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Speciation and biogeography of Vietnam's primates

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Summary

Vietnam is home to approximately 24 primate taxa including two lorises, five macaques, 11 colobines, and six gibbons. The biogeography of these primates is quite interesting with the vast majority being restricted to the region of Southeast Asia to the east of the Mekong River making this area, with Vietnam forming its heart, much richer in primate diversity than the area to the west of the river. This is quite interesting because the Mekong does not appear to be an important barrier for most other mammalian groups. In addition, within Vietnam, there is an interesting north – south distribution of primate taxa with closely related species replacing one another along this gradient. While this north – south distribution appears to be closely related to modern climatic conditions, the distinct distribution of primate taxa east of the Mekong appears to be related to Pleistocene climatic change caused by glacial cycles. A final fascinating feature of primate biogeography in Southeast Asia is the close association of a number of *Trachypithecus* species with the distinctive limestone geography of northern Vietnam – this union is so tight that the common name "limestone langurs" aptly characterizes the distribution of these taxa.

Sự hình thành loài và địa lý sinh vật học của các loài linh trưởng Việt Nam

Tóm tắt

Việt Nam là nơi cư ngụ của khoảng 24 loài và phân loài thú linh trưởng bao gồm, 2 loài culi, 5 loài khỉ, 11 loài voọc ăn lá, và 6 loài vượn. Địa lý động vật học của các loài linh trưởng này rất thú vị với đặc trưng như sau: phần lớn các loài phân bố khắp vùng Đông Nam Á đến phía đông sông Mê Kông với Việt Nam ở vị trí trung tâm, sự đa dạng thành phần loài ở khu vực này hơn hẳn khu vực phía tây của sông Mê Kông. Tuy nhiên sông Mê Kông lại không phải là yếu tố cách ly địa lý quan trọng đối với các nhóm động vật khác. Mặt khác, ở Việt Nam các loài linh trưởng lại phân bố theo trục Bắc - Nam với các loài gần nguồn gốc lần lượt thay thế nhau. Phân bố của các loài linh trưởng ở Việt Nam theo trục Bắc - Nam liên quan đến mô hình thay đổi của khí hậu theo vĩ độ, trong khi sự phân bố một cách tập trung ở đông sông Mê Kông lại liên quan đến sự thay đổi khí hậu ở thời kỳ Pleistocene gây ra bởi chu kỳ băng hà trên trái đất. Một đặc trưng thú vị khác về địa lý sinh vật của bộ thú linh trưởng ở vùng Đông Nam Á đó là mối liên quan giữa các loài thuộc giống *Trachypithecus* với hệ thống núi đá vôi biệt lập ở phía bắc Việt Nam. Mối liên hệ chặt chẽ đến mức các loài này thường được gọi là "voọc núi đá" để chỉ đặc trưng vùng phân bố của nhóm loài.

Introduction

There are perhaps 24 living species of primates in Vietnam (Table 1, Groves 2004). The uncertainty arises both because of queries about the validity of certain species, and because it is unclear whether a couple of them do actually occur within the territorial limits of Vietnam.

In what follows, I adopt the following definition of a species (based on the Phylogenetic Species Concept, or PSC):

Table 1. Primate Species in Vietnam

Suborder Strepsirrhini	
Family Loridae	
Genus Nycticebus	
Nycticebus bengalensis	Greater slow loris
Nycticebus pygmaeus	Pygmy slow loris
Suborder Haplorrhini	
Family Cercopithecidae	
Subfamily Cercopithecinae	
Genus *Macaca*	
Macaca arctoides	Stumptailed macaque
Macaca assamensis	Assam macaque
Macaca leonina	Northern pigtailed macaque
Macaca mulatta	Rhesus monkey
Macaca fascicularis	Crab-eating (Longtailed) macaque
Subfamily Colobinae	
Genus *Trachypithecus*	
*Trachypithecus crepusculu*s	Dusky langur
Trachypithecus margarita	Margarita langur
Trachypithecus germaini	Northern silvered langur
Trachypithecus francoisi	Francois' langur
Trachypithecus poliocephalus	Cat Ba langur
Trachypithecus hatinhensis	Hatinh langur
Trachypithecus ebenus	Black langur
Genus *Pygathrix*	
Pygathrix nemaeus	Red-shanked douc
Pygathrix nigripes	Black-shanked douc
Pygathrix cinerea	Grey-shanked douc
Genus *Rhinopithecu*s	
Rhinopithecus avunculus	Tonkin snubnosed monkey
Family Hylobatidae	
Genus *Hylobates*	
Hylobates pileatus 1)	Pileated gibbon 1)
Genus *Nomascus*	
Nomascus concolor	Western black gibbon
Nomascus nasutus	Eastern black gibbon
Nomascus leucogenys	Northern white-cheeked gibbon
Nomascus siki	Southern white-cheeked gibbon
Nomascus gabriellae	Buffy-cheeked gibbon

1) Note from the editor: There is no evidence that *Hylobates pileatus* occured in recent time in Vietnam.

A species is the smallest cluster of individual organisms within which there is a parental pattern of ancestry and descent and that is diagnosable distinct from other such clusters by a unique combination of fixed character states.

This concept of what a species is contrasts with the once widely-adopted Biological Species Concept (BSC), in which it is a requirement that different species do not 'actually or potentially' interbreed under natural conditions. There are numerous reasons why the BSC cannot be maintained: one is that 'potentially' is undefined, and probably undefinable, so that there can be no criterion for deciding whether allopatric forms are distinct species or not, and another is that we now understand that distinct sympatric species may interbreed widely and possess another species' mtDNA or Y chromosome DNA! The PSC also contrasts with the more recently proposed Genetic Species Concept (GSC), in which different species have to exhibit a given amount of genetic distance in a specified DNA sequence, usually a mtDNA locus. The reasons why this concept is unsatisfactory include the fact that perfectly distinct sympatric species may differ extremely little genetically, that some populations within a species may have greater genetic distances between them than some distinct species, and that different parts of the genome will show varying amounts of differentiation. The fact that non-recombining parts of the genome – mtDNA and Y chromosome DNA – may 'leak' across species boundaries argues against both BSC and GSC.

