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Systematics of the Genus *Nycticebus*

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The slow lorises, genus *Nycticebus*, are placed traditionally in the family Lorissidae; like the African potto and angwantibo, and the slender loris which is Asiatic like the slow loris, they move by 'slow climbing', a distinctive mode of locomotion with its own anatomical correlates. The galagos are also generally placed in the Lorissidae, but these are vertical clingers: swift-moving, long-legged animals normally vertical in posture, with elongated tarsal bones.

The wide separation of the Lorissidae from the Malagasy prosimians – and, by implication, the homogeneity of the family itself – has recently been challenged [CHARLES-DOMINIQUE and MARTIN, 1970]. The striking similarities between the Malagasy *Microcebus* and the African *Galago demidovi* are reinforced in their phylogenetic implications by the conclusions of NAVIER and WALKER [1967] that vertical clinging morphology was characteristic of all known Eocene primates. If the galagos are not a highly specialised group but in fact a diverse group of primitive primates similar to ancestral forms, then it becomes legitimate to look for species among them which may be closer to the 'slow climber' stock of lorises and pottos. Whether the galagos are in fact such a heterogeneous group, and whether one of them is closer to the potto-loris stem than the others, is a question to be determined by further research.

The 4 groups – traditionally, genera – of 'slow climbers' may or may not be of common origin: at least one author [GOODMAN, 1967] considers that they may not be. The African and Asiatic genera clearly form 2 distinct groups, each with a plump (potto, slow loris) and a slender (angwantibo, slender loris) type. The Asiatic group is characterized by the marked extension of the ectotympanic into a tubular meatus, the more

angular auditory bulla, the arched and elongated nasal bones, the more forward-facing and tubular orbits, and the more reduced incisors; the African group is specialized in fewer features, but most noticeably in the more reduced 2nd and 3rd digits of the manus.

In each geographical group, the slender type tends to be more specialized than the plump type; of the two, the slender loris is more divergent from the slow loris than is the angwantibo from the potto.

If it is indeed true that the pottos and lorises have a common origin, then this cannot have been since the upper Miocene: the latest date at which, by consensus, there was a forested Afro-Asian land bridge [NAPIER, 1970]. The palaeoecological data therefore provide an explanation for the wide divergence of the 2 groups of 'slow climbers'.

It seems reasonable, on present evidence, to retain 2 genera for the Asiatic lorises: *Loris* for the slender lorises of southern India and Ceylon, and *Nycticebus* for the slow lorises of south-east Asia. The latter has 2 species; the former is generally allotted a single species, but this may be in error.

The 2 species of *Nycticebus* overlap widely in distribution (fig. 1), and differ strongly in a number of features, so that it seems certain that they are reproductively isolated and should stand as full species. *Nycticebus pygmaeus* Bonhote 1907 is smaller in size, with larger ears (fig. 2; table I); in the skull the occiput is noticeably flattened, while the premaxillae are somewhat extended forward. In the toothrow, there is a diastema between the anterior upper premolar and the next, as well as between the first premolar and the canine; in the larger species, *N. coucang* Boddart 1785 only the canine-premolar diastema is evident. In the large species, the molars decrease in size in the upper jaw, progressively from front to back; in *N. pygmaeus*, they are all subequal in size. The palate often extends back as far as the back of M^3 in the small species, but never in the larger species. In *N. pygmaeus* the fur is fine and wavy; reddish or orange in colour, with a sprinkling of grey frosting on the back in young adult specimens, and the dorsal stripe is never very dark, and ends in the lumbar region; in *N. coucang* the fur is coarse and crisp, darker and duller in hue, with or without frosting, and with a more prominent, darker dorsal stripe which often runs almost to the root of the tail.

There is considerable geographic variability in *N. coucang* (fig. 3), and a number of geographic races have been described. In the present revision, quite large samples were available from Burma and Assam, Malaya, Sumatra, and Borneo; the smaller number of specimens available

