial shaft dorsoventral diameter
74. Tibial shaft mediolateral diameter
75. Fibular length
76. Calcaneal length
77. Calcaneal heel breadth
78. Talar length
79. Molar row area
80. Palatal width to length ratio
81. Upper face height to muzzle length ratio
82. Piriform aperture height to width ratio
83. Biorbital width to interorbital width ratio
84. Postorbital constriction width to cranial width ratio
85. Biorbital width to postorbital width ratio
86. Foramen magnum length to width ratio
87. Scapular length to width ratio
88. Intermembral index
89. Brachial index
90. Crural index
91. Skeletal trunk length to limb length ratio
92. Humeral robusticity index
93. Ulnar robusticity index
94. Femoral robusticity index
95. Tibial robusticity index
96. Medial humeral epicondylar width to lateral humeral epicondylar width ratio
97. Presence or absence of high, vertically oriented mandibular ramus
98. Presence or absence of a three-cusped upper third premolar

99. Presence or absence of wrinkled enamel on unworn molar surfaces
100. Presence or absence of accessory cusplets on molars
101. Presence or absence of "puffy"-looking molars
102. Consistent presence or absence of tuberculum sextum
103. Presence or absence of concave facial profile
104. Presence or absence of interorbital region oriented perpendicularly to occlusal plane
105. Presence or absence of mandibular body of uniform height from posterior to anterior
106. Presence or absence of upright mandibular symphysis
107. Presence or absence of greatly reduced or missing nasal bones
108. Presence or absence of short nasal bones
109. Presence or absence of double-chevron patterned nasal sutures
110. Presence or absence of long, narrow nasal bones
111. Presence or absence of triangular nasal bones
112. Ratio of tail length to body length
113. Degree of separation of male ischial callosities
114. Presence or absence of nasal flaps
115. Presence or absence of elongated nasal flaps
116. Presence or absence of relatively wide lower third premolars
117. Presence or absence of high molar relief, with deeply incised lingual notches evident on lower molars
118. Presence or absence of widely spaced molar cusp apices
119. Presence or absence of short trigonid and mesial shelf of molars
120. Presence or absence of asymmetrical distal edges of upper molars
121. Presence or absence of sacculated stomach
122. Presence or absence of sacculated fundus of stomach separated into two blind sacs by muscular septa
123. Presence or absence of cheek pouches
124. Presence or absence of telomeric Y chromosome
125. Diploid chromosome number
126. Presence or absence of lacrimal fossa in lacrimal bone
127. Presence or absence of median mental foramen
128. Color of crown hair
129. Color of temple hair
130. Color of temple patch
131. Color of forehead hair
132. Color of ear tuft
133. Color of whiskers
134. Color of hair on cheeks
135. Color of throat hair
136. Color of collar hair
137. Color of inner arm hair
138. Color of inner thigh hair
139. Color of hair on nape of neck
140. Color of hair over deltoid region
141. Color of hair on lateral aspect of arm
142. Color on hair over triceps region
143. Color of hair on lateral aspect of forearm
144. Color of hair on back of hand
145. Color of cape on upper back
146. Color of lower back hair
147. Color of sacral hair
148. Color of hair over iliac region
149. Color of hair around perineum
150. Color of hair on back of thigh
151. Color of hair on lateral aspect of thigh
152. Color of hair on leg
153. Color of hair on foot

154. Color of hair on tail
 155. Presence or absence of bicolored tail
 156. Color of tail tip
 157. Color of skin around eyes
 158. Presence or absence of blue skin around eyes
 159. Color of nasal skin
 160. Color of skin on philtrum
 161. Color of lips
 162. Presence or absence of pink lips
 163. Color of skin on ear
 164. Color of skin on palm of hand
 165. Color of nipples
 166. Color of ischial callosities
 167. Color of perineal and surrounding skin
 168. Color of penis
 169. Color of scrotum
 170. Length of tail hair
 171. Presence or absence of tail tuft
 172. Length of hair on withers
 173. Presence or absence of short hairs over sacrum
 174. Length of cape
 175. Presence or absence of ear tuft
 176. Presence or absence of whiskers
 177. Presence or absence of crest at vertex
-

APPENDIX B

The following is a list of the characters that describe the transformations enumerated in Table II. In this list, the number of the character is followed by the description of the transformation of the character. For instance, in the list of character transformations separating Node 2 from Node 3 below, the changes that occurred in characters 7 and 9 are designated as 7:1/0 and 9:0.1/0. This indicates that, for character 7, the character changed from state 1 at Node 2 to state 0 at Node 3. For character 9, the character changed from either states 0 or 1 at Node 2 to state 1 at Node 3.

