

CRANIOMETRY OF SLOW LORISES (GENUS *Nycticebus*) OF INSULAR SOUTHEAST ASIA

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ABSTRACT

We measured skulls of slow lorises (*Nycticebus*) from all over Sundaland, and compared them by multivariate and univariate analysis. There are slight differences of shape within Java, Borneo and Sumatra, and perhaps between those of the Riau Archipelago and Sumatra. Skulls from the Malay Peninsula average slightly larger than those from Sumatra, but otherwise are very similar. A skull from Bangka falls well within the range of variation of those from Borneo; one from P.Bunguran and one from P.Tioman (Malaysia) fall within the Sumatra/Malay range. Measurements from the literature of skulls from Tawitawi (Philippines) show that they do not differ from those from Borneo. The Sumatra/Malay/Riau/Bunguran/Tioman sample differs greatly on average from the Borneo/Bangka/Tawitawi sample, and they form two strongly distinct subspecies, *Nycticebus coucang coucang* and *N.c.menagensis*, respectively. The Java sample differs rather more from the others, and this, taken together with its apparently consistent external differences, induces us to recognize it as a full species, *N.javanicus*.

Key words: Slow loris, *Nycticebus*, Southeast Asia

INTRODUCTION

Biological taxonomy typically goes through two phases: a long period during which specimens are collected from ever more localities and new species and/or subspecies are described one by one, followed by a period of consolidation when the described taxa are compared in detail to each other and overall revisions are proposed. In this paper, we will briefly review the history of the taxonomy of Indonesian Slow Lorises (genus *Nycticebus*), then reconsider the position on the basis of our own cranial data.

During the collection/description phase the following taxa were proposed (Figure 8):

coucang Boddaert, 1785. "Bengal"; but *kukang* is the word for loris in some Melayu dialects."
javanicus E. Geoffroy St. Hilaire, 1812. Java.
malaiana Anderson, 1881. Melaka.
menagensis Lydekker, 1893. Referring to Nachtrieb's "A new lemur (Menagensis)"; Lydekker, in compiling the *Zoological Record* for 1893, listed Nachtrieb's paper under the name *Lemur menagensis*, so this is available (see Timm & Birney, 1992). Tawitawi, Sulu Is.

hilleri Stone & Rehn, 1902. Tanah Datar, Padang Highlands.

natunae Stone & Rehn, 1902. P. Bunguran.

borneanus Lyon, 1906. Sakaiam R., Sangau district, W. Kalimantan.

bancanus Lyon, 1906. Bangka.

philippinus Cabrera, 1908. Supposedly from Catagan, Mindanao (but see Fooden, 1991).

insularis Robinson, 1917. P. Tioman.

buku Robinson, 1917 (ex Martin, 1838, actually a langur). Sumatra.

ornatus Thomas, 1921. Batavia (=Jakarta).

brachycephalus Sody, 1949. Supposedly from P. Tebingtinggi.

The period of consolidation can be said to have begun with Osman Hill's (1953) monograph, in which all slow lorises were assigned to a single species, *Nycticebus coucang*, but with numerous subspecies. Groves (1971) revised these taxa and, after splitting off Indochinese *N. pygmaeus* a distinct species, divided *N. coucang* into four subspecies: *N. c. javanicus* (Java), *N. c. menagensis* (Tawitawi, Borneo and Bangka), *N. c. coucang* (Sumatra, Riau Archipelago, Malay peninsula, P.Bunguran and P.Tioman) and *N.c.bengalensis* (mainland Southeast Asia, from the Isthmus of Kra north to Assam and

southernmost China). Noteworthy in this arrangement was the allocation of the Bangka lorises to the Bornean subspecies, not to that of nearby Sumatra; and of those of P. Bunguran, in the North Natuna Is., to the Malay/Sumatran subspecies rather than to that of Borneo. Groves (1971) explained these curiosities by reference to the pattern of drowned rivers on the Sunda Shelf. His conclusions were confirmed and extended by Ravosa (1998). Later, Groves (1998) returned to the problem, and reconfirmed this arrangement on the basis of multivariate morphometrics, but without detailed analysis. The major novelty was the proposal to separate *N. bengalensis* as a distinct species.