The advantages of the Phylogenetic Species Concept are considerable:

- It relies on observable **pattern**, not on the **process** by which the pattern is supposed to have arisen or to be maintained;
- It is **objective**, not dependant on some hypothesis of evolutionary relatedness;
- It is **operational**, not dependant on a subjective assessment of whether "they might interbreed were their ranges to meet";
- It depends on whether the differences are **fixed** (as far as the available evidence indicates), not on the **degree** or **amount** of difference;
- It does not depend on speculation about **mechanisms** of speciation involved - even in the case of species of hybrid origin;
- No assumptions are necessary about the **time elapsed** since speciation was begun or completed;
- We do not need to speculate on the **functional significance** of species differences;
- There is no need to panic if **interbreeding** is detected between species;
- Species are the **units of evolution**: they have "their own unitary evolutionary role and tendencies" (the Evolutionary Species);
- Species are the **terminals** on a **cladogram**: below the species level, genealogy becomes reticulate;
- Species, being consistently defined, are suitable as **units of biogeographical analysis**;
- The species, finally, is suitable as the focus of conservation concern, being more or less equivalent to the **Evolutionary Significant Unit** (ESU).

Two of the primate species in Vietnam are strepsirrhines; 16 are Old World monkeys (5 macaques, 11 langurs); six are gibbons.

Biogeography

Some of Vietnam's primate species are endemic; some of them may extend over the border into Laos, a country whose fauna is less well-known than that of Vietnam; and others may nowadays be confined to Vietnam because they have recently become extinct in adjacent regions of China. What is perfectly true however is that, if we take the region east of the Mekong as a whole (that is to say, all of Vietnam except for the extreme south, all of Laos except for two small areas in the west and southwest, about one third of Cambodia, and a small part of China immediately north of the border), over half of the primate species of that region (and at least two genera, *Pygathrix* and *Nomascus*, and in one perspective a third, *Rhinopithecus*) are endemic, and Vietnam lies at the heart of this region.

An interesting aspect of this situation is that, with the exception of the gibbons at the generic level, and possibly of the *Trachypithecus cristatus* group at the specific level, vicariance is not involved: none of the species or species-groups that are confined to the east of the Mekong has representatives to the west of it. In other words, the primate fauna east of the Mekong is richer and more diverse than that elsewhere in mainland Southeast Asia. The primates are, in fact, unusual in this respect; very few other mammals are represented by ‘surplus’ species east of the Mekong in the same way as are primates (Meijaard & Groves, 2006).

Within Vietnam itself, there is also a division between the more seasonal northern half of the country and the more tropical southern half. All of Vietnam’s nonhuman primates, with the exception of the two species of loris and of one of the macaques, are affected by this division: either vicariant species replace each other in the two zones, or else (as in the case of the limestone langurs) they are restricted to one of the zones and absent from the other.

The reasons for this endemicity were briefly discussed by Groves (2004) and, in more detail, by Meijaard & Groves (2006). In summary, it involves the history of climatic fluctuations in the region and of the Mekong River itself. Studies of geomorphology (such as the filling rate changes of offshore sedimentary basins), and of the relationships of freshwater fish and mollusc faunas, all combine to suggest that the Mekong has moved sporadically eastward throughout the Plio-Pleistocene. In the Pliocene and most of the Pleistocene, the upper Mekong flowed along with the Salween into the Chao Phraya. The present-day middle course of the river was established in the Middle Pleistocene, though the lower Mekong still flowed into the Chao Phraya. Apparently the present lower course, south of Khong Island, was a separate stream until it captured the main river as little as 5,000 years ago.

Rainforest existed in Indochina in most of the Miocene and Pliocene, but was largely replaced by grassland and bush in the Late Pliocene and most of the Pleistocene. The climate was gradually cooling over this period, probably exacerbated by an extraterrestrial impact, centred in the Ubon district of eastern Thailand, about 800,000 years ago. During the Middle and Late Pleistocene, climates fluctuated in phase with the rise and fall of sea levels, but even during cool, dry climatic phases the Truong Son range remained forested throughout, so that it remained a refuge for rainforest taxa even when they disappeared elsewhere - and this is what permitted the distinctive East-of-Mekong primate fauna to differentiate in isolation.

The north/south zonation is explicable in terms of the modern climate. The northern and southern halves of the country contrast in their seasonality and consequent vegetation. Not surprisingly, species have spread as far as their ecological circumstances will allow, or until they are out competed by better adapted congenerics. But this north/south replacement is not a simple two-way affair. In two cases (*Macaca assamensis* and *M. leonina*; *Trachypithecus crepusculus* and *T. germaini/margarita*), congeneric species which are not sister species replace each other only approximately; in a third case (*Macaca mulatta* and *M. fascicularis*), two somewhat more closely related species hybridise extensively where their ranges meet; and in the other two cases (*Pygathrix nemaeus* and *P. nigripes*; *Nomascus leucogenys* and *N. gabriellae*), an arguably intermediate third species exists which, I will suggest, originated as a hybrid between the other two.

Finally, there is a unique habitat which is centred on the northern Vietnam and extends over the borders into northern Laos and southern China: the limestone hills. They are responsible for a wholly endemic species-group of primates, the so-called limestone langurs, as well as a number of endemic rodent genera (*Laonastes, Tonkinomys, Saxatilomys*). It has recently been argued (Li & Rogers, 2005) that limestone hills are not necessarily the preferred habitat for the limestone langurs – at least, in the case of the Southeast Chinese endemic *Trachypithecus leucocephalus* - rather, they are a refuge from human disturbance. It is certainly true that the various species of this group must theoretically be capable of traveling through suitable habitat beyond limestone hills, because each of them is found today in several separate limestone blocs; nonetheless, it is worth noting that the entire group is restricted to the (Northern) region where the limestone blocs occur, and that even in this area *Trachypithecus crepusculus* is found in forest areas away from limestone hills, which the limestone langurs are not.