Node 2 to Node 3

0:1/0; 1:1/0; 3:1.2/1; 4:0.2/0; 5:0.2/0; 6:3.4/4; 7:1/0; 9:0.1/0; 18:0.2/0; 19:3.4/4; 21:1.2/1; 22:2/1; 32:0.2/0.1; 34:0.1/1; 36:1.2/2; 40:0.1/0; 41:1/0; 43:1.2/0; 53:2.4/2; 54:1.3/1; 56:2.4/2; 57:1.3/1; 72:3.4/4; 79:1.2/1; 80:2/1; 82:2/4.6; 84:2/5.6; 90:2.3/2; 91:4.5/4; 92:2/5; 93:2/5; 94:1/5; 95:2.3/5; 96:2.3/2; 113:0/1; 124:0/1; 130:0/2; 131:0/1; 132:9/2; 137:0/1; 147:0/9; 148:0/1; 150:0/1; 154:0/9; 157:0/6; 159:6/9; 166:0/5; 170:1/0; 173:0/1.

Node 3 to *P. n. nemaeus*

2:1.2/1; 8:3.4/4; 11:1.2/2; 14:2.3/2; 16:4.5/5; 20:4.5/5; 23:0.1/1; 25:4/5; 26:3.4/4; 27:3.4/4; 28: 29:3.4/4; 30:3/4; 31:1.2/2; 32:0.1/0; 42:2.4/2; 44:2/1; 45:3.5/3; 47:3.4/3; 52:3/5; 59:1.2/0; 61:2.3/3; 63:3.4/4; 64:2.3/2; 67:2.3/3; 81:3.4/3; 82:4.6/6; 84:5.6/6; 85:3.4/4; 88:1.4/4; 89:2/7; 91:4/3; 93:5/6; 96:2/0; 135:6/9; 136:6/4; 143:0/9; 152:1/2.

Node 3 to Node 4

8:3.4/2; 10:1/0; 11:1.2/0; 15:2/1; 23:0.1/0; 24:3/2; 26:3.4/3; 27:3.4/3; 29:3.4/3; 31:1.2/1; 37:2/1; 44:2/2.3; 48:2/1.2; 50:3/2.3; 52:3/1.3; 61:2.3/0.3; 62:4/4.5; 65:2/0.2; 68:4/4.5; 75:4/4.5; 77:3/2.3; 79:1/0; 80:1/0; 81:3.4/4; 85:3.4/3; 92:5/5.6; 94:5/5.6; 128:0/1; 138:0/1; 165:1/5.

Node 4 to *P.n. moi*

2:1.2/2; 6:4/5; 13:3/2; 14:2.3/3; 16:4.5/5; 20:4.5/5; 28:2/3; 32:0.1/1; 34:1/2; 42:2.4/2; 81:4/5; 82:4.6/4; 84:5.6/6; 86:2/0.

Node 4 to *P. n. nigripes*

2:1.2/1; 12:3/2; 14:2.3/0; 16:4.5/4; 20:4.5/4; 21:1/0; 24:2/0; 30:3/2; 31:1/0; 32:0.1/0; 35:2/1; 37:1/0; 38:2/1; 39:1/0; 42:2.4/4; 44:2.3/3; 45:3.5/5; 48:1.2/1; 50:2.3/2; 52:1.3/1; 59:1.2/2; 61:0.3/0; 62:4.5/5; 63:3.4/3; 64:2.3/3; 65:0.2/0; 67:2.3/2; 68:4.5/5; 75:4.5/5; 77:2.3/2; 82:4.6/6; 83:0/1; 84:5.6/5; 86:2/3; 88:1.4/1; 92:5.6/6; 94:5.6/6.