Most recently, Supriatna & Hendras (2000) separated the Javan Slow Loris as a full species, *N. javanicus*, leaving just those from Sumatra, Borneo, Peninsular Malaya, and offshore islands in *N. coucang*.

MATERIAL AND METHODS

One of us (IM) measured the crania in the Museum Zoologicum Bogoriense, Research Centre for Biology-LIPI collection at Cibinong, Jawa Barat. CPG compared this dataset with that from the European and American collections, as described by Groves (1971), and incorporated the measurements of Tawitawi



Figure 1: Type localities of described taxa of Sundaland slow lorises

specimens given by Timm & Birney (1992). Both univariate and multivariate comparisons were made using SPSS version 11 for Windows. Because not all measurements were available for every specimen, a series of Discriminant Analyses and one Principal Components Analysis were run, each time using the measurements that were available for the largest number of specimens in each sample compared.

RESULTS

(1) Geographic variation within the Greater Sunda Islands

There is no evidence of variation in size, as measured by skull length, from west to east in Java (Figure 2). On a Principal Components Analysis, the first Component (accounting for 51.4% of the total variance) is strongly dependant on absolute size, but the second (which accounts for 32.4%) is a shape component, representing predominantly a contrast between wide posterior palate and narrow snout; values of PC2 tend to decline (very slightly) from west to east, meaning that the posterior palate becomes relatively narrower, the snout relatively broader (Figure 2b). Figure2b. This in fact depends entirely on two

specimens from the east, and does not counter our impression, gained from pelage characters, of an essential homogeneity within Java, and there's a single specimen from far west.

It would be interesting to test the possibility of variation with altitude within Java, but our material does not span sufficient altitudinal range to enable us to test this.

As Figure 3a shows, there may be an average difference between lorises from southeastern Kalimantan and Sabah on Discriminant Function 1, which accounts for 71% of the variance and contrasts large skull length with relative narrowness especially of the palate, but this is probably an effect of small sample size, because skulls from western Borneo span the entire range. As far as absolute size is concerned (Figure3b), Sabah skulls average somewhat larger than other samples, but there is almost total overlap. All Bornean skulls, like those from Java, will therefore be treated as a single sample.

Figure 4 compares skulls from northern and southern Sumatra and the Riau Archipelago (Kepulauan Riau), also the type of *brachycephalus* Sody, 1949 (a zoo specimen, reputedly from P. Tebingtinggi). In an analysis using only three variables, and so

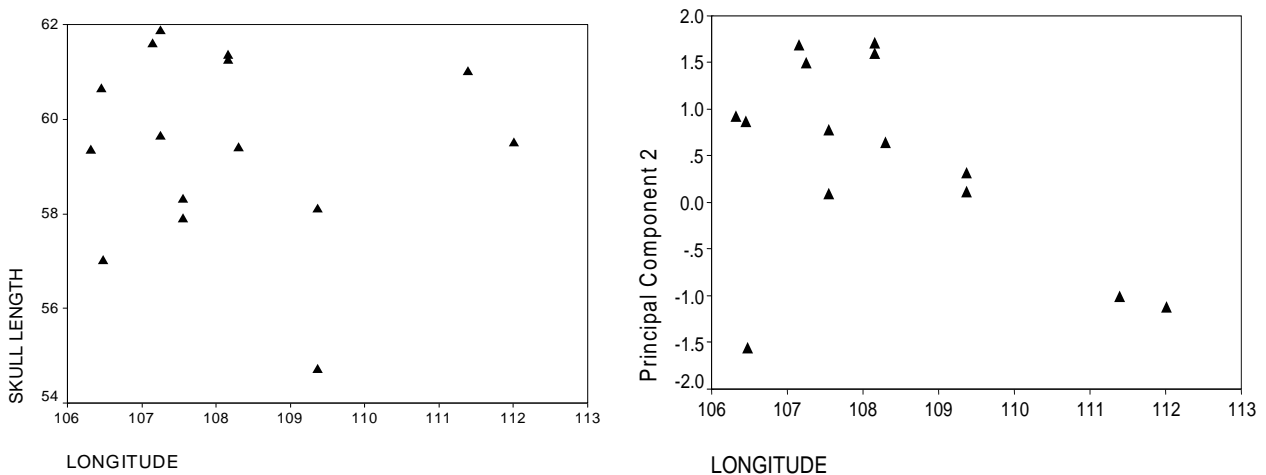


Figure 2: Variation by longitude in Java a: skull length, b: second principal component