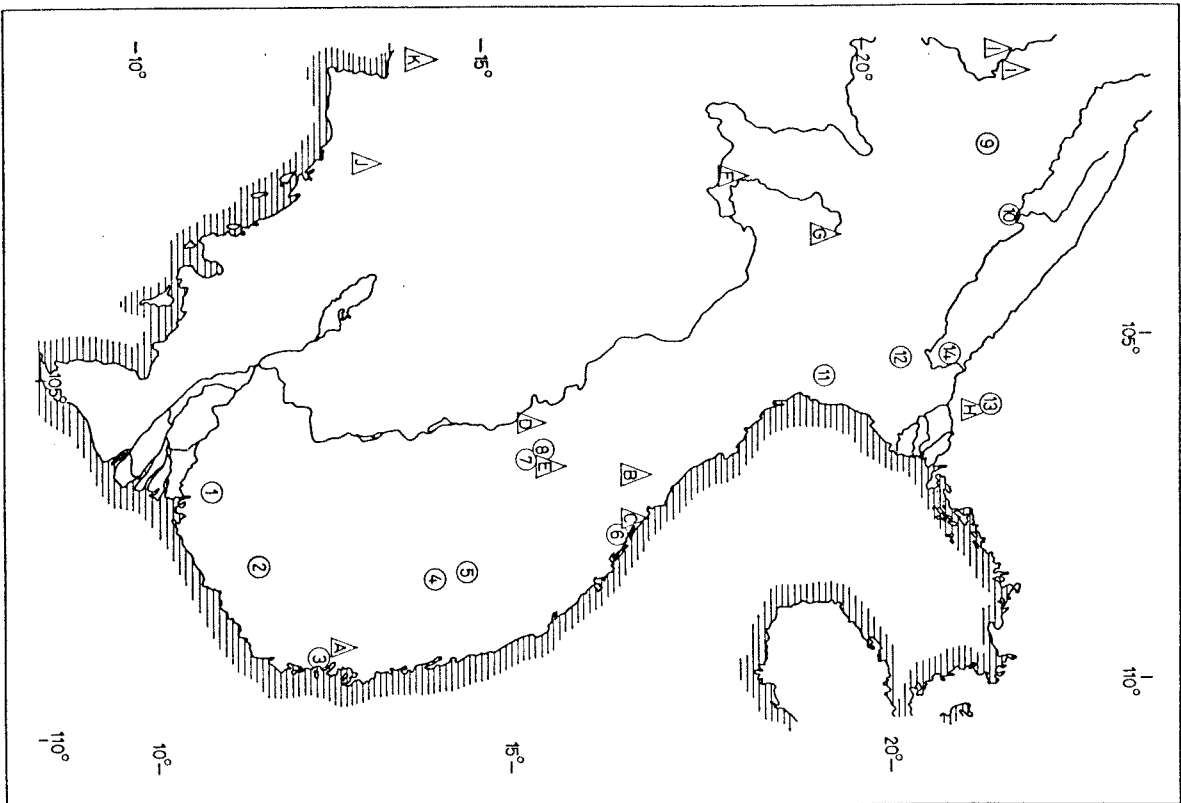


Fig. 1. Ranges of *Nycticebus pygmaeus* = O and *N. coucang bengalensis* = Δ in Indo-China.

Table 1. Distinguishing features of the species and subspecies of *Nycticebus*

	<i>N. pygmaeus</i>			
	<i>N. coucang</i>		<i>javanicus</i>	<i>bengalensis</i>
	<i>menagensis</i>	<i>coucang</i>		
Mean skull length (S. D.)	53.1 (10) 1.92	55.7 (23) 1.57	58.8 (41) 2.00	60.5 (12) 1.96
Percent with only I ¹ (no I ²)	6.7 (15)	100.0 (24)	20.0 (44)	100.0 (14)
Head + body length (mm)	230-287 (7)	265-300 (14)	265-330 (21)	330-367 (4)
Ear as percent of skull length	43.0-52.1 (6)	28.6-36.0 (4)	23.3-38.0 (9)	-
Body colour	red-yellow as body	light brown as body	light brown as body	yellow-grey creamy
Neck colour	as body	as body	as body	creamy-gre
Frosting	often strong	slight, flanks	slight, flanks	absent
Head-forks	unclear	broad, vague	well-marked	thin, dark unclear
Dorsal stripe	golden-brown	broad, dark	broad, dark	thin, black
Hair texture	fine, wavy	coarse, dense	coarse, dense	coarse, dense

N. pygmaeus

South Vietnam:

1. Saigon
2. Blao
3. Nhatrang (type locality of *N. pygmaeus*)
4. Pleiku
- . Kontoum
6. Hue

Laos:

7. Plateau Bolovens
8. Thateng
9. Phong Saly

North Vietnam:

10. Lai Chau
11. Phu Qui
12. Hoi Xuan
13. Thai Nien
14. Hoa-binh: type locality of *N. inter-*
medius

N. c. bengalensis

South Vietnam

- A. Nhatrang
- B. Lao Bao
- C. Hue

Laos:

- D. Pakse
- E. Thateng
- F. Vientiane
- G. Xieng Khouang

North Vietnam:

- H. Dinh-Ca
- China:
- I. Hsi-shuan-pan-na
- Thailand:
- J. Khao Soi Dow
- K. Bangkok

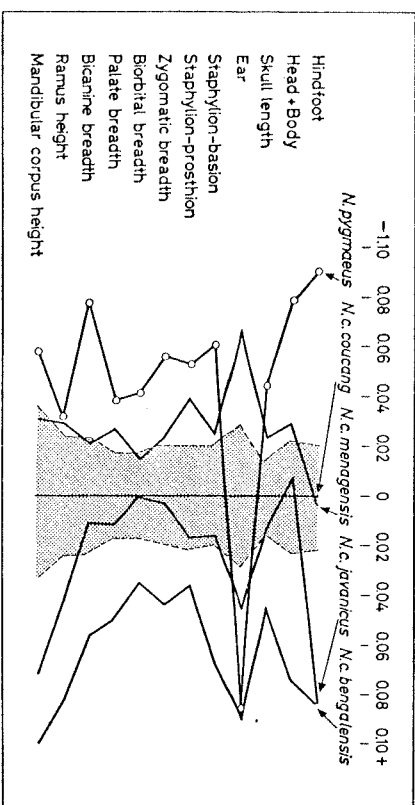


Fig. 2. Log ratio diagram comparing the taxa of *Nycticebus*, with the Malayan-Sumatran *N. c. coucang* taken as standard. The stippled area represents the Standard Deviation limits of *N. c. coucang*; means only are represented for the other taxa.

from other parts of the range were compared with these larger samples and their taxonomic position assessed according to whether they did, or did not, fall within the range of variation of the larger series. In this way, only 4 geographic forms proved to be recognisable; all the names listed in CHASEN [1940] and ELLERMAN and MORRISON-SCOTT [1952] are referable to one or other of these 4. They are:

1. *N. c. bengalensis* Lacépède 1800: from Assam, Burma, Thailand and Indo-China; southern limit, the isthmus of Kra. A large race, gingery in colour with the head and neck creamy, a colour which extends down the arms and along either side of the dorsal stripe as white frosting. On the head, as in all slow lorises, the dorsal stripe divides into four, sending branches to the eyes (uniting with the dark eye-rings) and to the ears. These forks are not very well expressed in the present race, except in a few individuals from Tenasserim. There is a cline from west to east across the range, with the amount of white frosting increasing somewhat, but otherwise the subspecies is quite homogeneous.

2. *N. c. coucang* Boddaert 1785: from Malaya, Sumatra, P. Tebing-tinggi, P. Tioman, the Rhio archipelago islands of Batam and Galang, and the North Natuna island of Bunguran. This race is a great deal smaller than the last, and generally more of a light brown in colour, without the creamy tint on the neck, but with the face still light. Frosting along the back is slighter; the dorsal stripe and head-forks are darker and better

developed. Sumatran skins average darker and greyer than Malayan. 20 skulls have been studied from Malaya and 20 from Sumatra; in 4 from each sample, the upper lateral incisors are missing, a trait which does not seem to occur in *bengalensis*.

3. *N. c. menagensis* Nachtrieb 1892: from Borneo, Bangka, Bongao in the Tawitawi islands, and recorded also from Catagan, Mindanao [CARRERA, 1908; TAYLOR, 1934] – perhaps deriving from a colony introduced to the island. Externally this race differs little from the last, but tends to be slightly darker with less well-expressed head-forks; it is however smaller, and every single skull (40 from Borneo, 4 from Bangka including those described by SODY [1937], and the types of *menagensis* and *philippinensis* described respectively by NACHTRIEB [1892] and CARRERA [1908]) lacks the upper lateral incisors on both sides.

4. *N. c. javanicus* Geoffroy St. Hilaire 1812: from Java. Although only 6 skins from Java have been seen in this study, they fall so clearly apart from all others that there can be no doubt of the validity of this race. They are yellowish-grey in colour with strongly contrasting creamy-hued head, neck and shoulders; the dorsal stripe is thin but bold and black, with clear head forks; and, as in the Borneo race there is no trace of I_2^3 , as can be seen in the 12 available skulls. This is a larger race than the others from Indonesia.