Loridae

There are two species of loris in Vietnam. The larger of the two, the Bengal slow loris (*Nycticebus bengalensis*), is one of a number of vicariant species into which the *N. coucang* group (sometimes called the greater slow lorises) is nowadays divided; the other species of the group live in the Malay peninsula, western Indonesia and the Tawitawi Islands of the southern Philippines. The Bengal species is much the largest of the group, and also the lightest in colour – white, or nearly so, on the foreparts, with rather poorly marked dorsal stripe and head markings. It is found all across mainland Southeast Asia, north of the Isthmus of Kra, from Bengal East across the Mekong, and north into southern China.

The smaller loris of Vietnam is the pygmy loris (*Nycticebus pygmaeus*). This is one of the species endemic to the region east of the Mekong. It is much smaller than any of the species of the *N. coucang* group, and is distinguished from all of them by various cranial, dental and external features - most characteristically by its large ears. It is reddish or brownish, with a dorsal stripe and dark fork-marks on the head; Streicher (2004) found that the colour changes, and the dark markings fade and reappear, according to season (and see also Groves, 2004). *Nycticebus intermedius*, still believed in by a few biologists, is a synonym of *N. pygmaeus*; *N. pygmaeus* was first described on the basis of a subadult specimen, and the species was so poorly known for the first half-century after its original description that, when the first adult was examined in detail, it was not recognized as being the same species and so described as something new!

How significant it is that the only taxa of the genus *Nycticebus* that exist in sympatry are the one that is largest and lightest coloured and the one that is smallest and darkest coloured? It is possible that we may have here an example of character displacement; after all, *N. pygmaeus* is only found where *N. bengalensis* is also found and could presumably have become more physically distinctive as a result. *N. bengalensis*, however, as a wide distribution west of the Mekong as well as east of it, and of course over most of this wide range it is the only loris, and it is therefore unlikely to have been changed just because of sympatry with *N. pygmaeus*. It may be simply that the two species are so very different that they are the only ones that are capable of existing in sympatry, and they have not affected each other morphologically.

We know little about how the two species differ ecologically, although Gause's Principle predicts that they must.

Cercopithecidae: Cercopithecinae

The five species of cercopithecine monkeys in Vietnam are all macaques. One of them, the stumptailed or bear macaque (*Macaca arctoides*), is found throughout Vietnam without, as far as is known, varying between the northern and southern regions, although no detailed study has been undertaken to verify this. Although it is not endemic to the east-of-Mekong region, it is of special interest as being a species of hybrid origin (Tosi *et al.,* 2000), and so potentially a model for the formation of a few other species in the region.

Among the other four species, there are two north/south pairs. The Assam macaque (*M. assamensis*) occurs in the north, and is replaced by the northern pigtail (*M. leonina*) in the south; but the replacement is not precise (they overlap very widely), and the two species belonging to different species-groups.

The species other north/south pair interbreed where their ranges meet. The rhesus macaque (*M. mulatta*) and the crab-eating or long-tailed macaque (*M. fascicularis*) are members of the same species group, but within it they are not themselves sister species; they nonetheless hybridise where their ranges meet along an approximately East-West line across mainland Southeast Asia, including Vietnam. North from the hybrid zone, rhesus monkeys extend far into China, and west into India and somewhat beyond; south of the zone, crab-eating macaques extend into western Indonesia and Philippines.

But the hybridisation between them is not a simple two-way affair: fewer genes appear to be flowing north than are flowing south, because whereas *M. mulatta* appears to be fairly typical right up to the hybrid zone, *M. fascicularis* shows signs of the presence of *M. mulatta* genes. Mainland

M. fascicularis, compared to those in the Malay peninsula and in islands of Southeast Asia, commonly have relatively short tails, especially towards the hybrid zone; they often possess cheek hair similar to *M. mulatta* (the so-called infrazygomatic crest, rather than the transzygomatic type which tends to be characteristic of the species elsewhere); and a *M. mulatta* Y chromosome has been recorded from a *M. fascicularis* in Vietnam.

Recently, I have put forward a hypothesis to explain this asymmetrical hybridisation (Groves, in press). I proposed that *M. fascicularis* evolved in Sundaland (islands of Southeast Asia) and that the original boundary between it and *M. mulatta* was the Isthmus of Kra, which for most of the Pleistocene was a seaway. When the land-bridge that is now the Isthmus was established, *M. fascicularis* spread north into the tropical rainforest on the mainland, replacing *M. mulatta* (a species better adapted to deciduous forests) and interbreeding with it along a moving frontier. The various *M. mulatta*-like features of mainland *M. fascicularis* are a legacy of this. On the other hand, as *M. mulatta* is the larger species, the males are likely to be dominant over males of *M. fascicularis*, so that the hybridisation would be mostly male rhesus with female crab-eaters.

Cercopithecidae: Colobinae

There are three genera of colobine monkeys in Vietnam: *Rhinopithecus* (snub-nosed monkeys, a more typically Chinese group), *Pygathrix* (the Douc langurs, a prime example of a genus endemic to the East-of-Mekong region) and *Trachypithecus* (more typical langurs, the genus being widespread throughout mainland and islands of Southeast Asia).