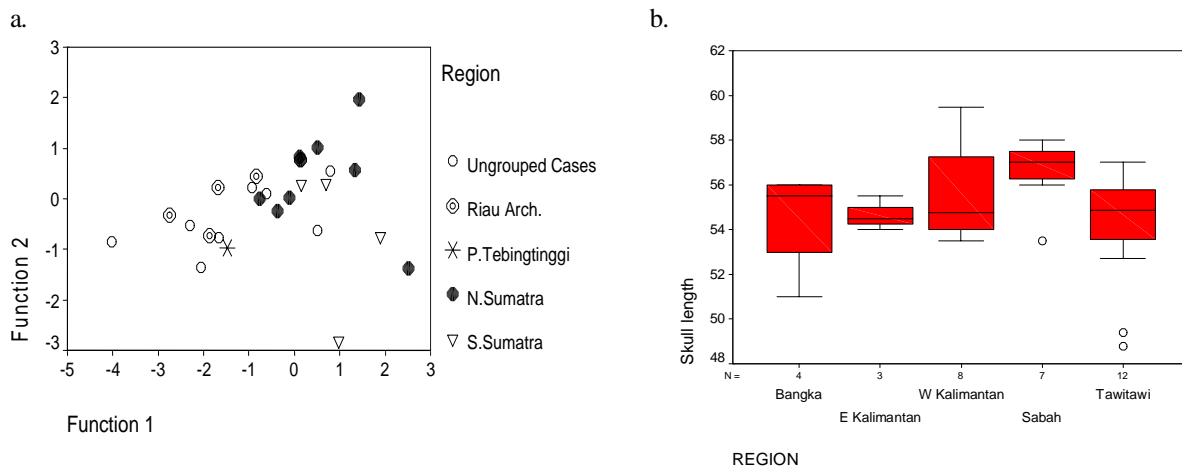


Figure 3: Geographic variation within Borneo a: Canonical Discriminant Functions Borneo (Gtl, Zyg, Palbr, Bican, Ramus), b: Skull length.

maximizing the number of specimens that can be analysed (Figure 4a), DF1 (accounting for 68.1% of the variance) contrasts wide zygomata with narrow snout; DF2 (29.7% of the variance) contrasts broad snout with short skull. In the analysis using six variables, and with a consequently smaller dataset (Figure 4b), DF1 (52.1% of the variance) contrasts large size and, especially, flaring zygomata with narrow biorbital breadth and palate; DF2 (42.5%) emphasizes in particular a relatively long basicranium (staphylion to basion distance). In neither analysis is there any difference between skulls from northern and southern Sumatra. Specimens from the Riau Archipelago appear at first sight to differ, especially in Figure 4a, but the series labeled “ungrouped” are specimens labeled “Sumatra” without more definite locality; as these cover the range of those from Kep. Riau, it would therefore seem, on the face of it, that no separation can be maintained. Using a larger set of variables, much smaller samples are available.

All Sumatran and Riau Archipelago specimens will therefore be treated as a single sample.

2. Geographic variation between Borneo and Sumatra

Using only four variables enables us to include the Tawitawi sample, using the measurements given in Timm & Birney (1992). This is necessary

because Tawitawi is the type area of *menagensis* Lydekker, 1893, the earliest available name for a Slow Loris in island Southeast Asia. The results are shown in Figure 4a. The first Discriminant Function, accounting for 88.9% of the variance, contrasts long skull and broad palate with narrow zygomata; the second, accounting for only 10.4%, contrasts skull breadth with skull length. There is an average difference between Borneo and Sumatra; 12 of the 20 Sumatran skulls are correctly classified. The 10 Tawitawi skulls and the single Bangka skull (type of *bancanus*) fall within the range of Borneo; none of them is misclassified as Sumatra, and only 2 of the 23 Bornean skulls are misallocated to Sumatra.