The nomenclature of slow lorises is a little confused. STONE and REHN [1902] used the name *coucang* for the Bengal form; this was shown to be in error by THOMAS [1922], and CHASEN [1940] restricted the type locality to Malacca. The name is in fact a westernization of the Malay *kukang*, for this animal. HUSSON and HOLTJUIS [1953] have shown that the correct name and authorship of the Bengal race is *bengalensis* Lacépède 1800. ROBINSON [1917] used the name *buku* Martin 1838 for the Malay slow loris, but reference to the description on which this name was based – RAFFLES [1821] – gives absolutely no reason to associate this name with a slow loris at all. The Bornean race is usually known as *bornanensis* Lyon 1908 but NACHTRIEB's name antedates it by 16 years. Finally, DAO [1960] described a new species from North Vietnam as *Nycticebus intermedius*, but this proves on the basis of 14 skins and skulls of *N. pygmaeus* to be merely the adult of latter, which was described on the basis of a young individual! DAO's paper is useful however in drawing attention to the skull features of the small species.

That *N. pygmaeus* is a more primitive species than *N. coucang* is shown by its intermediacy in many skull characters between the latter and

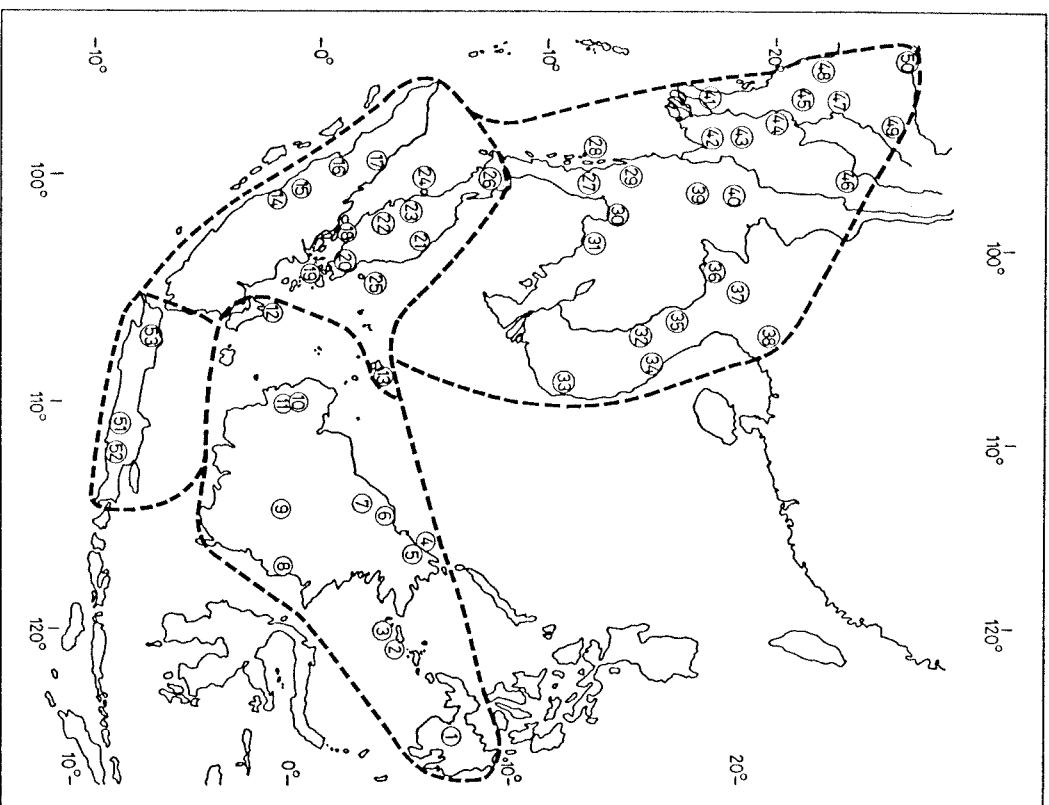


Fig. 3. Ranges of the 4 subspecies of *Nycticebus coucang*.

- N. c. menagensis*
- Philippines:
1. Catagan, Mindanao: type locality of *philippinus* Cabrera
 2. Tawitawi: probable type locality of *menagensis* Nachtrieb
 3. **BONGAO**
- Borneo:
4. Menggatal, 11 mi north east of Jesselton
 5. Ranau: Mt. Kinabalu
 6. Mainland opposite Labuan
 7. Mt. Duit
 8. **Samarinda**

the genus *Loris*: the more produced premaxilla, narrower interorbital septum, longer palate, subequal upper molars, canine-premolar diastema, and small size are all characters in which the lesser slow loris tends towards the slender loris. Among the races of *N. coucang*, it is the small insular form, especially *menagensis*, which most resemble *pygmaeus* in

