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THE TAXONOMIC AFFINITIES OF THE MENTAWAI ISLANDS SURELI, *PRESBYTIS POTENZIANI* (BONAPARTE, 1856) (MAMMALIA: PRIMATA: CERCOPITHECIDAE)

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ABSTRACT. - A review of the skeletal and external morphology of *Presbytis potenziani* demonstrates that, although marginal in some respects, the species is referable to the genus *Presbytis* (sensu stricto). Its cranial, pelage and adult male vocal characteristics indicate that its closest affinities are with Bornean and Sumatran populations of *Presbytis comata.* The type locality restriction for the nominate subspecies is amended, but the collector and date of collection of the holotype remain obscure. The generically atypical characters of *P. potenziani* are interpreted as the result of its being the sole representative of its genus to survive a severe cold and dry stadial of the most recent glaciation. The maritime climate of the Mentawai Islands enabled the archipelago to sustain the requisite *Presbytis* (sensu stricto) habitat when this had been eradicated elsewhere. Characters such as the polychromatism and reduced supraorbital torus of the rest of the genus are attributed to a relaxation of genetic stability during the rapid dispersal process that succeeded the glaciation, when the genus expanded geographically to its present distribution.

INTRODUCTION

The currently accepted subdivision of *Presbytis* (sensu lato) was established by Pocock (1928: 474), primarily on the basis of neonatal pelage colour. Later, Pocock (1935: 896) elevated his former species groups to generic rank, and the species group classification of *P. potenziani* implicit in his earlier work (Pocock, 1928: 666) was formalized with its allocation to the "genus", *Trachypithecus* (Pocock, 1935: 954). The characters cited as allying it with *Trachypithecus* were that: "The young is golden, the head of the adult is tufted, and the female has the white inguinal patch beneath the callosities which are common features in other species of *Trachypithecus*" (Pocock, 1935: 955). Pocock (1935: 957-958) was the first author to consider the cranial characters of *P. potenziani*, and the differences he evinced, coupled with the comparative shortness of the tail (both absolute, and relative to head and body length), persuaded him that it was not as closely related to the Indochinese pied leaf monkeys as Osgood (1932) had supposed. The resemblances restricted to pelage colour, might be convergent. Probably for similar reasons, Pocock (1935) had apparently abandoned his former conviction of its close kinship with *Semnopithecus (Trachypithecus) pileatus.*

Support for Pocock's generic separation of *Trachypithecus* from *Presbytis* was furnished by Washburn (1944), who found the two "genera" distinguishable both in cranial and post-cranial

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skeletal indices. However, as Washburn (1944: 292) acknowledged, the only available skeleton of *P. potenziani*, an incomplete male specimen from Pulau Pagai Selatan (USNM 121673), did not fall clearly into either group. In the series at the Museum of Comparative Zoology of Harvard University, *S. cristatus* specimens had shorter femora than *P. rubicunda* specimens of equal weight. This character, the intermembral index (81) and the femero-humeral index (75) led Washburn (1944: 293), undoubtedly influenced by Pocock's classification, to conclude that *P. potenziani* belonged to the "genus", *Trachypithecus*. In all three of the post-cranial skeletal indices available for measurement (brachial, intermembral and femero-humeral) however, the *P. potenziani* skeleton differed by only one unit from that of a male Sumatran *"[Presbytis] melalophus"*, USNM 49749 (from Tarussan Bay [=Teluk Tarusan, 1°13'S 100°25'E], V. Weitzel, *in litt.*). Its brachial index (106) was five units outside the range of variation found in *Trachypithecus* (91-101, mean=95). In the prognathism index (111), USNM 121673 differed by only two units from USNM 49749, falling within the range of variation in male *Presbytis* (100-115, mean=106), but four units outside the range of variation in male *Trachypithecus* (115-125, mean=119). With the exception of the femoral length, which might also become less anomalous if comparison were made with Sumatran material, the evidence presented by Washburn (1944) thus tends to refute, rather than corroborate Pocock's generic classification of *P. potenziani*. Nevertheless, Washburn's endorsement enabled Pocock's arrangement to prevail. Since 1944, the opinions of Thomas (1895) and Chasen (1940) have been ignored or rejected in most species group or genus-group subdivisions of the genus, *Presbytis* (sensu lato) (e.g. Fiedler, 1956: 202; Kuhn, 1967: 40; Napier & Napier, 1967: 353; Medway, 1970: 545). Groves (1970: 572) and Thorington & Groves (1970: 642) declined to recognize subgenera within the genus largely because of the supposed intermediate position of *P. potenziani* between two *Presbytis* sub-groups. It was probably instrumental in the decision by Chasen (1940) and Simpson (1945) not to follow Pocock's (1935) generic arrangement.

The classification of the Colobinae advocated by Brandon-Jones (1984) is here employed. The practice is maintained of adopting the Javan native name, "sureli" as a vernacular name for any species of the genus, *Presbytis* (sensu stricto), in order to stress the morphological and ecological divergence between this genus and the leaf monkeys and langurs (genus *Semnopithecus)*. The synonymies are restricted to the earliest detected publication of all the genus-group and species-group combinations to which the subspecies have been referred.

HISTORY OF THE SPECIES TYPE SPECIMEN

Before 1895, the only recorded specimen of the Mentawai Islands sureli was the mounted skin of an adult female (Peters, 1879: pl. IV B), preserved in the Museum für Naturkunde der Humboldt-Universität, Berlin. This specimen is the holotype of two species-group names, one published in 1856, the other in 1867, and both unaccountably employed by their respective authors as though they were already valid and available. Bonaparte (1856: 412) claimed to have established the name, *Semnopithecus potenziani* in 1850. Peters (1867: 429; 1879: 830: pl. IV B) treated *S. potenziani* as a junior synonym of "*Semnopithecus chrysogaster*", citing his authority as an exhibition of an illustration of the monkey to the Gesellschaft Naturforschender Freunde [Berlin] in 1840 by [M. H. C.] Lichtenstein. Neither Bonaparte nor Peters appended a bibliographical reference to the purported original description, and the absence of such references in all subsequent works, notably those of Blyth (1875, who had exchanged correspondence with Peters), Anon (1912) and Sherborn (1925: 1262, 1929: 5125) tends to confirm that the descriptions were unpublished, and therefore unavailable in zoological nomenclature.

Bonaparte's (1856) description appeared in a footnote to an article on European museum collections, and the definition mentioned only that the species "...se distingue éminemment par la brillante teinte dorée de son ventre" (is primarily distinguished by its bright golden ventral coloration). Blanford (1888b: 38) and Elliot (1913: 67) regarded this description as insufficient, and Blanford (1888a, b) treated the name as invalid and classified the monkey as "*Semnopithecus chrysogaster*", as validated by Blyth (1875: 10) (Blanford, 1888a: 627). Blanford's action however, was rejected by Thomas (1895: 663) who adopted the earlier name, setting a precedent which has won general acceptance. Bonaparte's definition, although meagre, does satisfy the provisions of Article 12 of the International Code of Zoological Nomenclature (1985), and *Semnopithecus potenziani* Bonaparte, 1856, is a valid and available species-group name.

Peters' (1879) report of Lichtenstein's notice on the monkey establishes that the holotype was received by the Berlin Museum not later than 1840. Bonaparte (1856) and Peters (1867, 1879) stated that it came from Tenasserim (south-east Burma). This was reiterated by Blyth (1875: 10) and Schlegel (1876: 33) who added that it had been collected by Helfer. With British Government patronage, J. W. Helfer conducted the first scientific exploration of the Mergui archipelago and Tenasserim from the mountains near the source of the Yinbaing Chaung (=tidal creek, c. 17°30'N 98°00'E) southwards to the Pakchan River estuary (c. 10°00'N). This preoccupied him from March 1837 until his murder by Andaman islanders on 30 January, 1840, six days before his thirtieth birthday (Nostitz, 1878).

That Helfer collected the holotype in Tenasserim is rendered highly improbable by his report of the existence there of only a single species of colobine, "*Symenopithecus* [sic] *Maurus*" (Helfer, 1838: 858). This name, unaccompanied by a description or authority, presumably refers to *Simia Maura* Schreber, 1774 (p. 107: pl. XXII B), sensu Geoffroy Saint-Hilaire (1812: 93), the ebony leaf monkey *(Semnopithecus auratus)*, or sensu Raffles (1821: 247), the banded sureli *(Presbytis femoralis)*. The banded sureli does occur within the area traversed by Helfer (Thomas, 1886: 66; Gairdner, 1915: 142; Wroughton, 1915: 702), but the encountered species is more likely to have been the more prevalent *Semnopithecus obscurus*, or possibly *S. barbei*, or any combination of the three species (see Fooden, 1976, where they are classified as four species, *Presbytis melalophos, P. obscura, P. phayrei* and *P. cristata)*.

Amongst the material collected by Helfer was a spirit specimen donated by J. T. Pearson to the Museum of the Asiatic Society of Bengal, Calcutta (subsequently incorporated into the Indian Museum). It was classified by E[vans] (1838) as "*Semnopithecus Maurus*" but owing to decay, had to be skeletonised (E[vans], 1838; Pearson, 1840: 526; Blyth, 1844: 466; 1863: 15; Anderson, 1881: 48). The cranial affinities of Helfer's specimen with *Semnopithecus obscurus* (apud Blyth, 1844, 1863) or with *S. auratus* (apud Anderson, 1881) preclude its identity as *P. p. potenziani* or as any golden-bellied species which might have been confused with the latter. Had Helfer collected the holotype of *P. potenziani* in Tenasserim, he could not have failed to recognize the existence there of more than a single species of colobine. The absence of such a strikingly pelage-coloured species in all subsequent collections from the area led Blanford (1888a: 627, 1888b: 38), as early as 1887 when no additional specimens of *P. potenziani* had been reported, to doubt the accuracy of the purported type locality.