Using 9 variables (Figure 4b) means that no Tawitawi skulls are now able to be included. DF1 (96.9% of the variance) contrasts palate breadth and length and biorbital breadth with skull length, ramus height and snout length; DF2 (only 3.1%) contrasts predominantly zygomatic breadth with skull length. Borneo and Sumatra now separate much better, though there is still an overlap; all but 3 of the 17 Sumatran skulls are correctly classified, and all but 2 of the 19 Bornean skulls. The Bangka skull again assorts with Borneo, even though it was entered as a separate group, which would give it a more-than-even chance to sort separately.

We conclude that (1) Borneo and Tawitawi skulls cannot be distinguished, so *borneanus* Lyon, 1906 is a synonym of *menagensis* Lydekker, 1893; (2) the Borneo-Tawitawi taxon can be distinguished, on average but not absolutely, from that from Sumatra; and (3) the single available Bangka skull allocates to Borneo/Tawitawi, not to Sumatra, so *bancanus* Lyon, 1906 is a synonym of *menagensis*.

3. The affinities of Malay peninsular lorises

Consideration of the taxonomic affinities of the lorises of the Malay Peninsula are necessary because the type locality of *Tardigradus coucang* Boddaert, 1785, was considered to be “probably Malacca” by Chasen (1939), and this was implicitly accepted as a valid fixation by Groves (1971). It is also convenient to consider the affinities of the lorises of two small islands in this context: P. Tioman, east of the Malay Peninsula, and P. Bunguran, in the North Natuna group, southeast of the peninsula and north of Borneo; these will be considered further below.

A single analysis was run (Figure 5), using 4 variables. DF1 (83.2% of the variance) largely contrasts long skull with narrow bizygomatic breadth; DF2 (16.8%) contrasts broad palate and snout with narrow bizygomatic breadth. The Malay and Sumatran samples differ weakly on average only. Consequently Sumatran lorises can be included in nominotypical

coucang. Tioman appears to fall at the edge of the Malay sample, but the two Bunguran skulls fall within it.

4. Comparing Borneo with Malay/Sumatran and insular lorises

Using 9 variables (Figure 7a), DF1 (62.8% of the variance) contrasts biorbital breadth to skull length, and DF2 (20%) contrasts palate breadth, basicranial length and mandible length to skull length and biorbital breadth. The substantial samples from the Malay Peninsula and Sumatra still overlap widely, though with somewhat different “centres of gravity”. The Borneo sample is largely separate from the Malay/Sumatran samples, though with overlaps; Bangka again falls within Borneo. Two from P. Bunguran (including the type of *natunae*) and one from P. Tioman (type of *insularis*) fall within the Malay/Sumatran dispersion, even though they were entered as separate groups. This confirms and extends the results of Figure 5.

As far as absolute size is concerned (Figure 7b), the Sumatran and Riau specimens average smaller than those from the Malay Peninsula, Bunguran and Tioman, but there is extensive overlap.

5. Comparing Java with other Sundaland lorises

Combining Borneo, Bangka and Tawitawi as *Nycticebus coucang menagensis*, and Malay peninsula,

