Systematics of Tarsiers and Lorises

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ABSTRACT. It seems probable that there are more species (in the sense of sharply diagnosable entities) than hitherto recognized among small Asian primates, and contrasting to some degree with larger-sized taxa. This presumably relates to their lesser vagility and consequent reduced potential for gene-flow. Even where some gene-flow can be demonstrated, as between *Nycticebus coucang* and *N. bengalensis*, this appears to be very limited and does not affect the essential homogeneity and diagnosability of the two taxa.

The biogeographic implications of the taxonomic findings of this study are noteworthy. They confirm the distinctness of Sulawesi in contrast to a Sundaland/southern Philippines link (*Tarsius*); the separation of the Indochinese and Sundaic faunal subregions (*Nycticebus*); and the uniqueness of the Sri Lankan "wet zone" (*Loris*). Much more work needs to be done on all three genera, but their great taxonomic interest, indicating much greater complexity than previously assumed, is apparent.

Key Words: Loris; Tarsier; Taxonomy; Morphometrics; Cladistics.

GENERAL INTRODUCTION

The Asian prosimians belong to both extant suborders of Primates: the Loriformes to the Strepsirrhini and the Tarsiiformes to the Haplorrhini. The term "prosimian" is no longer appropriate in a formal taxonomic sense, but is still acceptable as long as one realizes that it belongs in the realm of Folk Taxonomy, designating a small-brained primate, i.e. one that is not a monkey or ape.

The definitive revision of the genus *Tarsius* was published by HILL in 1953. Since that date, three papers have proposed innovations (MUSSER & DAGOSTO, 1987; FEILER, 1990; NIEMITZ et al., 1991).

Asian lorises (genera *Loris* and *Nycticebus*) were reviewed by HILL (1952), and GROVES (1971) revised *Nycticebus*. Since that date, no new contributions have been made.

This paper reports studies in progress on these three genera, and proposes preliminary changes to their taxonomy.

MATERIAL AND METHODS

1. *Tarsius*: As part of an ongoing study with G. G. MUSSER, I measured and took notes on tarsier skulls and skins in the collections of the Museum Zoologici Bogoriense, Bogor; Natural History Museum, London; and U. S. National Museum, Washington.

Skull measurements were as follows: greatest skull length, condylobasal length, biorbital width, breadth of left orbit, braincase width, braincase height, bizygomatic breadth, palate length, palate width (at widest point), bulla length (a) total, (b) anterior to, and (c) posterior to carotid foramen, bulla width, height, and width of nasal aperture, ascending ramus height, sigmoid notch depth.

Tooth measurements were as follows: lengths of maxillary and mandibular postcanine toothrows, crown heights of maxillary incisors and canines, lengths and breadths of all premolars and molars in both jaws.

External measurements were as follows: flesh measurements (lengths of head and body, tail, hindfoot and ear, and body weight) as recorded on label, length of pencilled portion on tail, length of middle finger and middle toe, length and width of terminal pad on middle finger and toe, length of nail on middle finger and toe. These were recorded where the skins in question did not appear to be unduly shrivelled.

Metrical data, both craniodental and external, were subjected to discriminant function analysis (DF) using SPSS for Windows. A cladistic analysis was run using 45 discrete characters, mostly observational but some metrical.

2. The *Loris* study is based on the collections in the Natural History Museum, London, and the United States National Museum. The skull measurements taken were greatest skull length, biorbital breadth, palate length, staphylion to basion length, palate breadth (widest), bicanine breadth, bizygomatic breadth, mandible length, and ramus height. No dental measurements were taken. Flesh measurements were recorded, as given on museum labels.

A Principal Components Analysis (PCA), using MVNutshell (R. V. S. WRIGHT, University of Sydney), was run using cranial (without mandibular) measurements; followed by a series of Discriminant Analyses, using SPSS for Windows, on both skull and external measurements.

3. *Nycticebus*: The specimens used were in the U. S. National Museum, Natural History Museum (London), Muséum National d'Histoire Naturelle, Paris, Museum Zoologici Bogoriense, and Zoological Reference Collection, Singapore. Measurements were the same as for *Loris*. As before, a PCA was run, followed by Discriminant Analyses. The PCA was restricted to the GROVES (1971) subspecies *bengalensis*, for which few sizeable samples from restricted localities were available. One of the DF analyses tested the separation of the various Sundaland populations from each other.