Nothing further was learnt of the species until 1894, when E. Modigliani collected an adult male (presumably deposited in the Museo Civico Storia Naturale "Giacomo Doria", Genova, Italy) and a subadult female specimen (ZD.1895.1.9.1) on Pulau Sipura, Kepulauan Mentawai, Indonesia (Thomas, 1895: 663). Subsequent knowledge has been derived exclusively from specimens collected (Lyon, 1916: 460; Chasen & Kloss, 1928: 811-813, pl. I) or observed (W. L. Wilson & C. C. Wilson, 1975; Tilson, 1976; Tilson & Tenaza, 1976; C. C. Wilson & W. L. Wilson, 1977) on the Mentawai Islands. Expeditions to Tenasserim since 1887, notably those of the Bombay Natural History Society's Mammal Survey (Wroughton, 1915; Lindsay, 1926), have not allayed Blanford's (1888a, b) doubts as to the occurrence there of *Presbytis potenziani*. It is now clear that the species is endemic to the Mentawai Islands. Specimens collected on Pulau Siberut in 1924, prompted Chasen & Kloss (1928: 811, pl. I) to separate them as a new subspecies with duller underparts. The holotype of the nominate subspecies was evidently from one of the Mentawai Islands other than Pulau Siberut, and Chasen & Kloss (1928: 811) restricted the type locality to Pulau Sipura. The present revision indicates its provenance on one of the Pagai Islands (see p. 342).

The species holotype was received by the Berlin Museum from "Professor Strempel of Rostock" (Blanford, 1888a: 627; Miller, 1908: 638; H. Hackethal, *in litt.*). The unreliability of the localities attributed to his material is confirmed by a squirrel also said to be from Tenasserim, and described as a new species, *Sciurus piceus* by Peters (1867: 429). The specimen remained the sole identified representative of the taxon until Schneider (1905: 109) provisionally allocated to the same taxon a series of specimens collected in north Sumatra. Schneider's identification was confirmed by Miller (1908) who in 1904 examined the holotype in the Berlin Museum, and recognized it as identical with the specimens he had previously segregated as a new species, *Sciurus erebus* Miller, 1903 (p. 456). The squirrel, classified by Chasen (1940: 128) as *Sciurus prevostii piceus* (a species referred to the genus, *Callosciurus* by Ellerman & Morrison-Scott, 1955: 32), occupies the "northern third of Sumatra, as far south at any rate as the neighbourhood of Deli on the east coast and Sibolga on the west" (Chasen & Kloss, 1925: 98). No record of a visit to the Mentawai Islands or Sumatra appeared in the account of Helfer's exploration of the Mergui archipelago and Tenasserim (Nostitz, 1878). Since this was his only expedition to east Asia, it can be safely concluded that Helfer never visited the Malay archipelago and therefore could not have collected Strempel's material.

The donor of the specimens was undoubtedly J. F. K. Strempel (1800-1872), a university lecturer, clinician, surgeon and medical reformer of some prominence in the history of Rostock, Germany. Strempel was also instrumental in the foundation or promotion of a natural history museum, a chemical laboratory and an astronomical observatory (Hofmeister, 1971). The only relevant record in the Berlin Museum is some brief correspondence relating to a stay Strempel apparently made in India (Hackethal, *in. litt.*). It is curious that an expedition which visited the Mentawai Islands and north Sumatra at such an early date did not excite sufficient zoological interest for its narrative to have been considered worthy of publication. A possible explanation is that its objectives were primarily botanical. This might account for the involvement of Strempel, whose dissertation topic was the ferns of Berlin (Strempel, 1822). I. Geißler of the Botanical Gardens at the Wilhelm-Pieck-Universität, Rostock, reported *(in litt.)* that a search in the university herbarium and at the university archives for material deposited by Strempel, has proved fruitless. He added however, that the basis for the herbarium was not acquired for the university until 1885.

TAXONOMIC HISTORY

Schlegel (1876: 32), Trouessart (1878: 118), Anderson (1879: 13; 1881: 14) and Forbes (1894: 103) included *Presbytis potenziani* as a synonym of *Semnopithecus pileatus* (Blyth, 1843: 174).

As recently as 1928, Pocock (1928: 666) regarded the two species as closely related, and suggested that *P. potenziani* would be treated as a "small, insular melanistic race of *pileatus*" were it not for differences in head hair length and disposition. "The species", according to Pocock (1928: 667), "serves in a measure to link *P[ithecus] pileatus* and *P. pyrrhus*". Peters' (1879: pl. IV B) illustration of the holotype was unpublished at the time the monographs of Schlegel (1876) and Anderson (1879) went to press. Their failure to distinguish the two species might be attributed to the inadequacy of Bonaparte's (1856) definition, were it not for the existence of Blyth's (1875: 10) fuller description. If published too recently for consideration by Schlegel (1876), it was certainly familiar to Anderson (1879). Blyth (1875: 11) reported that before seeing coloured drawings sent him by W. Peters, he too had suspected that *P. potenziani* would prove identical with *S. pileatus*.

Thomas (1892: 476-477) noted that *P. potenziani* (as figured by Peters, 1879) and *"Semnopithecus cruciger"* (a pelage colour aberration of *Presbytis femoralis*) were unique amongst *"Semnopitheci"* in sharing a combination of black, red and white in their pelage coloration. He conceded however, that the different colour distribution and the "conspicuous difference in the colour of the crown" widely separated the two forms. The receipt of Modigliani's freshly collected specimens offered Thomas (1895: 664) the opportunity to reappraise this opinion. *P. potenziani* now seemed to him "to be most nearly allied to *S[emnopithecus] hosei* and *S. everetti*, with which alone it shares the absence of any forwardly directed supraorbital or occipital hairs, combined with the presence of a well defined sagittal hair crest". Thomas' opinion was neglected, even by Chasen (1940: 78) who similarly suggested that, "taking an extremely broad view", *P. potenziani* "could be regarded as a very distinct race" of *"Pithecus aygula"* [=*Presbytis comata*, sensu lato]. This conclusion was reinforced by W. L. Wilson & C. C. Wilson (1975: 461) who found the adult male three-part spacing vocalization as similar to that of *Presbytis comata thomasi* "as are the calls of the [Sumatran] *P. melalophos* subspecies to one another" (C. C. Wilson & W. L. Wilson, 1977: 222).

A contrary view was expressed by Osgood (1932: 205) who, reviewing the Indochinese pied leaf monkey species including *Semnopithecus francoisi*, concluded that they were evidently related to *Presbytis potenziani*, "a very distinct species not heretofore closely associated with any other". Osgood's opinion was endorsed by W. C. O. Hill (1939: 292).

Trouessart (1879, 1904, 1911) and Elliot (1913) separated *P. potenziani* subgenerically from *S. pileatus*, but classified it with a heterogeneous assemblage of species, including both *S. francoisi* and the majority of the *Presbytis* (sensu stricto) species.

NEONATAL PELAGE COLOUR

The neonatal pelage colour of *Presbytis potenziani* has been described as "wholly pale ferruginous, somewhat darker on the hands and feet" (Blyth, 1875: 10), "roux" (Trouessart, 1879: 55), "wholly rufous white or pale isabelline" (Blanford, 1888b: 38), "yellow" (Elliot, 1913: 67), "golden" (Pocock, 1928: 666; 1935: 955; W. C. O. Hill, 1939: 292; Washburn, 1944: 293; Groves, 1970: 572) or "orange" (Medway, 1970: 536, 545). Most of these sources fail to acknowledge that the descriptions all derive from a single specimen, or from an illustration of that specimen. The specimen in question is the skin of a monkey neonate which was mounted on the same branch as the holotype of the species, and is preserved in the Museum für Naturkunde der Humboldt-Universität, Berlin (Catalogue no. 35; H. Hackethal, *in litt.*).

His preoccupation with the application of neonatal pelage colour in subdividing the genus *Presbytis* (sensu lato), perhaps led Pocock (1928, 1935) to undervalue tail length and cranial anomalies when primarily basing genus-group status on a single neonate not unequivocally assigned to the species under review. The need for caution should have been further emphasized by Colyer's (1936: 218) evidence that in both irregularity in the position of the incisors and in the number of specimens showing protrusion of the mandibular incisors, *P. potenziani* sorted with *Presbytis* rather than with *Semnopithecus* (sensu lato). This undue reliance on a neonate received by a museum before 1841, with erroneous data as to both the collecting locality and the identity of the collector should have been finally exposed by the skeletal indices published by Washburn (1944). A more thorough cranial examination, using his own criteria (Pocock, 1928: 675; 1935: 896-897) for distinguishing *Presbytis* from *Semnopithecus* (see p. 346), should have led Pocock to realize that the neonate was not the progeny of the holotype.