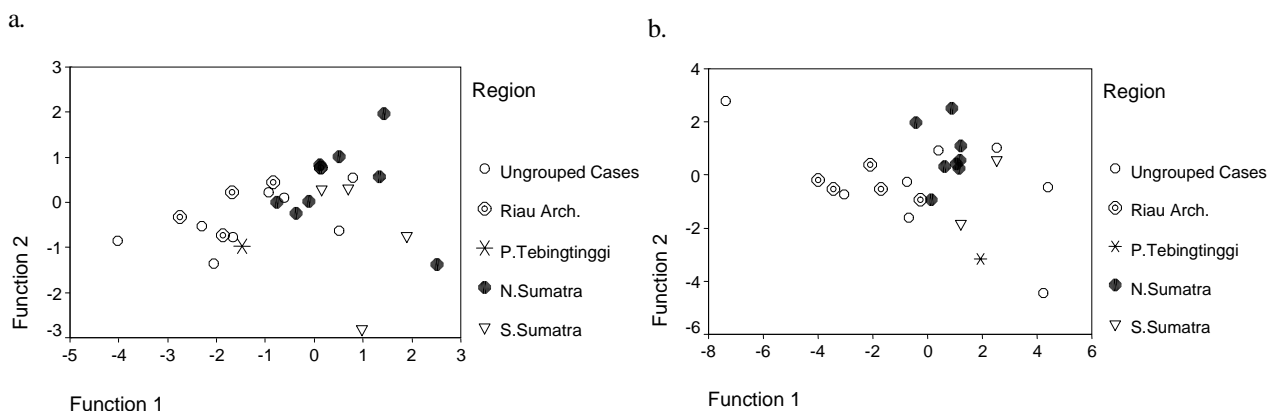


Figure 4: Geographic variation on Sumatra and its offshore islands. Canonical a: Canonical diskriminant functions (Reduce variable set: Gtl, Zyg, Bican), b: canonical discriminant functions (Reduce variable set: Gtl, Zyg, Biorb, Stbas, Stpros, Bican).

Sumatra, Kep.Riau, P.Tioman and P.Bunguran as *N.c.couang*, achieves samples large enough to make it worthwhile to perform a stepwise comparison with *N.c.javanicus*. A Stepwise Discriminant Function Analysis enters the variables separately, one by one, at each stage withdrawing those which add nothing to the discrimination (according to the criteria of the Mahalanobis method, partial F to enter >3.84, partial F to remove <2.71), until only a subset remains. In this case, after 16 enter-removal steps, four variables remained: Mandible Length, Posterior Palate Breadth, Biorbital Breadth, and Palate Length. DF 1, accounting for 85.9% of the total variance, contrasts low values for biorbital breadth with high values for the other variables; DF2 (14.1%) contrasts low values for Mandibular Length with high values for the rest. Figure 8a is the result. The three taxa are all separated but overlap, though *javanicus* overlaps less with they other two than they do with each other. The percentage of each taxon that is correctly classified is as follows: *javanicus* 84.6% (n=13), *menagensis* 95% (n=20), *couang* 65.8% (n=38).

Figure 8b shows the absolute size of the three Sundaland taxa. Of the three, *javanicus* averages largest, followed by *couang*, with *menagensis* much the smallest. The means, standard deviations and sample sizes are as follows:

<i>javanicus</i>	60.2 ± 2.22 (25)
<i>menagensis</i>	54.9 ± 2.25 (40)
<i>couang</i>	58.6 ± 2.36 (59)

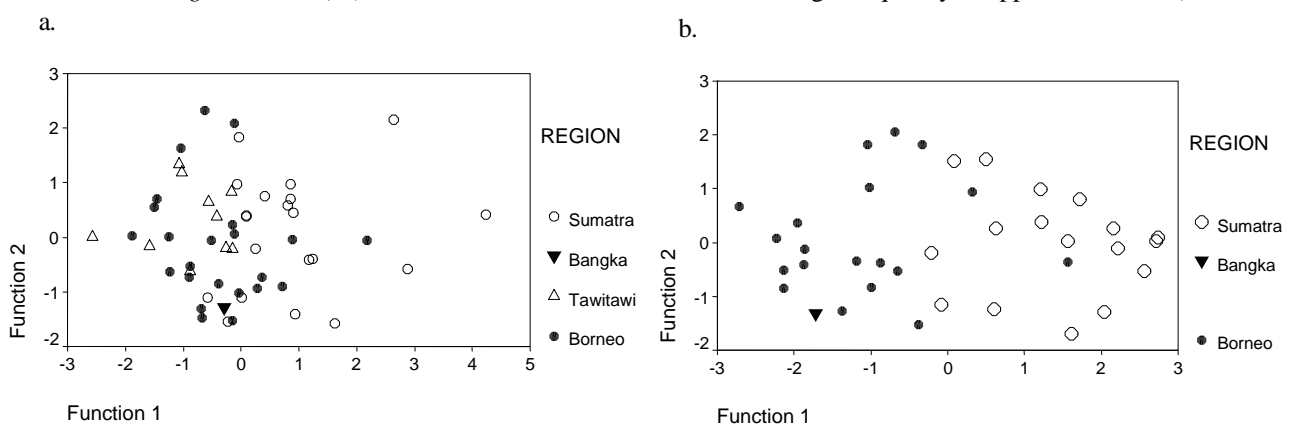


Figure 5: Comparisons between Borneo and Sumatra, and the position of Bangka a: canonical discriminant functions (reduced variable set: Gtl, Zyg, Palbr, Ramus), b: canonical discriminant functions (reduced variable set: 9 craniometric variables)