The Vietnamese species of snub-nosed monkeys is the Tonkin snubnosed monkey *Rhinopithecus avunculus* (Fig. 1). This is arguably the most important primate in the whole of Vietnam. This is because, while it is not alone in being endemic to Vietnam, it is a more thoroughly distinct species than any other Vietnamese primate, occupying an isolated position within its genus both morphologically (its long slender fingers and toes, its bizarre facial appearance) and ecologically (the only subtropical snub-nosed monkey); it numbers little more than 100 and is still declining because of hunting pressure despite ostensibly being protected by political decree (Government of Vietnam, 2006). While at least one other endemic Vietnamese species, *Trachypithecus poliocephalus*, is even more critically endangered in terms of absolute numbers, it has at least registered a slight increase in numbers over the past 2-3 years, and one might argue that the limestone langurs form a more close-knit group than do the snub-nosed langurs, and within them *T. poliocephalus* itself may be conspecific with a slightly more numerous Chinese taxon, the white-headed langur, *T. (cf. poliocephalus) leucocephalus*. Without wishing to be invidious in regard to which species is more critically endangered than any other, I would like to highlight the plight of the Tonkin snub-nosed monkey as of supreme national and global importance, and to emphasize that it will be an international scandal should it become extinct.

The east-of-Mekong endemic genus, *Pygathrix*, known as douc langurs, has a limited distribution in the southern and central parts of the region. The red-shanked douc, *Pygathrix nemaeus*, was the very first Vietnamese primate to be made known scientifically. It was described, as ‘le douc’, by Buffon (1766); on the basis of Buffon’s description it was given the scientific name *Simia nemaeus* by Carl Linnaeus, the founder of the modern system of biological taxonomy and nomenclature (Linnaeus, 1771), and later the species was placed in a special genus, *Pygathrix*, by Étienne Geoffroy St-Hilaire in a paper which may be said to mark the foundation of modern primate taxonomy. The specimen described by Buffon (1766), hence the type specimen of the species, still exists in the Muséum National d’Histoire Naturelle, Paris; its red shanks, although much altered in the original tone over the past 250 years, can be discerned (Fig. 2), even though Buffon did not actually mentioned them in his description. There is no doubt, therefore, that the name *Pygathrix nemaeus* is correctly applied to the northerly representative of the genus, the red-shanked douc, despite Buffon having given the place of origin as ‘Cochin-China’.

The distributions of the three species are given by Nadler *et al.* (2003). Essentially, the red-shanked douc (*Pygathrix nemaeus*) occurs from about 19°N south to nearly 13°N along the Lao border, but only as far as 14°33’N further seaward. The black-shanked douc (*Pygathrix nigripes*) occurs from 14°33’N as far south as Ho Chi Minh City; it overlaps with the red-shanked species in

Fig. 1. The type skin of Tonkin snubnosed monkey (*Rhinopithecus avunculus Dollman, 1912*). Photo: Colin P. Goves

Fig. 2. 'Le douc' described by Buffon & Daubenton in 1766, hence the type specimen of *Simia nemaeus* Linnaeus, 1771 (now *Pygathrix nemaeus*). Photo: Colin P. Groves

Kon Ka Kinh National Park[1], and hybrids are known. The grey-shanked douc (*Pygathrix cinerea*) has a very small range between the two, and overlapping with both; it occurs from 15°25'N (and possibly still further north) to about 14°25'N. Since its distribution is more or less confined to the overlap zone between the other two species, the question arises whether it might not be a stabilized hybrid between them. At least one species of hybrid origin is already known in primates, *Macaca arctoides* (see above). Roos (2004) found the mtDNA of *P. cinerea* to be closer to that of *P. nemaeus*, so that if it is indeed of hybrid origin it is likely to be ♀ *nemaeus* x ♂ *nigripes*, a proposition which could be tested by sampling Y chromosome DNA. As the mtDNA of *P. cinerea* and *P. nemaeus* are not identical, the presumptive hybridisation event is of some antiquity, and indeed the species is by now apparently perfectly homogeneous.

The third genus of colobine in Vietnam is *Trachypithecus*. A recent revision of the tropically distributed *T. cristatus* group (Nadler *et al.,* 2005) identified two separate species in the Indochinese region, *T. germaini* and *T. margarita*, which had not been distinguished by Groves (2001). They suggested that the boundary between these two might be the Mekong River, but as noted above the Mekong does not usually separate sister species, and, especially considering that the two have traditionally not been distinguished, caution must be expressed, and field surveys are desirable. One of these two species, presumably *T. margarita*, is found as far north as 16°37'N. a species belonging to a different species group, the dusky langur (*Trachypithecus crepusculus*), is found from about 18°N, north across the Chinese border. No lowland forest langur is known between the ranges of these two last species.

There is no doubt that the species group of *Trachypithecus* that is of most interest and concern here is the group known as limestone langurs: of most interest, because they are endemic to the East-of-Mekong region; of most concern, because every one of the species of the group is "Endangered" or (mostly) "Critically Endangered". They are glossy black animals, with a crest of hair on the scalp; a curved tract of elongated hair from mouth to ear, resembling a handlebar moustache; and (in all but one species) areas of white or yellowish on the head and, often, on the rump and/or tail. As in all species of *Trachypithecus*, the unweaned infants are a golden orange colour.

[1] Note from the editor: S. page 55-60: Ha Thang Long: Distribution of grey-shanked douc in Gia Lai Province.

Fig. 3. White-headed langur (*Trachypithecus leucocephalus*) in Fusui Nature Reserve, Guangxi Province, China. Photo: Tilo Nadler.

Fig. 4. Cat Ba langur (*Trachypithecus poliocephalus*) on Cat Ba Island, Vietnam. Photo: Stefan Kobold.

There are seven species, one of them rather controversial but I will treat it as a species in order to focus attention upon it until such time as it may be shown to be merely a colour morph. The species are as follows:

T. francoisi. The northernmost representative of the group; it occurs in suitable country north of the Red River, extending as far north as about 29°N in Guizhou Province, China. It is black, except for the handlebar moustache which is white as far as the upper edge of the ear.