Since 1928, the value of the usual yellowish-orange colour as a distinguishing character for the *Semnopithecus* subgenus *Trachypithecus*, has been lessened by reports that in at least two species, *S. pileatus* and *S. geei*, the neonatal pelage is apparently whitish (McCann, 1933: 626; Gee, 1961: 6; Khajuria, 1962: 125). Of greater significance is the process of development of pelage colour in the infant. Neonatal *Presbytis* (sensu stricto) skins in the Natural History Museum, London, the Rijksmuseum van Natuurlijke Historie, Leiden and the Sarawak Museum, Kuching collections examined by the author (see also Müller & Schlegel, 1841: 65, 70, 73, pl. 11, figs. 1, 2, pl. 12, fig. 2; Pocock, 1935: 897-898; Hooijer, 1962: 10; Medway, 1970: 529 (erratum), 530, 541-542; Schlosser, 1977) demonstrate that darker-pigmented hair invariably develops along the dorsal midline before its appearance on the forehead. *Semnopithecus* (*Trachypithecus*) neonates do not develop a continuous dorsal midline band of darker hair until after such hair has predominantly covered the arms, legs, head and anterior of the back (Bernstein, 1968: 3; Horwich, 1974: 165-167). Darker pigment appears initially in the hair of the dorsum of the hands, in the hair of the forehead, and at the bases of the tail hairs (Bornean *S. cristatus*, ZD.1845.10.2.4 and 1890.1.28.3 examined by the author).

The external characters of the neonate mounted alongside the holotype of *Presbytis potenziani*, as figured by Peters (1879: pl. IV B; Weitzel *et al.*, 1988: colour frontispiece), are as follows. The naked skin of the ears and of the face around the nostrils and eyes, is pink. The pelage colour grades from yellow around the face, to yellowish-orange on the arms and legs, where it is intermingled with orange which predominates on the back, rump and tail. The hair of the dorsum of the hands and feet, and in a small patch adjoining the upper border of the naked face, is blackish. The neonate is depicted in side view, squatting with its tail hanging straight down on the nearside of the branch and its head turned so that its gaze is directed at the artist. Sufficient of the back is visible to clearly demonstrate that it had no dorsal midline band of darker hair from the nape to the base of the tail, nor on the tail itself. Pelage colour may alter by immersion in preserving fluid, or may fade by prolonged exposure to light, but such processes are unlikely to mask a colour contrast of this type and had it existed, it would not have been overlooked by Peters (1879) or Blanford (1888b). It is therefore evident that both in pelage colour and in colour development, the specimen is a typical *Semnopithecus* (*Trachypithecus*) neonate.

The genus, *Semnopithecus* is absent from the Mentawai Islands, so the specimen could not have been collected there. The evidence from the amended type locality of *Sciurus piceus* Peters, 1867, cited above (p. 334), indicates that it is most likely that the specimen is a neonate of *Semnopithecus cristatus* collected in north Sumatra.

As for the true neonatal pelage colour of *P. potenziani*, this has recently been observed by Tilson (1976: 766), during field studies of the species in Siberut. He reported that: "Infants are born with a depigmented skin and a whitish pelage. The face becomes darkly pigmented in a few days, and after two to three weeks the pelage begins to darken, first along the dorsal midline and head, then laterally... Within 12 to 14 weeks the chest and belly are dark reddish-brown and the rest of the body is jet black; only the throat, cheeks and forehead, and the tip of the tail in some animals, remain white".

SYSTEMATICS

Presbytis potenziani potenziani (Bonaparte, 1856)
(Golden-bellied Mentawai Islands sureli)

Semnopithecus potenziani Bonaparte, 1856: 412
Pr[esbytis] Potenziani: Blyth, 1863: 15
Semnopithecus chrysogaster: Peters, 1867: 429
Presbytes chrysogaster Blyth, 1875: 10
Semnopithecus pileatus: Schlegel, 1876: 32
[Semnopithecus (Lophopithecus)] pileatus: Trouessart, 1878: 118
S[emnopithecus (Lophopithecus)] chrysogaster: Trouessart, 1879: 55
[Semnopithecus (Lophopithecus)] Potenziani: Trouessart, 1897: 10
Pygathrix [(Corypithecus)] potenziani: Elliot, 1913: 67
[Pithecus] potenziani: Wroughton, 1916: 653
Pithecus potenziani potenziani: Chasen & Kloss, 1928: 811
Trachypithecus potenziani: Pocock, 1935: 954
P[resbytis (Trachypithecus)] potenziani: Fiedler, 1956: 202
P[resbytis] p[otenziani] potenziani: Napier & Napier, 1967: 353
Lophopithecus potenziani: Krumbiegel, 1978: 71

Type specimen. - The holotype, catalogue no. 34, an adult female mounted skin (Peters, 1879: pl. IV B; Weitzel *et al.*, 1988, colour frontispiece) formerly exhibited in the Museum für Naturkunde der Humboldt-Universität, Berlin, could not be located by an exhaustive search through the primate collection in 1979 (H. Hackethal, *in litt.*).

Type locality. - "Tenasserim" (Bonaparte, 1856: 412), corrected by Thomas (1895: 663-664) to the "Mentawei Islands", and restricted by Chasen & Kloss (1928: 811) to "Sipora Island", but this restriction is here provisionally amended (p. 174) to Pulau Pagai Utara, Kepulauan Mentawai, Indonesia.

Distribution. - Pulau Sipura (Thomas, 1895: 663; Chasen & Kloss, 1928: 811), Pulau Pagai Utara and Pulau Pagai Selatan ("North and South Pagi Islands": Lyon, 1916: 460), Kepulauan Mentawai, Indonesia.

Specimens examined. - The subadult (permanent third molars incompletely erupted) female skull and round skin (ZD.1895.1.9.1) from "Sereinu ([=]Sipora), Is. Mentavei [sic], Magg[io=May] 1894" preserved at the Natural History Museum, London, and the four specimens at the Zoological Reference Collection (ZRC), National University of Singapore, catalogued by Weitzel *et al.* (1988: 66-67). C. P. Groves *(in litt.)* has very generously placed at the author's disposal his measurements and brief descriptions of the latter specimens and of those examined by him at the Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia. From Pulau Sipura, these comprise two adult males (MZB 2864 and ZRC 4.333), one adult female (ZRC 4.334) and one infant (ZRC 4.335, its apparently separated callosities indicate that it is a female); and from Pulau Pagai Utara, four adult males (MZB 6622, 6624, 6627, 6629), two juvenile males (MZB 6625 and ZRC 4.332), four adult females (MZB 6626, 6628, 6630 and 6631) and one juvenile female (MZB 6623).

Presbytis potenziani siberu (Chasen & Kloss, 1928)
(Sombre-bellied Mentawai Islands sureli)

Pithecus potenziani siberu Chasen & Kloss, 1928: 811
Trachypithecus potenziani: Pocock, 1935: 954
Presbytis potenziani siberu: J. E. Hill, 1960: 33
[Presbytis (Trachypithecus) potenziani] siberu: Kuhn, 1967: 40

Type specimens. - The holotype, ZD.1928.11.2.1, collector's no. 2005, is an adult male skull and round skin collected by C. B. Kloss on 13 September, 1924 (Chasen & Kloss, 1928: 811) and preserved in the Natural History Museum, London. Two of the paratypes, adult female, ZRC 4.336, collector's no. 2024, and juvenile male, ZRC 4.337, collector's no. 2159, listed by Chasen & Kloss (1928: 812-813) are preserved in the Zoological Reference Collection, National University of Singapore (Weitzel *et al.*, 1988: 66-67). The two other paratypes, adult male, USNM 252315, collector's no. 2065, collected on 25 September, 1924 and subadult (third permanent molar incompletely erupted) female, USNM 252314, collector's no. 2025, collected on 16 September, 1924, are preserved in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (J. P. Angle, *in litt.*; V. Weitzel, *in litt.*).

Type locality. - Siberut Island [=Pulau Siberut, Kepulauan Mentawai, Indonesia] (Chasen & Kloss, 1928: 811).

Distribution. - Confined to the type locality.

Specimens examined. - Paratypes, ZRC 4.336 and ZRC 4.337, and the holotype. Its canine and premolar morphology and its pendulous nipples, confirms that ZRC 4.336 is a female, contrary to its listing by Chasen & Kloss (1928: 812); but the penis and contiguous callosities in ZRC 4.337, diagnose it as a male.

ADULT EXTERNAL CHARACTERS

This description, derived primarily from the above listed examined skins of *Presbytis potenziani*, is supplemented with information from Chasen & Kloss (1928) and from C. P. Groves *(in litt.)*. Tilson & Tenaza's (1976: 320) implication that the male only has a white genital fur patch is refuted by the presence of such a patch in all examined specimens. Apart from minor differences associated with the sexual dimorphism in the position of the ischial callosities (contiguous in the male; separated, with the vulva situated in the intervening area, in the female), the pelage colour differences between the specimens which form the basis of this description, are evidently taxonomic and not sexual.