DISCUSSION AND CONCLUSION

This study has shown that, while there are slight variations in loris craniometrics within each of the three Greater Sunda islands, it is between them that the major differentiation occurs. This corroborates their separation as three distinct taxa. In addition, multivariate analysis supports the proposition that the Bangka loris is consubspecific with that of Borneo, as are those of Tawitawi in the Philippines, whereas those of Kepulauan Riau, P.Tebingtinggi, P.Bunguran, and the Malay Peninsula and P.Tioman in Malaysia, are consubspecific with the Sumatran loris.

How should these be classified? Our craniometric analyses indicate that, while all three taxa overlap, the Bornean and Sumatran forms overlap with each other more than either does with Java. Groves (1998) retained them as three subspecies of a single species, *Nycticebus couang*, whereas Supriatna and Hendras (2000) separated Javan lorises as a full species *Nycticebus javanicus*. We are inclined to accept their revision, given that it is, in our experience, absolutely different in its colour pattern (see also Groves 2001). We note that Ravosa (1998, see especially Figure 8b) likewise found that *javanicus* is strongly differentiated from other slow lorises. Ravosa (personal communication) has suggested to CPG that there might be a case for giving species rank to *menagensis* in addition; its high frequency of upper I2 absence (see

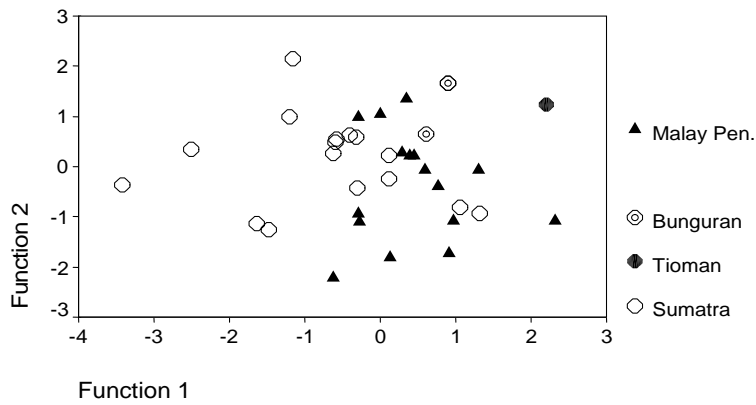


Figure 6: Comparison of Malay and Sumatran lorises by canonical discriminant functions (Reduced variable set: Gtl, Zyg, Palbr, Bican, Ramus)

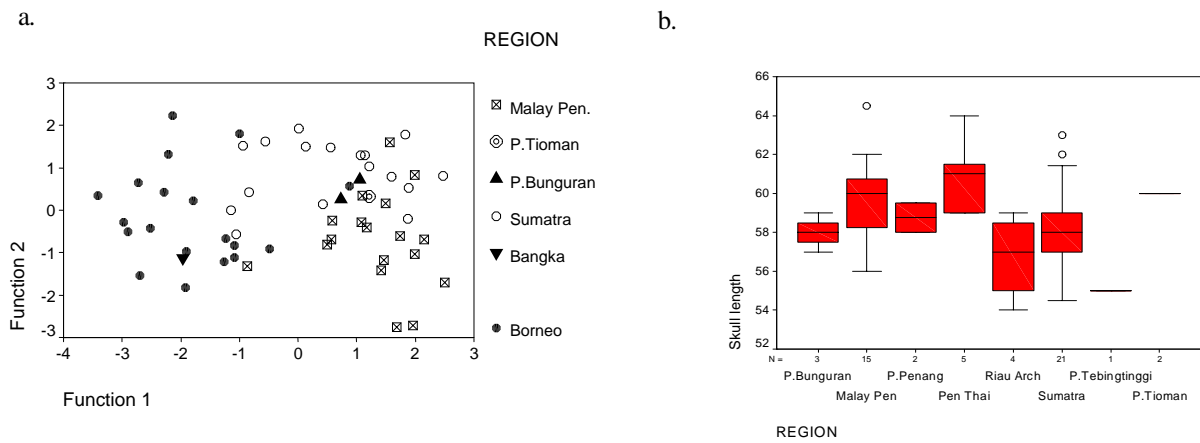


Figure 7: Comparison of Borneo with Malaya and Sumatra and island lorises a: canonical discriminant functions (9 craniometric variables), b: skull length