GENUS *Tarsius*

Introduction

After at least half a century of confusion, HILL (1953) straightened out the nomenclature and demonstrated the existence of three sharply distinct taxa, which he awarded specific rank as *Tarsius spectrum* (Sulawesi and neighbouring islands), *T. syrichta* (southern Philippines), and *T. bancanus* (Sumatra, Borneo, and intervening islands).

MUSSER and DAGOSTO (1987) showed that a fourth species, *T. pumilus*, was present in the highlands of Sulawesi. Despite its poor representation in museum collections (they could find only two specimens), this species differs so sharply from all others that there can be no doubt about its validity. They divided the genus into two informal groups: (1) *T. syrichta* and *T. bancanus* and (2) *T. spectrum* and *T. pumilus*. The zoogeographic implications of this are interesting: an early separation of the Sulawesi representative, but a late dispersal between Borneo and the southern Philippines.

FEILER (1990) briefly described the type of *Tarsius sangirensis* MEYER, 1895, from the Sangihe Islands north of Sulawesi, and drew attention to features in which it appeared to differ from *T. spectrum* as described by MUSSER and DAGOSTO (1987). He proposed that *T. sangirensis* be restored to specific rank as a fifth species.

NIEMITZ et al. (1991) described a sixth species, *Tarsius dianae*, from low altitudes in Central Sulawesi. It could not be confirmed whether the new species replaced *T. spectrum* in Central Sulawesi, or was sympatric with it. There were now six species recognized in the genus.

The measurements and descriptive notes on *Tarsius* specimens were in part designed to test the taxonomic claims of HILL (1953), MUSSER and DAGOSTO (1987), FEILER (1990), and NIEMITZ et al. (1991).

RESULTS

In the first Discriminant Analysis using craniometric data (Fig. 1), the samples were analyzed at species level as determined by HILL (1953), except that the single available skull of *T. pumilus* was entered as an unknown. The three quasi-specific units are clearly separated, but *T. syrichta* and *T. bancanus* almost form a continuum, while *T. spectrum* is strongly separated from them. This supports the groupings proposed by MUSSER and DAGOSTO (1987). The single skull of *T. pumilus*, however, is far from any of the three samples. Almost all the discrimination (95%) resides in the first Discriminant Function, which is most highly correlated with orbit width, anterior bulla length, palate width, whole bulla length, biorbital breadth, maxillary toothrow length, and bulla breadth. The second Function (5%) correlates with skull length, toothrow length, sigmoid notch depth, and anterior bulla length (positive) versus posterior bulla length (negative).

A separate analysis using dental measurements gives much the same picture (Fig. 2), except that *T. syrichta* is better separated from *T. bancanus*, while *T. pumilus* is less far removed from *T. spectrum*.

Inspection of the individual cranial and dental measurements shows that *T. spectrum* has, compared to the other two species samples, a short and narrow bulla, especially short anterior to the carotid foramen; small orbits; narrow palate; low snout; short toothrows; and small molars, especially M3. *T. syrichta* differs from *T. bancanus* in having a deeper sigmoid notch, longer toothrows, and higher-crowned incisors.
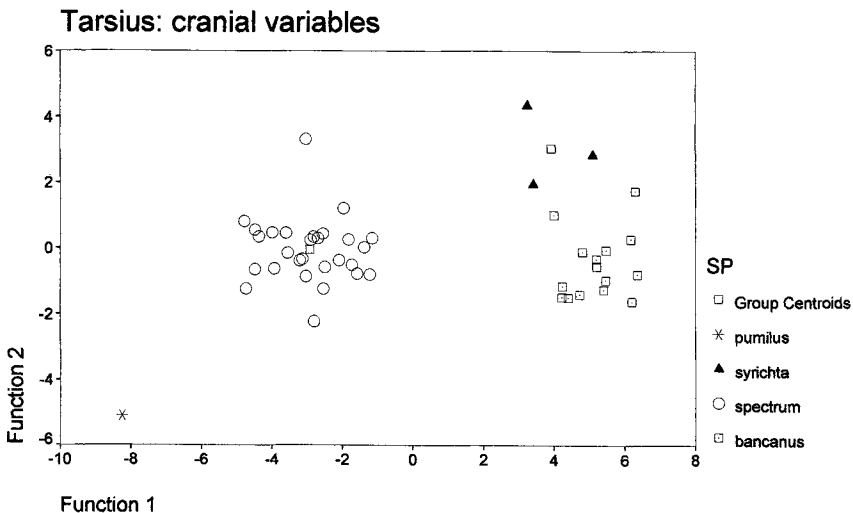