Node 2 to Node 5

0:1/2; 2:1.2/2; 3:1.2/2; 7:1/2; 12:3/4; 13:3/4; 14:2.3/4; 15:2/4; 17:3/5; 18:0.2/2; 19:3.4/1.2; 21:1.2/2; 23:0.1/0; 26:3.4/4; 27:3.4/4; 28:2/3; 29:3.4/4.5; 38:2/3; 40:0.1/2; 41:1/2; 42:2.4/5; 43:1.2/3; 46:3/3.4; 47:3.4/3.5; 48:2/2.3; 50:3/3.4; 51:2/2.4; 54:1.3/1.4; 60:4/4.5; 61:2.3/2.5; 63:3.4/3.5; 66:4/4.5; 67:2.3/2.4; 69:3/3.5; 70:3/3.5; 71:3/3.5; 74:3/3.4; 76:4/4.5; 77:3/3.5; 78:3/3.4; 79:1.2/2; 81:3.4/4; 85:3.4/4; 87:1/0.1; 103:0/1; 104:0/1; 105:0/1; 106:0/1; 107:0/1; 112:3/0; 113:0/2; 115:0/1; 122:0/1; 128:0/0; 138:0/6.7; 141:0/1; 142:0/9; 143:0/1; 145:0/3; 148:0/9; 158:0/1; 159:1.6/1; 162:0/1; 168:9/19; 174:0/1; 175:0/1; 176:0/1.

Node 5 to *R. (Presbytiscus) avunculus*

4:0.2/0; 5:0.2/0; 6:3.4/2; 8:3.4/3; 9:0.1/0; 10:1/0; 11:1.2/1; 14:4/5; 16:4.5/4; 19:1.2/0; 20:4.5/4; 29:4.5/5; 31:1.2/1; 32:0.2/0; 34:0.1/0; 36:1.2/0; 85:4/5; 86:2/8; 128:0/1; 129:0/9; 130:0/1; 131:0/9; 135:6/4; 136:6/9; 137:0/8; 138:6.7/7; 147:0/5; 154:0/5; 156:9/8; 157:0/8; 160:9/5.

Node 5 to Node 6

0:2/2.3; 1:1.2/4; 2:2/4; 3:2/5; 4:0.2/1.3; 5:0.2/2; 6:3.4/4; 7:2/3.4; 9:0.1/1.2; 10:1/2; 11:1.2/1.3; 12:4/4.6; 13:4/5.6; 15:4/5; 16:4.5/5; 17:5/5.6; 18:2/2.4; 20:4.5/4.6; 21:2/4; 22:2/3; 25:4/5; 26:4/5; 27:4/5; 28:3/4; 30:3/5; 31:1.2/2; 32:0.2/1.2; 33:2/5; 34:0.1/3; 35:2/4; 36:1.2/3.4; 37:2/2.4; 38:3/4.5; 39:1/3; 40:2/4; 41:2/4; 43:3/4; 45:3.5/5; 46:3.4/4; 47:3.5/5; 48:2.3/3; 50:3.4/4; 51:2.4/4; 53:2.4/4; 54:1.4/4; 56:2.4/4; 57:1.3/3; 61:2.5/5; 63:3.5/5; 66:4.5/5; 67:2.4/4; 69:3.5/5; 70:3.5/5; 71:3.5/5; 74:3.4/4; 77:3.5/5; 78:3.4/4; 79:2/2.5; 81:4/5; 88:1.4/3.4; 112:0/5; 128:0/3; 134:9/0; 137:0/9; 138:67/6; 139:0/3; 146:0/2; 150:0/9; 170:1/1.2.