T. hatinhensis. The southernmost representative of the group, found from about 19°40'N south to about 16°N in Vietnam; it probably extends over the border into Laos. Superficially looks very similar to *T. francoisi*, but the white tract extends behind the ear, approaching the midline of the nape sometimes very closely.

T. poliocephalus. Restricted to Cat Ba, the largest island in Ha Long Bay. The head is creamy white or golden yellow, this colour extending down the neck to the shoulders; the tips of the crest hairs remain black. There are yellow-brown hairs on the feet, and grey hairs on the sacral region and, generally, the thigh-backs.

T. leucocephalus. Not known from Vietnam; known from a small range in Guangxi Province in China; it hybridizes with *T. francoisi* where their ranges meet. The head is white (not creamy or yellow), and this colour extends further onto the chest and shoulders than in *T. poliocephalus*; the feet and sacral region have white hairs, and the tail is terminally white, this colour extending to as much as three-quarters of the tail length in some individuals. Differences between this species and *T. poliocephalus*, which it very much resembles, can be seen in Fig. 3 and 4.

T. laotum. This species is not known from Vietnam, but only from a small region of Laos, about 17°50'-18°30'N (Duckworth *et al.,* 1999). The head is white except for the black crest and a black strip down the nape from the crest to the shoulders (Fig. 5 and 6).

T. delacouri. From south of the Red River, to only about 20°N, and known only from Vietnam. This species and *T. poliocephalus* are therefore the only members of the group that are strictly Vietnamese endemics. It is the most distinctive in appearance of the group, with white hindparts and thighs, and long grey cheek whiskers; the tail is curiously bushy.

Fig. 5. The type specimen of Laos langur (*Pithecus laotum* Thomas, 1921 - now *Trachypithecus laotum*). Photo: Colin P. Groves.

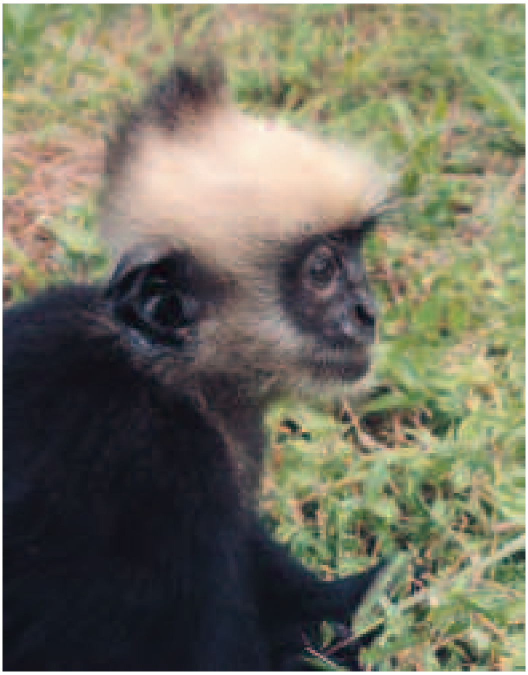

Fig. 6. Laos langur (*Trachypithecus laotum*) at the Endangered Primate Rescue Center, Vietnam. Photo: Tilo Nadler.

T. ebenus. Known from the Nui Giang Man proposed nature reserve in Quang Binh Province, Vietnam (Le Khac Quyet, 2004), extending westward apparently as far as the Mekong in Laos (Duckworth *et al.,* 1999). It is completely black, with just faint yellow tipped hairs on cheeks, chin and upper lip, and around palms and soles, and whitish hairs at front of ear. The very existence of this species is controversial; it is said to form homogeneous troops in its Vietnam range, but it is unclear whether it does so in Laos, or whether it behaves as merely a polymorphic variant of *T. laotum* or perhaps *T. hatinhensis*.

The relationships of these species, according to the evidence of cytochrome b sequences (Roos 2004), are as follows: [((*francoisi* (*poliocephalus*, *leucocephalus*)) ((*delacouri* (*laotum, hatinhensis+ebenus*))].

They divide, therefore, into a northern and a southern group, with the Red River as the boundary; the superficially similar *T. francoisi* and *hatinhensis* belong to different groups. The sequences for the two available specimens of *T. ebenus* were intermingled among those of *T. hatinhensis*; Roos (2004) interpreted this to mean that the all-black *T. ebenus* is simply a colour morph of the latter, but, as discussed above, past or even continuing hybridisation events between the two could be an alternative explanation. The genetic distances between *T. poliocephalus* and *leucocephalus*, and between *T. laotum* and *hatinhensis*, were low, and Roos (2004), basing himself implicitly on the GSC, proposed to unite the first two as subspecies of *T. poliocephalus* and the second two as subspecies of *T. laotum*. Again, as discussed above, application of the PSC requires that all of them be maintained as distinct species, the differences between them being, as far as the evidence goes, fully consistent; this applies not only to external morphology, but apparently to the cytochrome b sequences themselves, which have quartet puzzling support values of 93% (*T. hatinhensis* from the single specimen of *T. laotum*) and 97% and 99% (*T. leucocephalus* and *T. poliocephalus* respectively).

Because these species are so poorly studied, I collected together all the measurements I could find (mainly from Brandon Jones, 1995), and here present graphs of them. External measurements must always be used with some caution, as different collectors may have used slightly different techniques, but there is a certain consistency about the measurements for each taxon in this sample, regardless of who took the measurements.

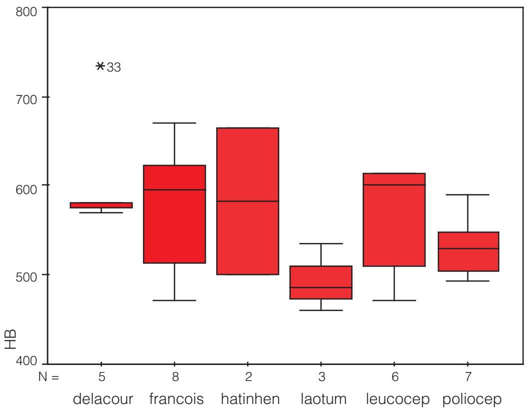

Fig. 7. Head and body length in limestone langurs.