Fig. 1. *Tarsius*, cranial variables: Discriminant Functions 1 and 2.
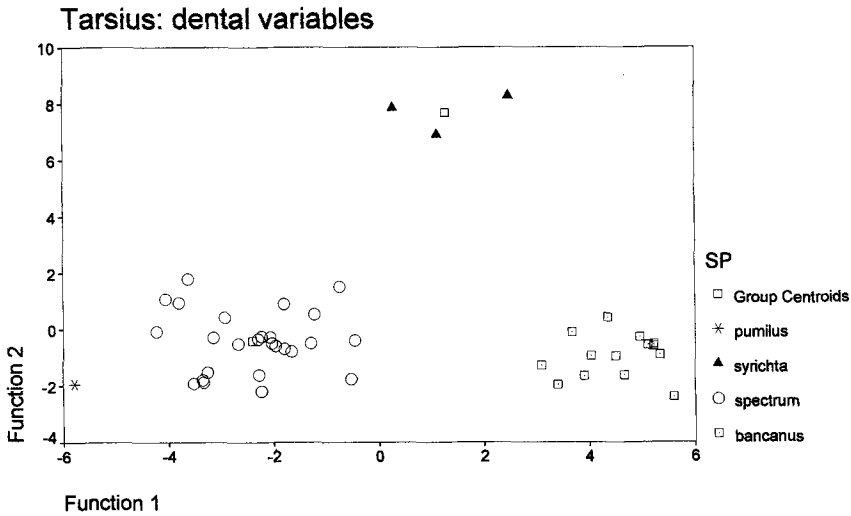
Tarsius: dental variables

Fig. 2. *Tarsius*, dental variables: Discriminant Functions 1 and 2.

The discriminant analysis on external measurements show exactly the same picture as those for cranial and dental measurements, except that the axes are reversed. All four species are again well separated; *T. pumilus* (two specimens) and *T. spectrum* are reasonably close, as in the case of the dental variables. Function 1 (89% of total variance) correlates positively with length of tail pencil and negatively with length of third finger and of its terminal pad. Function 2 (9%) correlates positively with pencil length, length and breadth of pad, and finger length, negatively with length of nail on third finger.

A striking aspect of all three of these figures is the degree of separation of the taxa, the scale being in standard deviation units. In Figure 1 the centroid of the *T. spectrum* scatter is sepa-
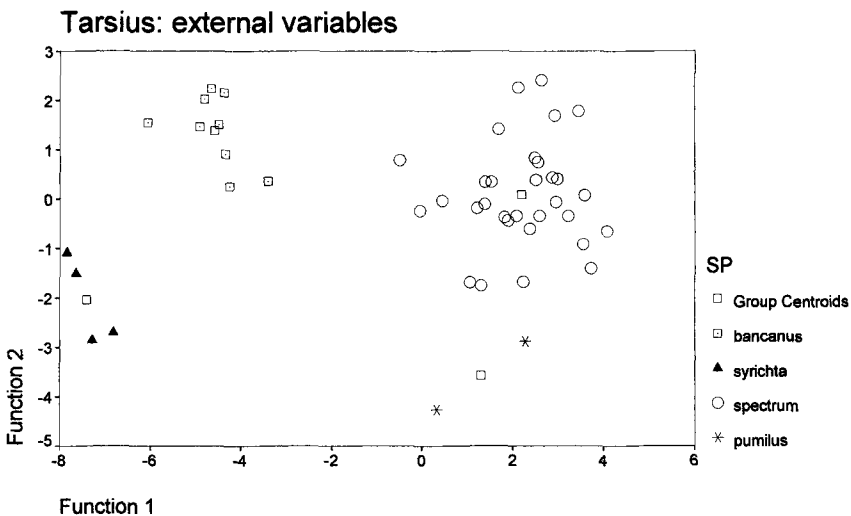
Tarsius: external variables

Fig. 3. *Tarsius*, external variables: Discriminant Functions 1 and 2.