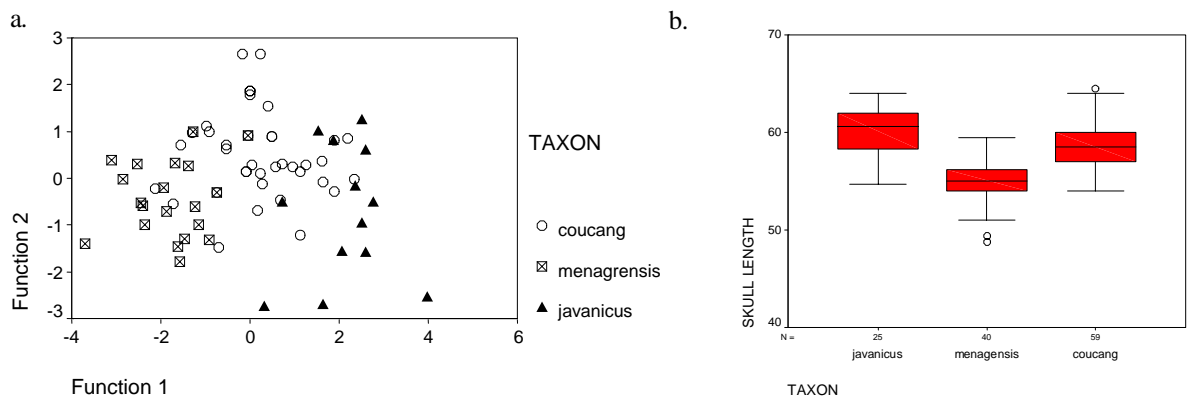


Figure 8: Comparison of Java with other Sundaland lorises a: canonical discriminant functions (8 variables entered 4 selected), b: skull length

below) differentiates it strongly from *coucang* and brings it close to *javanicus*. While it is true that *menagensis* is strongly differentiated (see Figure 8b), in ways unrelated to allometry as was shown by Ravosa (1998), the available evidence does not indicate that they are 100% different. We await future DNA studies, which may alter our opinion.

Of other characters found to be useful in loris taxonomy, the only other that is applicable to Sundaland forms is the number of upper incisors. In our sample, all 13 skulls of *N. javanicus* in which the character can be confidently detected have a single pair of upper incisors, as do all 22 skulls from Borneo and Bangka. Ravosa (1998), however, found that this character is not completely fixed: on the basis of larger samples than available to us, he found a single upper incisor pair present in 84% from Borneo, and 95% from Java (see Ravosa, 1998, Table II). Of 42 skulls of the Sumatra/Malay taxon, however, 34 have two pairs of incisors on each side, 6 have a single pair, and two skulls have one pair on one side, two on the other. Out of 84 sides, therefore, 17% have a single pair, 83% have two pairs. This strong difference greatly adds to the case for subspecific differentiation between *N.c.coucang* (Sumatra/Malay) and *N.c.menagensis* (Borneo/Bangka).

The taxonomy of Sundaland lorises therefore is as follows:

- 1) *Nycticebus javanicus* E.Geoffroy St.Hilaire, 1812. Synonym *ornatus* Thomas, 1921. Java.
- 2) *Nycticebus coucang* (Boddaert, 1785).
 - a) *Nycticebus coucang coucang* (Boddaert, 1785). Synonyms *malaiana* Anderson, 1881; *hilleri* Stone & Rehn, 1902; *natunae* Stone & Rehn, 1902; *insularis* Robinson, 1917; *buku* Robinson, 1917; *brachycephalus* Sody, 1949. Sumatra, Riau Archipelago, P.Tebingtinggi, P.Bunguran, Malay Peninsula, P.Tioman.
 - b) *Nycticebus coucang menagensis* (Lydekker, 1893). Synonyms *borneanus* Lyon, 1906; *bancanus* Lyon, 1906; *philippinus* Cabrera, 1908. Borneo, Bangka, Tawitawi (Philippines).

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