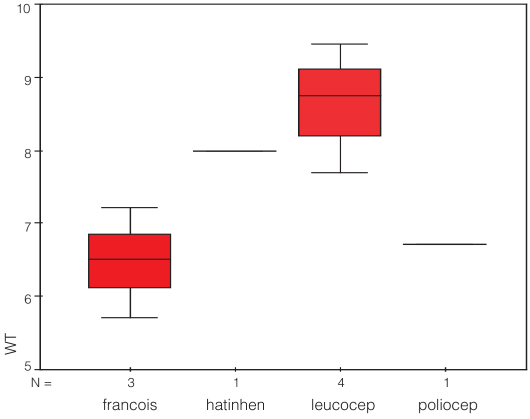

Fig. 8. Weight in limestone langurs.

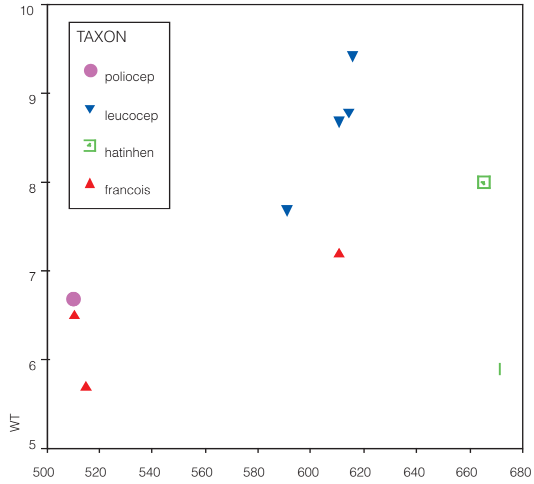

Fig. 9. Weight compared to head and body length in limestone langurs.

As far as linear size is concerned (head and body length), *T. laotum* seems to be somewhat smaller than the others; *T. delacouri* appears strikingly homogeneous, whereas the two available specimens of *T. hatinhensis* are strikingly different in size (Fig. 7). In linear size, *T. leucocephalus* is much the same as *T. francoisi*, whereas its weight is much greater (Fig. 8). When weight is graphed against head and body length, the apparently heavier build of *T. leucocephalus* is very clear; a single specimen of *T. poliocephalus* is relatively heavy (for its rather small size) like *T. leucocephalus*, whereas a single specimen of *T. hatinhensis* is lightly built for its linear dimensions like *T. francoisi* (Fig. 9).

T. leucocephalus and *hatinhensis* would seem to be relatively smaller-eared than other species according to these data; *T. laotum* and *delacouri* apparently have rather large ears (Fig. 10). Relative tail length (Fig. 11) shows less consistent differences; *T. laotum* has a long tail, *T. leucocephalus* averages shorter-tailed than *T. poliocephalus*, *T. delacouri* is fairly short-tailed, but plots for *T. francoisi* and *hatinhensis* are inconsistent.

Putting all these together into a Discriminant Analysis (Fig. 12) gives good separation between the closely related *T. poliocephalus* and *leucocephalus*, and separates *T. laotum* from all the others. There is clearly a need for longer series of measurements, taken by a single person, to test these provisional results.

From photographs, and from my personal observations of living animals and museum skins, it is clear that there are consistent differences among the species in the form of the crest on the crown. The crest of *T. delacouri* is distinctively high and thin, very upright anteriorly, but sloping forward posteriorly; in this species, the ears noticeably stand out from the head. The crest of *T. francoisi* is thicker, but still well-defined, and stands upright both anteriorly and posteriorly; the ears are adpressed to the head. *T. hatinhensis* is very different from *T. francoisi*: the crest is low, scruffy in appearance and relatively poorly defined both anteriorly and laterally, but it is upright posteriorly; the ears are very adpressed, flat against the temples; those of *T. ebenus*, *laotum* and *leucocephalus* most closely resemble this shape from the front, but like *T. francoisi* they are upright anteriorly instead of sloping backward. The crest of *T. poliocephalus* is distinctively low, wide and conical.

There also differences in the way each species tends to hold its tail (Nadler & Ha Thang Long, 2000). Other features, such as gait and sitting postures, remain to be studied.

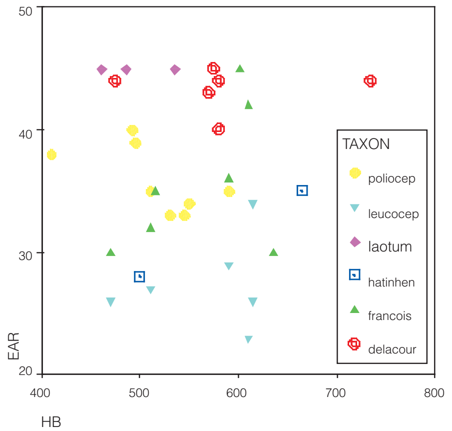

Fig. 10. Relative ear size in limestone langurs.

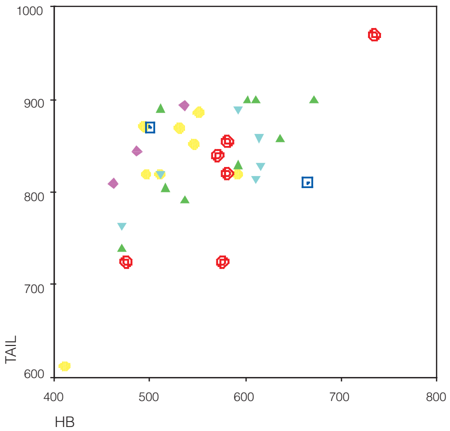

Fig. 11. Relative tail length in limestone langurs.