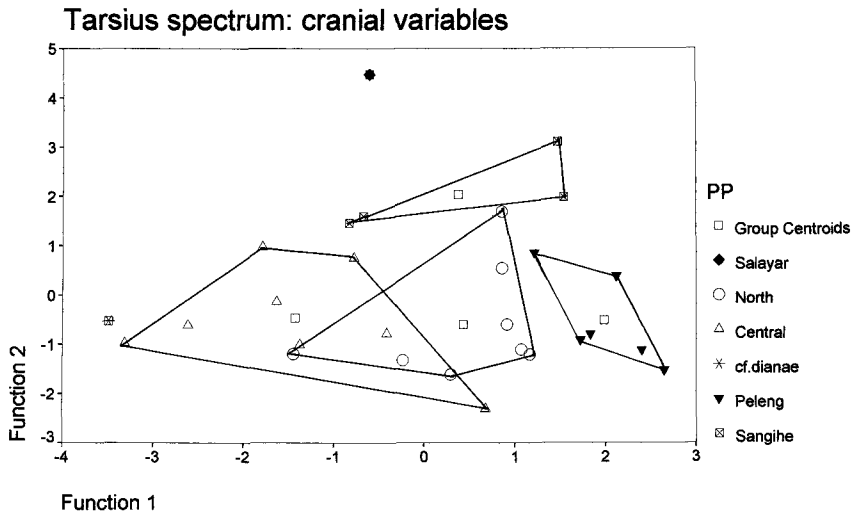## Tarsius spectrum: cranial variables

Fig. 4. *Tarsius* cf. *spectrum*, cranial variables: Discriminant Functions 1 and 2.

rated from that of *T. bancanus* by more than seven units, and from that of *T. syrichta* by as much (combining the separation on the two axes). Figures 2 and 3 show similar degrees of separation; in these cases, *T. syrichta* is almost as well separated from *T. bancanus*. *T. pumilus* is also strongly separated from *T. spectrum*, at least in Figure 1. The large separations are not due to combining different types of measurements: thus cranial variables, which are subject to ontogenetic increase, have been carefully separated from dental variables, which are not. Professor CHARLES OXNARD has pointed out to me, commenting on an earlier draft of this paper, that such separation is more in line with what one would expect when comparing different genera rather than species within a genus.
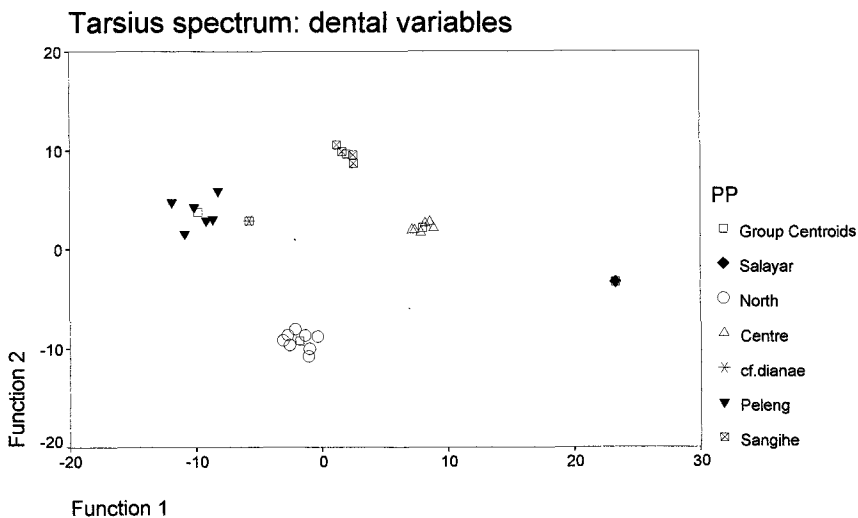
Tarsius spectrum: dental variables

Fig. 5. *Tarsius* cf. *spectrum*, dental variables: Discriminant Functions 1 and 2.

Samples within *T. bancanus* and *T. syrichta* were not large enough to make it worthwhile analyzing geographic variation within either of them. Within *T. spectrum*, however, there were four geographic samples containing a reasonably large number of specimens: the northern arm of Sulawesi; Central Sulawesi; Peleng; and Sangihe. In addition, there was a specimen from Salayar; and a specimen from Central Sulawesi which appeared to show some of the external features ascribed by NIEMITZ et al. (1991) to *T. dianae* (shape of eye, median nasal cleft, larger black paranasal spots, and dark nails). These specimens were kept apart in the intraspecific analyses.

In the analysis of cranial measurements (Fig. 4), Central is distinguished on average from North (though overlapping), and Sangihe, Peleng, and Salayar are distinguished from both, but

Table 1. Characters used in cladistic analysis of *Tarsius*.