9. Puruk Tiahu, Barito river
 10. Sungai Landak
 11. Sungai Kapuas; S. Sakaiam, Sanggau district: type locality of *borneanus* Lyon
- Bangka:
12. Klabat Bay: type locality of *bancaeus* Lyon
- N. c. coucang*
- North Natuna:
13. Sibintang; Bunguran: type locality of *natunae* Stone and Rehn
- Sumatra:
14. Padang highlands: type locality of *hilleri* Stone and Rehn
 15. Batu Sangkar; Tarussan Bay
 16. Tapanuli Bay
 17. Padang Bahrang; Tandjong Morawa; Siantar
 18. Pulau Tebingtinggi: type locality of *brachycephala* Sody
- Rhio archipelago:
19. Batam
- Malaya:
20. Johore Lanau; Jambu; Biserat
 21. Trengganu
 22. Kepong; Ulu Gombak; Kuala Lumpur
 23. Rumpin river; Batu Gantong; Changkat Mentri; Pulau Pangkor; Dindings
 24. Penang
 25. Pulau Tioman: type locality of *insularis* Robinson
- Thailand:
26. Khaw Song Mt., Trang
- N. c. bengalensis*
27. Mergui town
 28. King's island, Mergui archipelago
 29. Paungdaw; Hinlhem; Amherst: type locality of *tenasserimensis* Elliot
 30. Bangkok: type locality of *cinerus* Milne-Edwards
 31. Khao Soi Dow
 32. Thateng
 33. Nhatrang
 34. Lao Bao; Hue
 35. Pakse
 36. Vientiane
 37. Xieng Khouang
 38. Dinh-Ca
 39. Raheng
 40. Chienamai
 41. Bassein
 42. 50 mi north of Pegu
 43. Toungoo East; Thaundang
 44. Taungyi; Kyeikpadein: type locality of *incanus* Thomas
 45. Chin Hills
 46. Bhamo; Sumprabum
 47. Kindat, west bank of Chindwin
 48. Tipperah; Chittagong
 49. Naga Hills; Changpang
 50. Goalpara
- N. c. javanicus*
51. Lodojo Kediri
 52. Tiaruban (Cheribon)
 53. Djakarta (Batavia): type locality of *ornatus* Thomas

size and colouration: the occasional lack of I² in the latter species increases this resemblance.

CHASEN [1940] invokes an 'eastern drift' of faunal dispersal into Indonesia to explain such resemblances between Indochinese forms and Indonesian; such a route must have been open at some rather remote time, perhaps in the early Pleistocene, when the Sunda shelf was dry land but the great river flowing into the South China sea had not yet arisen. If a small, reddish-brown loris with a tendency towards incisor reduction was dispersed down this route early in the Pleistocene, the formation of the South China river would have provided the isolation necessary for speciation to take place, so that by the time slow lorises had re-invaded Indochina from the west, reproductive isolation had been achieved.

Within Indonesia itself, the pattern of subspeciation is readily explainable on palaeogeographic grounds. UMBROVE [1949] shows that Bangka formed part of a divide between the river systems flowing north and east from Sumatra, and that this divide (running via Billiton and the Karimata islands to Borneo) made an excellent faunal dispersal route. Thus, until the drowning of the Sunda shelf, the fauna of Bangka was largely isolated from that of Sumatra (all but the southeastern portion) but in contact with that of Borneo. When the Sunda shelf was drowned, the shapes of the remaining islands were very different from those of today: for example, the whole of the east Sumatran lowlands postdate this time, having been formed by accretion at the rate of between 75 and 125 m per annum [VAN BEMMELLEN, 1949]. Thus the southeastern portion of Sumatra, originally populated by Bangka fauna, was swamped, and gradually reformed and repopulated by Sumatra fauna. The two great Sunda rivers, therefore, separated the 3 Indonesian subspecies of slow loris even while the Sunda shelf was dry land; the modern pattern of islands is much more recent.

This pattern of subspeciation in Sundaland may perhaps be found to apply to other mammals, although a surprising number (notably, among primates, the gibbons) are inexplicably absent from all but the Greater Sunda islands – even from such a relatively large island as Bangka; indeed the slow loris itself seems not to have been recorded from either Billiton or the Karimata islands, although it must once have lived all along the Bangka-Borneo divide. The distribution of the tarsier makes immediate sense on this basis; presumably it represents a Pleistocene dispersal from Celebes into Borneo, having reached Bangka by the time the sea re-invaded; its restricted range in south-east Sumatra evidently represents a recent re-occupation from Bangka.

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