The pelage in *Presbytis potenziani* is of moderate length, longer on the dorsum of the shoulders and the anterior of the flanks, and shorter on the face, throat, posterior part of the abdomen and ventrum of the thighs. It is generally rather recumbent, and is distally directed on the limbs and tail. The dorsal hairs of the head and trunk are posteriorly directed, with the exception of a small patch at the vertex which is erected and somewhat anteriorly directed. This hair patch, which is very small in some specimens, tapers and disappears towards the nape. Below and, in some specimens, anterior to the pinna, the hairs of the side of the throat are laterally directed. Under the chin and towards the cheek the throat hairs are anteriorly directed. Their alignment therefore opposes that of the posteriorly directed chin and cheek hairs, producing a ridge which runs from the pinna anteriorly across the cheek towards the corner of the mouth, and then transversely across the chin. This ridge is more conspicuous in the more blackish Siberut specimens, owing to the abundance along its course, of distally blackish hairs. The throat hair is parted along the midline (in ZRC 4.337 the parting is very nearly reduced to a whorl) and posteriorly its direction is caudal, as is that of most of the chest, although towards the flanks and especially towards the arms, the hairs become more laterally directed. The hairs of the anterior of the abdomen are lateral or in some specimens, predominantly rostral in direction, producing a line of conflict which approximates to the lower edge of the rib cage. In some specimens this line is broken at the midline (about 320 mm anterior to the tail base in ZD.1928.11.2.1; 210 mm in ZRC 4.337; and 290 mm in ZD.1895.1.9.1) by a peninsula of caudally directed hair which intrudes into the abdomen along the midline for about 50 mm in ZD.1928.11.2.1, and for about 40 mm in ZRC 4.337 and ZD.1895.1.9.1. In ZD.1928.11.2.1, the abdominal hairs bordering this peninsula are more laterally directed, conspicuously displaying their white to reddish basal portions. Towards the posterior of the abdomen the hair direction again radiates about the midline until it is caudal anterior to the callosities.

The facial skin pigmentation in *Presbytis potenziani* was reported as "black, fading to dusky fleshy round the mouth" (Chasen & Kloss, 1928: 813). The shortness of the hair between the eyes and the nostrils renders it inconspicuous against the skin pigmentation and its colour difficult to discern, but it appears to be whitish, intermingled in Siberut specimens, with blackish. In specimens other than ZRC 4.332, a tiny patch of slightly longer blackish hairs occurs within the ventral hollow of each nostril. Along the upper lip are some sparse blackish hairs, marginally whitish at their bases and increasing in length as they approach the corners of the mouth where they extend onto the cheeks in Siberut specimens. The upper border of the facial skin is rimmed by a line of similarly pale-based long blackish hairs which marginally encroach onto the midline of the face. Immediately behind these blackish hairs is a radiation of yellowish white hairs whose blackish distal bands form an arc about 15 mm in medial width whose span is equidistant to that between the lateral corners of the eyes.

The remainder of the dorsal pelage in *Presbytis potenziani* is predominantly blackish, but only on the paws does the colour pervade the whole hair shaft. From the frontal arc, the blackish colour extends posteriorly. Its lateral borders circle the vertex and skirt the pinnae narrowly in most specimens, but by a margin of about 10 mm in ZD.1895.1.9.1, ZRC 4.332 and ZRC 4.336. In the latter specimens the blackish circle is almost completed on the occiput. The blackish along the ridge of the sagittal crest, and more diffusely to either side, links it with the nape. Here it widens again, although still somewhat diffusely, to the extent that in ZD.1895.1.9.1, it approaches closely behind and as far as the lower end of the pinna. In other specimens, a fairly uniform blackish colour is maintained throughout the width of the nape with only a slight medial recession of the colour between the nape and the shoulder. In ZD.1895.1.9.1 and ZRC 4.332 there is almost complete recession here to form a "collar" which virtually separates the diffusely blackish nuchal hair from the more intense blackish of the hair of the back. The remainder of the dorsal pelage is superficially blackish, with the exception of the tail tip where there is individual variation in the presence of whitish hairs. In ZD.1928.11.2.1, ZRC 4.332 and 4.337 these whitish hairs are largely concealed by the surrounding blackish ones. Their conspicuousness in ZD.1895.1.9.1. is probably partly attributable to damage resulting in the loss of the distal parts of both the whitish and the blackish hairs in this specimen, but Tilson (1976: 766) confirms that the tail tip is white in some individuals.

The ventral and dorsal tail pelage colour in *Presbytis potenziani* are identical and, in the darker specimens (ZRC 4.333 and those from Siberut), the ventral pelage of the limbs is also blackish, becoming somewhat diluted to brownish on the proximal part of the brachium. In all but the palest examined skins, ZD.1895.1.9.1. and ZRC 4.332, this blackish brown colour also encroaches onto the pelvic part of the abdomen almost to its midline. In these latter specimens, a similar dilution extends further to include the entire inside of the thigh and in ZD.1895.1.9.1, the ventral midline of the shank. There is only the faintest blackish encroachment onto the abdomen. On the inside of the forearm in ZD.1895.1.9.1, the blackish, which is very evident immediately above the wrist, becomes progressively more restricted to the tips of the hairs until it is almost absent from those of the posterior part of the inside of the brachium and, in ZRC 4.332, throughout the midline of the arm. It is completely absent from the hairs of the pubic region and from most of those of the throat, chin, cheeks and abdominal midline. Ventral blackish is readily evident only in the distal parts of the hairs forming, on each side of the chest, an ill-defined baldric-like arc which runs obliquely from the anterior of the brachium to the anterior of the abdominal peninsula of caudally directed hairs where it widens, predominantly on the thoracic side of the line of conflicting hair direction, before merging with the dorsal pelage colour midway along the opposite flank. (In ZRC 4.332 there is apparently even less ventral blackish, but adequate examination was precluded by the mounted state of the skin.) In an arc along the pectoral girdle, and in a broad thoracic midline band which includes the abdominal peninsula of caudally directed hairs and the adjacent laterally directed ones, the distal part of the hairs in ZD.1928.11.2.1 is almost as black as is that of the dorsal pelage. Throughout the rest of the ventrum, including the cheeks and chin, the distal blackish in the hair shaft is diluted until it persists only as grey at the tips of the central throat hairs. In the remaining examined skins, ventral blackish is largely restricted to the thoracic midline. It is most restricted in ZRC 4.334 and most widespread (but less intense than in ZD.1928.11.2.1) in ZRC 4.337. It is completely absent from the hairs on and around the scrotum. In ZD.1895.1.9.1, 1928.11.2.1, ZRC 4.333 and 4.337 the distal part of the hairs on the upper rim of the pinnae are brownish, with a blackish tinge in ZD.1928.11.2.1. Pinnal hairs are wholly whitish in other specimens.

The central portion of the hair shaft throughout most of the ventrum posterior to the pectoral girdle in ZD.1928.11.2.1, is a reddish orange which is strongest on the anterior of the upper thigh, anterior of the abdomen and the posterior of the chest but, at about the level of the axillae, begins to fade out towards the throat. It also fades out towards the wrist, and towards the shank. It is absent from the pubic hairs, but intensifies in the blackish hairs which surround them laterally and posteriorly. Dorsally, its presence is evident midway along the shaft of the hairs of the nape (where its conspicuousness amongst the blackish distal bands produces a speckled effect), anterior part of the flank and to a lesser extent, on the anterior of the back and on the vertex. In ZD.1895.1.9.1 the orange is a shade more reddish except on the inside of the thighs. Its distribution is similar, but it is absent from the abdominal midline, from the hair laterally adjacent to the pubic hair and it barely extends from the forearm onto the brachium and, on the chest, begins to disappear about 40 mm posterior to the level of the axillae. Conversely, it is more pervasive midway along the shaft of the hairs on the inside of the shank, and dorsally is absent only in the pelage of the paws, tail and lower forearm. It is visible without displacing the hairs in the nuchal "collar" and as speckling on the nape itself.

The hairs of the pubic region are whitish yellow in all examined specimens of *Presbytis potenziani.* In ZD.1928.11.2.1 they form a rhomboidal patch whose marginally longer axis, about 80 mm in length, passes transversely across the anterior base of the penis. The posterior apex of this rhomboid abuts onto the ventral end of the line of juncture of the callosities, and is flanked by distally blackish hairs whose shafts grade through reddish to yellowish at their bases. Anteriorly the yellowish white pubic hairs extend along the midline to merge indiscernibly with the blackish-tipped buffy ones of the lower abdomen. In ZD.1895.1.9.1. the pubic patch is more oval in shape, sparse whitish-yellow hairs occur between the callosities and the hairs immediately anterior to the pubic patch are distinguishable only by their faint brownish orange tinge.

Most of the hairs on the throat, cheeks and chin in ZD.1895.1.9.1, and in both specimens on the lower lip and amongst the sparse blackish hairs on the upper lip are wholly yellowish white; as are the proximal parts of most of the hairs whose shaft coloration has not so far been fully described. This proximal colour grades through grey where the adjacent shaft colour is blackish, or through yellowish where it is orange. The exceptions are the paw and tail hairs of ZD.1895.1.9.1 where there is little colour separating the yellowish white proximal part from the blackish distal portion. In ZD.1928.11.2.1 the whitish proportion increases in the hairs surrounding the nipples and at the posterior end of the abdominal peninsula of caudally directed hairs, rendering these hairs conspicuous. The enhanced whitish around the nipples connects with that anterior to the pectoral girdle. A similar increase in proximal whitish in the hairs on the nape and occiput of the Sipura specimen accounts for the diffuse nature of the distal orange and blackish in these hairs.

In short, *Presbytis potenziani* has the appearance of an animal whose pelage is undergoing a blanching process from glossy black via reddish to white, commencing at the base of the hair shaft and in two anatomical centres, one on the throat, the other in the pubic region. The blackish, succeeded by reddish, having completely receded from the pubic patch, and almost entirely from the facial margin and throat, continues its withdrawal along the lateral parts of the nape towards its midline, along the lateral parts of the chest and along the inside of the arms towards the wrists. From the pubic region its retreat proceeds initially along the abdominal midline, and latterly along the inside of the legs towards the ankles. The blackish, and to a lesser extent, the reddish pigment has also receded from the proximal part of the hair shaft in much of the rest of the body, notably at the tip of the tail. This representation is of course reversible, and the species could be envisaged as an originally white-haired animal in the process of assuming a blackish pelage by way of a reddish transitional coat. This alternative might better accord with the whitish neonatal pelage colour, but it would also involve pigmental invasion of the hair shaft in a distal to proximal direction, with at least five centres of origin of the pigment: namely on the paws, proximal part of the tail, and probably another one on the vertex. Be that as it may, the former concept can suffice for the purpose of illustration, and the Sipura skin will be seen to represent a more advanced stage in the blanching process than does that from Siberut. The Pagai Utara skins, as described by C. P. Groves *(in litt.)*, would appear to represent, in some respects at any rate, an even more advanced stage.