Node 6 to *R. (Rhinopithecus) roxellana*

0:2.3/3; 1:2.4/4; 2:4/6; 4:1.3/3; 7:3.4/4; 8:3.4/4; 9:1.2/2; 11:1.3/3; 12:4.6/6; 13:5.6/6; 17:5.6/6; 18:2.4/5; 19:1.2/1; 20:4.6/6; 24:3/2; 29:4.5/4; 32:1.2/2; 36:3.4/5; 37:2.4/4; 38:4.5/5; 42:5/6; 46:4/6; 47:5/6; 59:1.2/1; 60:4.5/5; 62:4/5; 64:2.3/1; 72:3.4/3; 76:4.5/5; 79:2.5/6; 81:5/6; 86:2/0; 87:0.1/0; 88:3.4/4; 90:2.3/0; 91:4.5/5; 95:2.3/2; 96:2.3/5; 129:0/4; 134:0/4; 140:1/0; 141:1/3; 143:1/3; 144:1/3; 147:0/6; 151:1/3; 152:1/3; 153:1/8; 154:0/2; 164:1/8; 165:1/6; 170:1.2/2; 172:0/1; 174:1/2; 177:0/1.

Node 6 to Node 7

5:2/2.4; 6:4/4.6; 19:1.2/2; 21:4/5; 22:3/3.5; 24:3/4; 28:4/5; 29:4.5/5; 34:3/4; 35:4/5; 39:3/4; 43:4/4.6; 48:3/6; 50:4/5; 51:4/5; 52:3/4; 53:4/5; 56:4/5; 57:3/5; 59:1.2/3; 64:2.3/4; 65:2/6; 67:4/5; 72:3.4/4; 73:4/6; 74:4/5; 78:4/6; 80:2/2.3; 82:2/1; 89:2/3; 90:2.3/3; 91:4.5/3; 96:2.3/0.3; 131:0/5; 133:9/6.9; 145:3/1; 148:9/8.9; 149:9/8.9; 154:0/1.

Node 7 to *R. (Rhinopithecus) bieti*

0:2.3/6; 1:2.4/4; 4:1.3/3; 5:2.4/4; 6:4.6/6; 7:3.4/4; 8:3.4/6; 9:1.2/2; 11:1.3/4; 12:4.6/7; 13:5.6/7; 14:4/7; 15:5/6; 17:5.6/6; 18:2.4/4; 19:2/4; 20:4.6/7; 21:5/6; 22:3.5/5; 23:0/1; 24:4/5; 27:5/7; 28:5/6; 29:5/6; 30:5/6; 31:2/4; 32:1.2/1; 36:3.4/4; 37:2.4/5; 38:4.5/5; 43:4.6/6; 45:5/6; 57:5/6; 74:5/6; 76:4.5/4; 79:2.5/5; 80:2.3/3; 84:2/1; 85:4/6; 87:0.1/0; 88:3.4/3; 93:2/1; 94:1/0; 95:2.3/0; 96:0.3/0; 128:3/7; 129:0/5; 133:1.6/1; 134:0/3; 138:6/8; 139:3/1; 146:2/3; 147:0/1; 148:7.8/7; 149:7.8/8; 157:0/5; 163:1.5/1; 166:0/3; 168:19/1; 170:1.2/2; 171:0/1; 172:0/2; 177:0/1.

Node 7 to *R. (Rhinopithecus) brelichi*

0:2.3/2; 1:2.4/2; 4:1.3/1; 7:3.4/3; 8:3.4/3; 9:1.2/1; 11:1.3/1; 12:4.6/3; 13:5.6/5; 17:5.6/5; 18:2.4/2; 20:4.6/4; 32:1.2/4; 33:5/6; 34:4/6; 36:3.4/3; 37:2.4/0; 38:4.5/4; 39:4/5; 40:4/5; 41:4/6; 42:5/3; 44:2/5; 49:4/6; 50:5/7; 51:5/6; 52:4/5; 53:5/6; 54:4/6; 55:4/6; 56:5/7; 58:4/6; 59:3/6; 62:4/3; 64:4/5; 66:5/7; 67:5/6; 68:4/5; 69:5/6; 70:5/6; 71:5/6; 72:4/6; 75:4/6; 76:4.5/6; 79:2.5/2; 82:1/0; 84:2/3; 87:0.1/1; 88:3.4/6; 90:3/6; 91:3/0; 94:1/2; 95:2.3/4; 112:5/1; 129:0/3; 133:1.6/6; 134:0/6; 135:6/4; 136:6/0; 137:9/6; 147:0/3; 148:7.8/8; 149:7.8/7; 150:9/6; 151:1/0; 164:1/7; 170:1.2/1; 175:1/0.