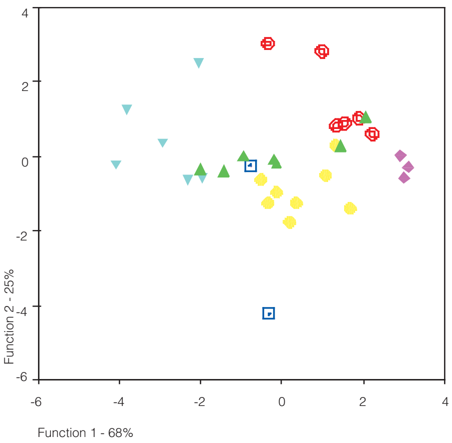

Fig. 12. Discrimant analysis of external measurements in limestone langurs.

Hylobatidae

Gibbons, the long-armed 'lesser apes' of Southeast Asia, are noted for their social monogamy, unusual among catarrhines. Among their conspicuous vocalisations is a morning duet, the Great Call, in which the female's contribution is, in three out of four genera of the family, much more striking and conspicuous than the male's. The exception to this is the genus *Nomascus*, which is endemic to the region east of the Mekong.

It is probable that, in the past, *Hylobates pileatus* occurred in Vietnamese territory to the west of the Mekong Delta; but east of the Mekong only the genus *Nomascus* occurs. It is interesting that three of the four genera of gibbons are strictly allopatric: *Nomascus* occurs east of the Mekong (except for a small population of *N. concolor* in Yunnan, perhaps cut off west of the Mekong by a meander); *Hoolock* occurs west of the Salween; *Hylobates* occurs between these two rivers, and extends further south into Sundaland. The fourth genus, *Symphalangus* (the siamang), is sympatric with *Hylobates* in the Malay peninsula and Sumatra; it is much larger than other gibbons, and presumably it is this size difference that enables this coexistence (as in the case of the lorises, above).

In *Nomascus* (as in fact is the case in *Hoolock* as well), the unweaned infant is buff, and juveniles of both sexes are black, with such facial adornment as may occur in a given species; at sexual maturity, the female turns buffy, with just a black streak on the crown and nape, whereas the male remains coloured like the juveniles. A troop of *Nomascus*, therefore, may include several black individuals, among them two or three juveniles of either sex as well as the adult male, but will have only a single buff coloured individual (the adult female). An exception to this may be the three northernmost species, the ones in which the black phase has no whitish areas on the face. The existence of polygynous troops has from time to time been claimed for *Nomascus concolor*; recently it was confirmed that the two remaining troops of *Nomascus hainanus* both contain two buff-coloured females, despite the additional presence of two solitary males (Zhou *et al.*, 2005), and of five troops of *Nomascus nasutus* recorded by La Quang Trung & Trinh Dinh Hoang (2004) three had two buff-coloured females. (At least two troops in the latter sample were listed as having two adult males, but it might be hard to distinguish a fully mature male from a subadult).

In *Nomascus*, there are three species in which the black phase is without any white or whitish

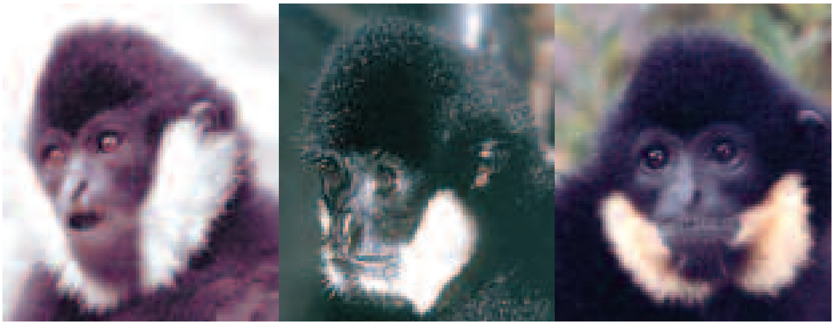

Fig. 13. Left to right: *Nomascus leucogenys*, *N. siki*, *N. gabriellae*. Photos: Colin P. Groves.

facial adornment, and three (or at least three?) in which black individuals have white or whitish patches on the cheeks. The six species are as follows:

Nomascus concolor. Found between the Red and Black Rivers, from Vietnam northwest into Yunnan; and there is an isolated population in Laos, on the Mekong at about 20°N. Black individuals (adult males and juveniles of both sexes) are completely black and adult females have a large black patch on the chest and belly; the pelage is full and plush. Several subspecies, of uncertain validity, have been described; the isolated population in Laos, *N.c.lu*, in particular, needs further investigation.

Nomascus nasutus. Found north of the Red River, in Cao Bang Province, where they were recently rediscovered by La Quang Trung & Trinh Dinh Hoang (2004). In the black phase, there is a characteristic brown zone on the chest; to judge by descriptions of skins by Dao Van Tien (1984), the adult female lacks black on the chest.

Nomascus hainanus. Restricted to Hainan. Externally, this species would seem to be distinguished from *N. nasutus* by its short, thin pelage.

Nomascus leucogenys. Found southwest of the Black River (except where *N. concolor lu* is found), south to about 19°N in both Vietnam and Laos. In the black phase, there is a conspicuous white streak on the cheeks, running in a thick straight line from the level of the eye to the corner of the chin; in the adult female, there is a thin white edging round the face, and there is no black on the ventral surface. The pelage is full and plush. This species has evidently, in comparatively recent times, extended its range northwest, replacing *N. concolor* which has been reduced to a larger area on the left bank of the Black River and a tiny area in far western Laos.