Chasen & Kloss' (1928: 813) description of the Siberut subspecies, and an examination of the two paratype skins, indicate that there is negligible variation in the dorsal pelage colour, but that in ventral pelage colour, the holotype is amongst the darkest of the type series. Chasen & Kloss

(1928: 813), presumably following the colour nomenclature of Ridgway (1912: pl. XV), described the underparts as "between tawny and ochraceous-tawny (type)". Ridgway's colour "ochraceous-tawny" is applicable only to some of the hairs of the abdomen, and to only the more proximal parts of the hairs of the mid-ventrum of the holotype. It is therefore assumed that Chasen & Kloss' description refers to the range of colour in the holotype, rather than the range of colour in the type series. They did however state that there "is never any approach to the bright [ventral] colouring of *P. p. potenziani.* While the colour of the abdomen of the more brightly coloured examples of *siberu* is tawny, the dullest Siporan animals are ferruginous below". The ventral pelage between the pectoral girdle and the pubic patch in paratype ZRC 4.336, is reddish yellow with a blackish sagittal band on either side of the midline. Adjacent to the abdominal peninsula of caudally directed hairs, anterior to the nipples, and about midway between these two points, the blackish tinge diffuses laterally. ZRC 4.337 is ventrally orange white with a blackish sagittal band on either side of the midline of the chest and anterior abdomen. The blackish colour of the flanks encroaches onto the ventrum more strongly than in ZRC 4.336. The ventral pelage of the Sipuran specimens, ZRC 4.333 and 4.334, is reddish, the hair tips tinged with blackish towards the midline of the chest. The reddish and the blackish colour are more intense in ZRC 4.333. ZRC 4.335 is ventrally reddish yellow with a blackish tinge. C. P. Groves *(in litt.)* described MZB 2864 as: "Underside very red, with black tips on lower chest; upper chest reddish-white; red doesn't extend to legs, and hardly (very blackened; humeri only) to arms".

The belly and lower chest of most of the Pagai Utara skins examined by C. P. Groves *(in litt.)* are described as "red-brown" rather than red. The exceptions are MZB 6627 which is described as "very red below" with a "tinge of black", and MZB 6631 described as "very pale buff below, little red". The ventral pelage between the axillae and hips in ZRC 4.332 is reddish yellow with blackish tips to the hairs towards the centre of this area. Limb colour seems less variable than in Sipuran specimens. The inner side of the thigh is concolorous with the belly, darkening distally until the belly colour disappears halfway along the shank. The inner side of the brachium is whitish, becoming "dirty red" distally as far as the mid forearm. The only exception is MZB 6625 in which the inside of the brachium is red and red extends only along the proximal half of the inside of the thigh. Pagai Utara skins have a broader whitish brow band and a correspondingly smaller blackish area on the crown. The whitish area also extends further down the chest. In other respects Pagai Utara skins appear indistinguishable from Sipura specimens.

The holotype of *Presbytis potenziani potenziani* as figured by Peters (1879: pl. IVB) and described by Blyth (1875: 10), Blanford (1888b: 38) and Elliot (1913: 67) resembles the Pagai Utara, rather than the Sipuran skins. The reddish inside of the brachium resembles the exceptional MZB 6625.

The distinctions between the Sipuran and the Pagai Utara specimens raise the possibility that the species is represented by three rather than two subspecies, although Chasen & Kloss (1928: 811) reported that two "faded mounted specimens from the Pagi Islands (1902) do not appear separable" from Sipuran skins. One of these specimens is presumably ZRC 4.332 collected in Pagai Utara on 11 November 1902 by W. L. Abbott (Weitzel *et al.*, 1988: 66). At 12 mm, the medial width of its brow band is at least 2 mm wider than in any of the examined Sipuran skins and, rather than abutting onto the pinna, the blackish crown hairs are separated from it by a whitish band approximately 9 mm in width. A more precise determination of the type locality of the nominate subspecies will depend on whether Pagai Selatan specimens are separable from Pagai Utara specimens. Although the evidence clearly contradicts Pocock's (1935: 956) view that "the Siberu skin" (ZD.1928.11.2.1) is quite inconclusively racially distinct from the nominate subspecies, the establishment of a third subspecies would be unjustified without a personal examination of a comprehensive series of specimens. Some authors might prefer to refer the Sipuran population to the subspecies, *P. p. siberu.*

TAXONOMIC AFFINITIES BASED ON ADULT PELAGE CHARACTERS

As already mentioned (see pp. 334-335), the adult pelage characters of *Presbytis potenziani* have indicated to different authors, taxonomic affinities with *Semnopithecus pileatus;* with *S. francoisi* and its allied species; with *Presbytis femoralis;* and with *P. comata.* It therefore seems appropriate to review its adult pelage character affinities with each of these species in turn. The *S. pileatus* subspecies most closely resembling *P. potenziani* in adult pelage colour is *Semnopithecus* (*Trachypithecus*) *pileatus tenebricus* (Hinton, 1923: 81). The following comparison is derived primarily from the adult male holotype, ZD.1921.7.13.8, from the Matunga River [26°45'N 91°33'E], North Kamrup, [Assam,] India.

The pelage of *S. p. tenebricus* is sparser and, especially around the vertex and on the shoulders and flanks, less recumbent than that of *P. potenziani.* The hair direction is generally similar, but the anterior abdominal hairs are more laterally than anteriorly directed; there is no abdominal peninsula of caudally directed hairs; there is a hair whorl on the chin instead of a sagittal parting of the throat hairs; and above all there are no anteriorly erected hairs on the vertex. The hairs immediately anterior to the lower half of the pinna are very elongated in relation to those on the nape and cheeks, and the "cap" which characterizes the species results from the elongation of the lateral hairs of the vertex in relation to those between the facial margin and the upper part of the pinna. The tail hairs, which are relatively uniform in length in *P. potenziani*, are elongated along the proximal quarter and distal quarter of the tail in *S. pileatus.*

The dorsal pelage colour of *S. p. tenebricus* resembles that of *P. potenziani* only on the anterior part of the "cap", on the hands excluding the distal phalanges, on the proximal phalanges of digits II-V of the feet, and along the distal third of the tail. The hairs of the halluces are predominantly reddish yellow and the dorsum of the distal phalanges of the remaining digits is fringed with brownish grading to yellowish white hairs. The blackish hairs of the tail are without pale bases and the few yellowish white hairs at the tip of the tail are without blackish tips. From these blackish areas the dorsal pelage colour grades through dark grey to a fairly uniform pure grey on the nape, trunk, limbs from the wrists and ankles, and on the proximal quarter of the tail. The bases of the greyish hairs are somewhat paler, and those of the hairs of the head, upper trunk and upper arms are somewhat tinged with reddish. The majority of the grey hairs of the nape, anterior two-thirds of the back, and metatarsals II-V, are distally yellowish white.

The ventral pelage of *S. p. tenebricus*, including the sides of the head immediately below the "cap" from the face to the pinna, a post-auricular area about 15 mm in width, most of the girth of the neck, the inner surface of the limbs to the hairless palmar pads, the abdomen to the base of the callosities and the proximal 40 mm or so of the tail, is entirely without blackish tips. The ventral pelage colour grades from yellowish orange on the sides of the head, upper chest and inner half of the hollow of the shoulders, to yellowish white on and behind the pinna, on the chin, on the lower forearm and posterior part of the brachium, on the lower chest and throughout the rest of the ventrum. The coloration of the shorter hairs on the face contrasts with the apparent condition in *P. potenziani*, it being blackish along the nose and whitish laterally and exclusively blackish along the lips. The hairs bordering the lateral margin of the facial skin are whitish intermingled with a few blackish hairs at nose level, but there are no whitish or basally whitish hairs along the upper facial margin.

The Asian pied leaf monkeys, including *Semnopithecus* (*Trachypithecus*) *francoisi*, have been reviewed by Brandon-Jones (in prep., a). When compared with them, *P. potenziani* most closely resembles *S. laotum* in hair length, although the flank hair is shorter than in any Indochinese pied leaf monkey. The disposition of the head hair resembles *S. delacouri*, but the crest hairs are less than a third the length; the whiskers are about half the length; there is no hair whorl behind the pinna; and *S. delacouri* resembles *S. pileatus* in the presence of a hair whorl on the chin. With the apparent exception of *S. delacouri*, the Indochinese pied leaf monkeys do share with *P. potenziani* the presence of an abdominal peninsula of caudally directed hairs.

In dorsal pelage colour *P. potenziani* superficially resembles *S. francoisi* in the amount of whitish pelage behind the pinna, but is distinguished by the whitish brow band which is considerably narrower than in *S. laotum*; and by the pale throat which resembles only that of *S. johnii* and albinotic *S. francoisi*. As in *S. johnii* the roots of the dorsal hairs are pale, but the intervening colour is reddish, rather than brownish. Only male *S. johnii* share with male *P. potenziani* the presence of the pale hairs surrounding the penis, and none of the Asian pied leaf monkeys show even the limited ventral paling present in *P. p. siberu*.

The parallelism between *P. potenziani* and the aberrantly black-red-white pelaged specimens of *Presbytis femoralis*, noted by Thomas (1892), is instructive, and apart from some differences in the disposition of the hair of the head, and some reversion to reddish of pelage areas such as the forehead, whitish in *P. potenziani*, these aberrant specimens could well be regarded as yet a further stage in the pelage colour blanching process displayed by the Siberut, Sipura and Pagai Utara populations of *P. potenziani*.

The hair length and disposition of *P. femoralis*, including the presence of an abdominal peninsula of caudally directed hairs, is similar to *P. potenziani*, but on the head the line of conflict of hair direction is orientated almost horizontally towards the centre of the cheek where it abruptly turns downwards towards the corner of the mouth, isolating a narrow tract of laterally directed hairs along the lateral facial margin. In most specimens the line then circumvents the mouth to terminate on the throat where the midline hairs are posteriorly directed, not parted. A sagittal crest of semi-erect posteriorly directed hairs extends from the facial margin, where it is flanked by a semi-whorl of radiating hair to either side, to the occiput where it is dissipated by a medial patch of erect elongated hairs. The elongated hairs to either side of the occipital crest tend to be swept round behind it. The hairs of the chin, cheeks and side of the neck are also longer than in *P. potenziani*.

In skins of *P. femoralis* examined by the author, the greatest extent of blackish in the pelage is shown by an adult female from "Batang Lupar [c.1°15'N 111°26'E], Sarawak" (Hooijer, 1962: 15, specimen no. 9); the least in an adult female skin, ZD.1895.5.7.2, from Sungai Miri [4°23'N 113°59'E], Sarawak. Both skins are dorsally reddish orange (yellowish orange in an adult female, ZD.1900.2.2.1, from "Baram District, Sarawak") with a faint ventral encroachment (very faint in ZD.1895.5.7.2) to the midline between the chest and abdomen. The rest of the ventrum is yellowish white. Some sparse hairs immediately above the corners of the mouth, and in a line along the upper facial margin are blackish. Overlying part of the orange colour or, in the darker skins replacing part of it, the blackish in its minimal expression, covers the paws, forearm, anterior of the brachium, dorsal midline from the shoulders where the blackish band is about 100 mm wide, to the hips where it is about 40 mm wide, and for about one-fifth of the distal dorsum of the tail. Blackish hairs occur very sparsely throughout the rest of the dorsum of the tail, but sparse yellowish hairs are intermingled with the blackish caudal, arm and foot hairs, and even along the periphery of the hand. Orange hairs are strongly intermixed directly above the wrists and directly below the elbows, and in patches along the midline of the dorsal blackish band. In its maximal expression the dorsal blackish colour consolidates on the paws, arm, torso, basal third of the tail, and distal posterior of the shank; and suffuses through the orange of the nape (from pinna to pinna), the occipital crest, the flank, the distal tail, the anterior of the shoulders and shank, and the midline of the thigh. Yellowish hairs are visible at the tail tip and along the periphery of the paws. Unlike ZD.1895.5.7.2, the throat and pectoral girdle are faintly tinged with orange, and all the ventral orange hairs are intermingled with sparse blackish hairs, especially along the midline and postero-lateral parts of the chest.

Evidence for recognizing *Presbytis comata everetti* as a sexually dichromatic, inland subspecies; and for restricting *P. c. hosei* as a chromatically monomorphic subspecies endemic to coastal north Sarawak, was presented by Brandon-Jones (in prep., b). Of the described subspecies of *P. comata, P. potenziani* most closely resembles the adult female phenotype of *P. c. everetti*. The following comparison is made primarily with the holotype, ZD.1892.10.19.1, of *Semnopithecus everetti* Thomas, 1893 (p. 582), from Mt. Kinabalu [6°05'N 116°33'E], and with a paratype, ZD.1892.10.20.1, from Mt. Dulit [3°21'N 114°11'E]. The paratype parallels Miller's (1934: 16) two specimens of *P. c. canicrus* from Klambu Harbor [=Labuhankelambu, 1°14'N 118°44'E], in the blackish brown cast that sullies the grizzled grey of its shank, brachium and upper torso, and tinges the blackish of its crown.

In hair length and disposition, both specimens of *P. c. everetti* differ from *P. potenziani* only in that the tail hairs are longer, especially in ZD.1892.10.19.1, and the midline parting on the throat is replaced by two transversely aligned hair whorls. Apart from the absence of any reddish colour in the hair shaft, and the presence of whitish rather than blackish nasal hairs, and taking into account individual variation; head pelage coloration in *P. c. everetti* is to all intents and purposes identical with that in *P. potenziani*. The sexual dichromatism in *P. c. everetti* shows an intriguing parallel with the geographic variation in *P. potenziani*. The adult female more closely resembles the Siberut population, and the adult male and juvenile, the Pagai island population.

Presbytis c. everetti is distinguished from *P. potenziani* by the admixture of whitish and whitish-banded hairs to the brownish black hairs of the tail, and to those of the dorsal pelage of the rest of the body other than the paws; its uniformly whitish non-caudal ventral pelage; and the absence of reddish colour. The differences in pelage colour between the holotype and paratype, and between the black-red-white aberrants of *P. femoralis* and its normal phenotype, throw this divergence into perspective. In external morphology, *P. potenziani* shows closer affinities to *P. c. everetti* than to any other extant colobine.

TAXONOMIC AFFINITIES BASED ON ADULT CRANIAL CHARACTERS

This analysis is primarily based on ZD.1895.1.9.1 and 1928.11.2.1, and ZRC 4.333, 4.334 and 4.336. The left side of the maxilla of ZD.1895.1.9.1 is congenitally distorted (see Colyer, 1936: 220).

Lyon (1907: 568) enumerated eight cranial characters which distinguished Bornean *Presbytis femoralis* from Bornean *Semnopithecus cristatus*. Pocock (1935: 896-897) recapitulated these as generic characters which distinguished *Presbytis* from the "genus", *Trachypithecus*. In addition, he noted that the anterior nares were less elongated; the nasal region was usually prominently convex; the upper edge of the orbit was straighter, giving a "frowning" aspect to the brow; and the occipital region had a weaker crest. The cranial characters described by Lyon and Pocock, were reiterated by Hooijer (1962: 21).

The five *Presbytis potenziani* skulls which were examined share with most *Presbytis* the following cranial characters, paraphrased from Lyon and Pocock. There is a convexity at nasion (also present in *Semnopithecus johnii poliocephalus*, ZD.1933.4.1.9 and 1933.4.1.10). The anterior nares are short in proportion to their breadth (16 X 11mm in ZD.1928.11.2.1; 14 X 9 mm in ZD.1895.1.9.1). Their rim contracts towards prosthion at a less obtuse angle. Medial to the zygo-maxillary suture, there is a marked emargination of the inferior edge of the orbital bar. (This character also generally distinguishes *Semnopithecus obscurus* from *S. cristatus*.) The mandibular corpus is shallow and the ascending ramus is not unusually expanded. (Many of the *"Presbytis phayrei crepuscula" [=Semnopithecus barbei]* specimens listed by Napier, 1985: 67-68, especially those from Thailand, are indistinguishable from *Presbytis* on this character.)

In an attempt to objectively assess Lyon's and Pocock's claim that the rostrum is more abbreviated in *Presbytis*, the calvarium was viewed in profile so that the maxillary canines were silhouetted against each other and a measurement was taken to the nearest millimetre from a transparent rule held parallel to the long axis of the skull and to the Frankfort plane, between prosthion and the point where the zygo-maxillary suture crossed the rim of the orbit. On the small sample tested, this measure tend to confirm Lyon's and Pocock's statement, but the rostral and palatal length placed *P. potenziani* in an intermediate position between the two genera.

The "well-marked swelling of braincase just beneath lambdoid suture" results from lambda being relatively high and the occipital crest relatively low and poorly developed. It is a character which is not constant in *Presbytis femoralis chrysomelas*, let alone other *Presbytis*, and is valueless in generic diagnosis. It is absent in ZD.1928.11.2.1 and ZRC 4.333, but partially developed in ZD.1895.1.9.1, ZRC 4.334 and 4.336.

Presbytis potenziani resembles *Semnopithecus* in the considerable constriction behind the orbits. Skulls ZD.1928.11.2.1 and ZD.1895.1.9.1 are narrow by both *Presbytis* and *Semnopithecus* standards in their interorbital (both 7 mm) and postorbital (38 mm in ZD.1928.11.2.1; 39 mm in ZD.1895.1.9.1) widths. Groves (1970: 583) has shown that the species is intermediate in the index of these two measurements. The orbital bar, especially in ZD.1928.11.2.1 and ZRC 4.333, is robust even by *Semnopithecus* standards, and the horizontal flattening of the frontal bone behind glabella and the more perpendicular interorbital profile, resemble *Semnopithecus* (sensu stricto) rather than *S. (Trachypithecus)*.

It is necessary to emphasize that Pocock's (1935: 896) characterization of the *Presbytis* supraorbital torus as weaker than in *S. (Trachypithecus)*, with the upper edge of the orbit straighter, is a general character which will not discriminate every specimen. The series of 249 adult skulls at the Natural History Museum, London, the Zoological Reference Collection, National University of Singapore, and the Sarawak Museum, Kuching, show considerable individual variation. In some specimens, notably those of *Presbytis comata thomasi*, and to a slightly lesser extent, the Riau archipelago *Presbytis siamensis*, there is considerable development of the supraorbital torus. In most cases, however, there is no "raised eyebrow" appearance typical of *S. (Trachypithecus).* In some specimens, especially *P. c. thomasi,* ZD.1938.11.30.7 and ZD.1938.11.30.8, it is as if a *P. potenziani* supraorbital torus has "melted" at glabella and sagged onto the interorbital region, sometimes producing a transverse crease between glabella and nasion.