Nomascus siki. The distribution of this species begins, or began, immediately south of that of *N. leucogenys*, and extends an unknown distance to the south. The black phase also has white cheek whiskers, but these do not form a long straight line, but surround the corners of the mouth in a wide bushy arc; the adult female seems to be indistinguishable from *N. leucogenys*. This gibbon is currently referred to as *Nomascus leucogenys* siki by Geissmann *et al.* (2000), Roos (2004) and Konrad & Geissmann (2006), but clearly it is consistently different from the more northerly *leucogenys*, and indeed (see below) it would appear to be its relationship to *N. gabriellae* which needs attention. Black-phase examples of these three pale-cheeked species are in Fig. 13.

Nomascus gabriellae. This species is certainly found south of about 13°N, and extends in more or less to the Mekong Delta. The black phase resembles *N. siki*, except that the white of the cheeks is replaced by buffy, occasionally red-tinged, and does not extend so far along below the mouth but extends further down the sides of the chin, and also there is some brown on the chest; the adult female lacks the white facial edging.

According to Geissmann *et al.* (2000), all of these species can readily be distinguished by their different vocalizations. *N. concolor*, *leucogenys*, *siki* and *gabriellae* have slightly different karyotypes, although not enough specimens have been studied to verify that the differences are consistent. The baculum also differs between different species.

According to Roos (2004), the phylogeny (*N. hainanus* was not studied) is: [(*nasutus* (*concolor* (*leucogenys*, *gabriellae*)].

Fig. 14. "Patzi" as juvenile. Photo: Tierpark Berlin.

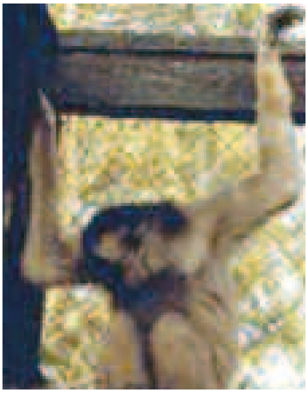

Fig. 15. "Patzi" as adult about 1980.

For his phylogenetic study, Roos (2004) also included five individuals of *N. siki*. Two of these clustered with *N. gabriellae*, forming a separate subclade from the three individuals of the latter, and the other three clustered with *N. leucogenys*, two of these forming a separate subclade and the other clustering with the six *leucogenys* individuals. On the face of it, this might suggest that *siki* is a species of hybrid origin, which has not yet achieved full reciprocal monophyly with respect to its parent species in some characters. But the situation seems to be more complicated than that.

Geissmann *et al.* (2000) found a complex mosaic of character states between *N. siki* and *N. gabriellae*. Males resembling *siki may have gabriellae*-like features in vocalizations; wild-caught individuals resembling *gabriellae* in appearance and in song, may have *siki* karyotypes or hybrid karyotypes. Of interest, three captive-bred hybrids resembled *gabriellae* but the songs were intermediate, and the two males lacked brown on chest. The type specimen of *siki* is from Thua Luu, south of Hue, and close to Bach Ma National Park (16°13'N), but a second museum specimen from that locality is *gabriellae*; on the other hand, a museum specimen from southern Laos - well to the south of the latitude of Bach Ma - is intermediate between the two. Putting all this together with their observations that the large area in northern Cambodia, southern Laos and central Vietnam has gibbons of indeterminate or intermediate traits, they proposed three hypotheses to explain the odd situation in this large intervening area: (1) it is inhabited by an undescribed taxon, or (2) it is a wide intergrade area between *gabriellae* and *siki*, or (3) a combination of the two.

The vocalizations of *N. gabriellae* and *siki* have been further explored by Konrad & Geissmann (2006). Typical *N. gabriellae* songs were recorded in Samling logging concession, at about 12°20'N, and sightings were of individuals typical of that species. Yet, in northeastern Cambodia at about 14°N, apparent *N. gabriellae* were making vocalizations much more like those recorded at Bach Ma, virtually the type locality of *N. siki*, as noted above. Vocalisations at the three northeastern Cambodian sites were not precisely identical to each other or to those at Bach Ma, nor in fact were they identical to those of captive gibbons identified phenotypically as *N. siki*, but they were very unlike those of *N. gabriellae*.

Konrad & Geissmann (2006) consider these new findings in the light of the three hypotheses of Geissmann *et al.* (2000), and argue that they support the first hypothesis - that the area is inhabited by an undescribed taxon, and that the two different clusters formed by *N. siki* in Roos's (2004) phylogeny 'may be geographically separated taxa'. Alternatively, one notes that, as far as external appearance is concerned, the dividing line between the *gabriellae* and *siki* phenotypes may slant southwest from Bach Ma to southernmost Laos, and if future research on vocalizations proves to substantiate this, the hybrid zone hypothesis may not be ruled out after all. Whether indeed *Nomascus siki* is itself a species of hybrid origin, as proposed by both Groves (2004) and Roos (2004), would still be interesting to investigate.

There remains a final conundrum. "Patzi", a female gibbon that lived in Tierpark Berlin from 1952 (at an estimated age of 1 year or slightly more) until 1986, was unlike any other known individual, particularly in her extensively blackened underside, connected to an extraordinarily wide and long crown streak (in fact, covering almost the entire width of crown, and extending backward onto the shoulders) by a narrow black circumfacial ring (Fig. 15). All that is known of her is summarized extensively by Geissmann (1989). When young, she was of course black, but I cannot find whether she had a brown zone on the chest or not (Fig. 14). She was reputed to have been captured in the hinterland of Hon Gai, just northeast of the Red River delta on Halong Bay; there would seem to be no plausible barrier between this locality and the area further northeast where *Nomascus nasutus* still exists, yet she is entirely unlike the females of that population as described by Dao Van Tien (1984). According to Geissmann, her vocalizations were very like those of the surviving northeastern gibbons. A possibility might be that she was a hybrid between *N. nasutus* and *N. concolor*; it seems hardly possible that she was an extreme variant of *N. nasutus*, nor that she could have represented yet another (extinct) species. Two photos of her, in adult and in juvenile phase, are given in Fig. 14.

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