In order to investigate its geographic distribution, the development of the supraorbital torus was quantified as follows. 4 = continuous across glabella with shelf behind. 3 = continuous across glabella without shelf behind. 2 = medial hiatus at glabella. 1 = lateral development only (absent from glabella). 0 = completely absent. To date, only the collections at the Natural History Museum, the Zoological Reference Collection, and the Sarawak Museum have been subjected to this analysis. Southern Borneo and most of Sumatra were unfortunately poorly represented by the 249 adult skulls involved, but averaging the scores from the individual localities indicate there was geographic variation. In addition to the above mentioned populations, there were clusters of localities with relatively high scores centred on Gunong Mulu [4°03'N 114°56'E], Sarawak, Borneo, for *Presbytis comata*, but not for *P. femoralis* nor *P. rubicunda*, and centred on Klong Tung Sai [7°58'N 98°22'E], Thailand, for *P. femoralis.* Conversely, most *Presbytis siamensis siamensis* (from West Malaysia) and many *P. rubicunda* skulls, consistently scored only 1. It is noteworthy that the sample included only six skulls with supraorbital torus completely absent.

There is an anteriorly adjacent duplication of the greater palatine foramen in ZD.1895.1.9.1, the left duplicate being more medially positioned than the right one. (5.1% of the NHM *Presbytis* skulls, and 4.0% of the NHM *S.* (*Trachypithecus*) skulls show such a duplication.) V. Weitzel *(in litt.)* observed that *P. potenziani* conforms with *Presbytis* in that the greater palatine foramen is broad in relation to its sagittal length, with a less acute angled posterior outline and a razor-edged, rather than smooth, medial (palatine) margin. This is substantiated by the NHM specimens in which a razor-edged medial margin was found in 90.7% of *Presbytis* and 43.0% of *S. (Semnopithecus)*, but in *S. (Trachypithecus)* only in the holotypes of *S. delacouri* and *S. laotum*, in *S. johnii* ZD.1845.9.20.4, in *S. obscurus shanicus* ZD.1914.7.8.5 and ZD.1937.12.3.72 and on the right foramen of *S. f. francoisi* ZD.1928.7.1.8. Of the *P. potenziani* skulls in which this character was determined, ZD.1895.1.9.1, 1928.11.2.1, ZRC 4.333 and 4.336 have razor-edged medial margins, and ZRC 4.334 has a sharp-edged medial margin.

Presbytis potenziani resembles *Presbytis* in being without a marked constriction of the mental region of the mandible between the bases of the canine root sockets.

TAXONOMIC AFFINITIES BASED ON THE DENTITION

Colyer (1936: 218) investigated positional variations in the incisors of most of the *Presbytis* and *Semnopithecus* species recognized by Pocock (1928, 1935). When adjusted so that the *"Semnopithecus senex" [=S. vetulus]* data is transferred from the genus, *Semnopithecus* to the "genus", *Trachypithecus;* and the *"Trachypithecus potenziani"* data is isolated to facilitate comparison with that of *Presbytis* and *Trachypithecus;* his figures reveal that the percentage showing irregularity in the position of the incisors was 12.8 in *Presbytis* (n=311), 8.3 in *P. potenziani* (n=12) and 25.2 in *Trachypithecus* (n=429). The percentage showing protrusion of the mandibular incisors was 77.2 in *Presbytis,* 66.7 in *P. potenziani* and 19.3 in *Trachypithecus.*

Colyer's (1936: 207) definition of "inferior protrusion" as where "the mandibular incisors project beyond the maxillary teeth to the extent of at least half the externo-internal diameter of the tooth" is arbitrary, and begs the question of how this diameter is defined. A more objective definition of what may be termed "underjet", is that it is the condition where the labial occlusal edge of the mandibular incisor occludes anteriorly to that of the maxillary incisor. When subjected to this criterion, 93% of 359 *Presbytis* skulls examined by the author, showed underjet of both the central and lateral incisors. Of the remainder, twelve showed a predominantly underjet incisal occlusion, twelve had a mixed bite with the mandibular central incisors either occluding edge to edge or lingually to the maxillary central incisors, and one skull had an asymmetrical incisal occlusion with the right side underjetted and the left side overjetted. Only 17.6% of 512 *S. (Trachypithecus)* had a fully underjetted incisal occlusion. Zingeser (1970: 179) reported that the "aberrant Mentawai leaf monkeys *(T[rachypithecus] potenziani)*" housed at the U.S. National Museum "are exceptional in having a high incidence of underbites". Of six specimens examined by the present author, five had complete underjet, and ZD.1928.11.2.1 had predominant underjet.

Delson (1973: 175) found that of 18 *Presbytis potenziani* from "the Mentawai (Pagai) islands", six males and six females lacked a hypoconulid bilaterally, one male lacked it unilaterally (with the opposite side "normal"), four males had rather small hypoconulids bilaterally, and only one female had "normal" hypoconulids bilaterally. Of five specimens examined by the present author, the two NHM specimens had "normal" hypoconulids bilaterally, while three ZRC skulls each asymmetrically had one small hypoconulid and lacked the other. The 15.2% of normal hypoconulids in the combined above sample compares well with the 17.7% in a sample of 685 *Presbytis* mandibular third molars. *P. potenziani* appears abnormal only when compared with the 96.7% incidence of normal hypoconulids in a sample of 958 *Trachypithecus* mandibular third molars. In the small sample available, *P. potenziani* actually exceeds *Presbytis* by 11.2% (see Table 1) in its incidence of specimens lacking a hypoconulid, and exceeds by almost 60% the 0.9% of such specimens in *Trachypithecus*. In order to allow for asymmetry and absent molars, these percentages were based on individual rather than pairs of molars. The sample size of skulls examined was therefore rather more than half the above quoted molar sample sizes. Hypoconulids were regarded as absent if the development of the mesial and distal shelves on the molar was symmetrical. If the distal shelf was more developed, the hypoconulid was regarded as vestigial or present, depending on its degree of development.

Table 1. Percentage cusp incidence on the mandibular third molar.

Taxon	4	4.5	5	5.5	6	Molar Sample Size
Presbytis	49.6	32.7	17.7	0	0	685
P. potenziani	60.9	23.9	15.2	0	0	46
Trachypithecus	0.9	0.2	96.7	1.5	0.7	958

Kay (1978: fig. 7), in a principal coordinates analysis of the molar dimensions of Asian cercopithecid primates, found that *P. potenziani* had a larger first coordinate value than the four *Semnopithecus* species he measured, and clustered with the four *Presbytis* species. Weitzel (1983: 300) considered the dentition of *P. potenziani* consistently *Presbytis*-like. In his sample of 19, none had an articular facet on the distal surface of the maxillary third molar, although the molar row approached "*Trachypithecus*" in its increased length. The maxillary incisors were strongly homodont, symmetrical and broad. The mandibular incisors were "chair-shaped" lingually, forming a lingual incisal basin. The mandibular incisors of MZB 6622 were poorly tuberculated, other specimens were rather strongly tuberculated. In the skulls examined by the author, the incisors were found to resemble those of *Presbytis* except that the mandibular incisal lingual cingulum was low as in *Semnopithecus (Trachypithecus)*.

TAXONOMIC CONCLUSIONS

The sole available skeleton of *Presbytis potenziani* falls at the low end of the range of variation in *Semnopithecus (Trachypithecus)* intermembral and femero-humeral indices, and only one unit higher than these indices in a skeleton of the Sumatran *Presbytis melalophos*. Its brachial index is at the low end of the range of variation in *Presbytis*, but five units above the range of variation found in *S. (Trachypithecus)*. Its prognathism index falls four units below the maximum recorded for male *Presbytis*. This maximum index for male *Presbytis* is also the minimum for male *S. (Trachypithecus)* (Washburn, 1944).

This characteristic of usually falling within, but near the extreme of *Presbytis* variability, is typical of much of the *P. potenziani* morphology. It is typically *Presbytis* in most other cranial characters, but is extreme in its postorbital constriction and robust development of the orbital bar; is rivalled only by *P. comata thomasi* in its development of the supraorbital torus; and is intermediate with *S. (Trachypithecus)* in its rostral length, palatal length and interorbital index. With the exception of the low mandibular incisal lingual cingulum, it is also typically *Presbytis* in its dentition.

In tail shortness (Pocock, 1935: 957) and neonatal pelage coloration (Tilson, 1976) *P. potenziani* is typically *Presbytis*. In adult pelage coloration and disposition it most closely affiliates with the adult female phase of the north Bornean *Presbytis comata everetti*, but shows convergence with other species such as the Laotian *Semnopithecus laotum*. The adult male three-part call of *P. potenziani* closely resembles that of the north Sumatran *P. comata thomasi* (C. C. Wilson & W. L. Wilson, 1977), which in turn closely resembles that of *Presbytis comata canicrus* in east Kalimantan (C. C. Wilson & W. L. Wilson, 1975: 265). The vocalizations of all three have more in common with each other than they do with the geographically intervening south Sumatran *P. melalophos* (W. L. Wilson, pers. comm.).

PHYLOGENETIC CONCLUSIONS

Kloss (in Chasen & Kloss, 1928: 799) speculated that the narrow sea-bottom ridge of less than 100 fathoms between the Mentawai Islands and the Batu Islands to the north-east, might not be as unbroken as most contemporary bathygraphical charts indicated. He emphasized that elsewhere the archipelago is surrounded by depths of 100-500 fathoms of water. This implication that it is the sea as a barrier to dispersal that has rendered *Presbytis potenziani* "aberrant", has been repeated by Medway (1970), Zingeser (1970), Delson (1973) and Tilson (1976). Biogeographic evidence however, suggests that perhaps the reverse is the case, and that *P. potenziani* is "normal" while its congeners are "aberrant".

The glaring zoogeographic evidence unexplained by the conventional view is that its fellow endemic, *Nasalis concolor* has its nearest relative, *N. larvatus* on Borneo with no relative on Sumatra. *P. potenziani* has its closest pelage colour affinities with an animal from Borneo. Its closest cranial affinities are with an animal from Sumatra. It apparently shares its closest vocal affinities with the two latter animals. Its closest Sumatran relative however, is not *P. melalophos*

Table 2. Collectors' measurements (in millimetres) of *Presbytis potenziani*.

Locality	Acc. No.	Collector	Coll. No.	Age	H&B	Tail	HF.	Weight
Male								
Siberut	ZD 1928.11.2.1	C. B. Kloss	2005	Adult	500	580	155	-
Siberut	USNM 252315	C. B. Kloss	2065	Adult	485	550	150	-
Siberut	ZRC 4.337	C. B. Kloss	2159	Juv.	390	450	130	-
Sipora	MZB 2864	C. B. Kloss	2349	Adult	540	610	162	-
Sipora	USNM 252313	C. B. Kloss	2389	Adult	495	595	160	-
Sipora	ZRC 4.333	C. B. Kloss	2313	Adult	505	590	160	-
Pagai Utara	MZB 6627	J. J. Menden	-	Adult	[522]*	592	172†	-
Pagai Utara	MZB 6629	J. J. Menden	-	Adult	536	562	164	-
Pagai Utara	MZB 6622	J. J. Menden	-	Subad.	[506]*	560	154	-
Pagai Utara	MZB 6624	J. J. Menden	-	Subad.	512	558	158	-
Pagai Utara	USNM 121664	W. L. Abbott	2025	Juv.	460	585	-	10 lb
Pagai Selatan	USNM 121667	W. L. Abbott	2109	Adult	495	640	-	15 lb
Pagai Selatan	USNM 121668	W. L. Abbott	2118	Adult	575	610	-	15 lb
Pagai Selatan	USNM 121670	W. L. Abbott	2121	Adult	525	590	-	16 lb
Pagai Selatan	USNM 121672	W. L. Abbott	2126	Adult	-	-	-	12 lb
Pagai Selatan	USNM 121673	W. L. Abbott	2192	Adult	525	590	-	15.75 lb
Pagai Selatan	USNM 121669	W. L. Abbott	2119	Subad.	470	590	-	11 lb
Female								
Siberut	ZRC 4.336	C. B. Kloss	2024	Adult	435	495	148	-
Siberut	USNM 252314	C. B. Kloss	2025	Juv.	465	545	150	-
Sipora	USNM 252312	C. B. Kloss	2314	Adult	510	605	152	-
Sipora	ZRC 4.334	C. B. Kloss	2365	Adult	485	640	156	-
Pagai Utara	MZB 6628	J. J. Menden	-	Adult	[518]*	552	149	-
Pagai Utara	MZB 6631	J. J. Menden	-	Adult	548	554	154	-
Pagai Utara	MZB 6626	J. J. Menden	-	Juv.	[495]*	550	152	-
Pagai Utara	MZB 6630	J. J. Menden	-	Juv.	456	485	137	-
Pagai Selatan	USNM 121666	W. L. Abbott	2116	Adult	515	640	-	15 lb
Pagai Selatan	USNM 121671	W. L. Abbott	2123	Adult	520	600	-	13.25lb

H&B = Head and body length; HF = Hind foot length

*Computed by subtraction of tail length from total length.

†Perhaps lapsus for "162".

inhabiting the adjacent Sumatran coastline, nor even *P. femoralis* whose distribution includes the Batu Islands (Lyon, 1916: 459), but *P. comata thomasi* whose north Sumatran distribution approaches Siberut no closer than 375 kilometres across open sea.

This evidence strongly substantiates Chasen's (1940) hypothesis that the distribution of *P. comata* is disjunct and that *P. potenziani* is conceivably "a very distinct race". His conjecture that *P. comata* reached Java and Sumatra from Indochina via Borneo "by the eastern drift" (Chasen, 1940: xv) fails to identify its progenitor, fails to account for its absence in southwestern Borneo and southern Sumatra, and fails to account for *P. potenziani* having attained a degree of distinctiveness sufficient to have misled taxonomists into referring it to a different species group or genus-group.

This morphological imbalance between *P. potenziani* and *P. comata* cannot be dismissed as the result of geographic isolation. *P. potenziani* is no more geographically isolated from *P. comata* than are the Bornean, Javan and Sumatran populations of *P. comata* from one another. Its skeletal resemblances to the subgenus, *Trachypithecus*; its development of a supraorbital torus comparable with that of *Pygathrix* and *Semnopithecus* (sensu stricto); and its convergences in pelage colour with the Indochinese pied leaf monkeys indicate however, that it is more ancestral than *P. comata*. This indication is apparently substantiated by the prominent call which according to Kawamura (1984: 42), resembled that of *P. c. thomasi* only in the latter protion of its long phrase, while the earlier part included some phonetic elements comparable with those of *S. cristatus* and others evocative of those of *S. entellus*.

Brandon-Jones (1978, in prep., c) has recounted how Asian colobine geographic distribution, supported by other biogeographic evidence, indicates that the Asian rainforest was fragmented by the cool and dry climate which accompanied the most recent glaciation. The biogeographic evidence implies that during this era the central geographic distribution of *P. comata* was eradicated. The squirrel genus, *Callosciurus* and the gibbon, *Hylobates* are both represented by a subspecies endemic to the area of north Sumatra inhabited by *P. comata*, but *Macaca* and *Semnopithecus* are not so represented. This implies that the latter genera were absent from Sumatra at the advent of the cold dry episode that created this north Sumatran endemism. They must however, have been present at some earlier period in order for the macaque, *Macaca pagensis* to have colonized the Mentawai Islands and the leaf monkey, *Semnopithecus auratus* to have reached Java. The absence of a macaque and *Semnopithecus* endemic to north Sumatra therefore indicates the intervention of an earlier and more severe arid period. This earlier glacial drought was presumably also responsible for the eradication of both *Nasalis* and the significant number of animals found on the Asian mainland and Java, but not on Sumatra (Dammerman, 1929). It is inferred that *Callosciurus*, *Presbytis*, *Hylobates* and the orang-utan, *Pongo* recolonized Sumatra after this drought and their present distribution is the result of a second and less severe climatic deterioration. The most parsimonious explanation of the distinctiveness of *P. potenziani* is that it was the sole representative of its genus to survive the first arid period, and that it evolved ("degenerated" might be a more appropriate description) into *P. comata* during the interstadial. The relevance of the deep sea channel surrounding most of the Mentawai Islands is that it furnished the archipelago with a maritime climate which buffered it from the extremes of the glacial drought.

Brandon-Jones (in press) presented a synopsis of the evolution of the remaining species of the genus from *P. comata*. Their phylogeny involves a unidirectional integumental colour degradation in a sequence expressed simplistically as grey to brown and, in some instances to red and albinotic. This chromatic succession has also characterised the post-glacial dispersal of *Semnopithecus* (Brandon-Jones, 1978, in prep. c) and is comparable to those identified by Hershkovitz (1968, 1977). In both *Presbytis* and *Semnopithecus*, the pelage colour of what is interpreted as the pre-glacial relic species is predominantly glossy black (Brandon-Jones, in prep., a). It is therefore probably not coincidental that not only are most of the Mentawai Islands mammal fauna characterised by their very dark colour (Chasen, 1940: vii), but that the Siberut populations tend to be darker than those of the southern islands (Chasen & Kloss, 1928; Whitten & Whitten, 1982). This indicates that at the height of the glaciation even the southern Mentawai islands became inhospitable.

Chasen & Kloss (1928: 811) recorded that: "A juvenile *[P. p. potenziani]* taken from the breast on Sipora Island is...far more like the Siberut form than its own parents. It differs from *P. p. siberu* in having a little grey-white on the crown and hind limbs, the lower side of the tail greyish-white for two-thirds the length basally, rufous on the shoulders, and in being less blackened on the lower side of the trunk. It would seem therefore that *P. p. siberu* is the more primitive form". In the pelage colour dilution that characterises the insular variation from Siberut to the Pagai islands, *P. potenziani* appears to some extent to anticipate the chromatic phylogeny of its congeners. The tegumentary chromatic degradation of its congeners relative to *P. potenziani* also parallels what may be regarded as a degradation in the development of the cranial supraorbital torus. It is tempting, but perhaps premature, to parallel this latter degradation with the cranial differences between archaic and modern man.

Hershkovitz (1968) interpreted the tegumentary chromatic degradation as a long term evolutionary process affecting all mammals. It would seem more probable that it is a relatively short term process perhaps attributable to a relaxation in genetic stability associated with the rapid dispersal of populations as they expanded to their present geographic distribution during the interstadial and subsequent to the glaciation.

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