1. M3 hypoconulid: short, elongated*
2. Talonids cf. trigonids: broader, equal in width
3. Dentition: very small (<11mm), small (12.0−13.5), larger (>13.5)
4. Paraconids: very mesial*, less so, level with protoconids
5. Upper molars, distolingual corners: absent*, very slight, bigger, strong
6. P^2 cf. canine: reduced in size, larger
7. Molar wear compared to premolars: equal, much heavier
8. Lower incisors: spaced but slant medially, closely apposed*
9. Maxillary incisor-canine diastema: present, usually absent*
10. I^1 height: high (>3.6mm)*, low (3.3−3.6), very low (<3.3)
11. I^2 height: high (>2.5mm)*, medium (1.9−2.2), low (1.7), very low (<1.7)
12. Upper lateral incisor: upright*, slanting forward
13. Upper canine height: very high (>2.8mm)*, high (2.3−2.8), low (<2.3)
14. Incisor and canine cingulum: slight, well-developed
15. Lateral projection of orbital rims: little*, enormous
16. Dorsal projection of orbital rims: little*, enormous
17. Interorbital space: wide*, narrow, very narrow (rims touch)
18. Lateral emargination in orbit: small*, deep
19. Nasal bones: short (not projecting), medium, long (projecting)
20. Pyriform aperture: narrower, wider
21. Bulla length anterior to carotid foramen: <4mm*, 4.7−6.6, >6.6
22. Palate: narrow (<15.7mm), wide (>15.7)
23. Median occipital convexity: absent*, prominent
24. Inion: flattened, slightly ridged, prominent
25. Sides of rostrum: evenly converge, pinched in behind premolars
26. Occipital condyles: rim-like, prominent
27. Foramen magnum: rounded, elongated (lozenge-shaped)
28. Cranial vault: flattened, arched
29. Coronoid process: high and vertical, low and slopes back, very low
30. Gonion: produced backward, not produced
31. Sigmoid notch: deep (>1.5mm), shallow (<1.5)
32. Fur: woolly, finer, silky
33. Black paranasal spot: absent*, poor if present, present, expanded
34. Bare subauricular patch: no, no or slight, yes
35. Postauricular light spot: none*, slight, prominent
36. Tarsus: naked, sparsely haired, fully haired*
37. Tail ventral surface: smooth*, ridged, scaly
38. Tail tuft length: none, short (39−61mm), intermediate (95), long (>100)*
39. Tail tuft colour: none, light brown, black
40. Eyes and orbits: smaller (orbit breadth <17mm)*, larger (>17)
41. Ears: short, relatively short, long
42. Nails: well-developed, somewhat reduced, very reduced
43. Third finger: short (usually <25mm), longer (25), very long (>25mm)
44. Vocal duets: no, yes
45. Diploid chromosome number: 80, 46

*Presumed primitive states. All multistate characters are ordered (unpolarized).

Peleng is, counterintuitively, closest to North. The "cf. *dianae*" specimen is just outside the Central polygon. The first function (58% of variance) correlates positively with bulla length and breadth, negatively with orbit breadth; the second (19%) positively with toothrow length, palate breadth, bulla length, orbit breadth, and biorbital breadth, negatively with bulla breadth and basion-bregma height.

In an analysis based on dental variables (Fig. 5), Central is again distinguished from North, Peleng, and Sangihe, and Salayar is far from all others. Function 1 (62% of total variance) correlates positively with upper canine and incisor crown heights and negatively with second molar length; Function 2 (15%) positively with breadth of first and second molars and length of first molar, negatively with lateral incisor and canine crown heights.

Comparing individual measurements, Sangihe is distinguished from mainland Sulawesi samples in being large and broad-skulled, with long toothrows and short lateral incisors and canines. The Salayar specimen has a very long maxillary toothrow and very long lateral incisors and canine. Peleng is less distinctive, but tends to be large, with short third lower molars. The mainland samples differ only slightly from each other. The cf. *dianae* specimen is noticeably longer-skulled than other Central Sulawesi specimens, but not different in breadth; with shorter toothrows.

The 45 characters used for the cladistic analysis are listed in Table 1. The two sharply distinct cf. *spectrum* samples, Sangihe and Salayar (the latter represented by a single specimen), are scored separately. With an isolated genus like *Tarsius* there is of course no logically satisfactory outgroup; in this case some (dental) characters were polarized by reference to the states depicted in the descriptions of fossil species (*T. eocaenicus*: BEARD et al., 1994; *T. thailandicus*: GINSBURG & MEIN, 1987), others by assumptions of global plesiomorphy (thus, less expanded orbits were considered more primitive than more expanded ones).

Sangihe tarsiers have a higher, less sloping coronoid process, a more poorly marked pale postauricular spot and finer, less woolly fur; the Salayar specimen has a deeper sigmoid notch, a much shorter tail tuft, longer fingers; they both have more sparsely haired tarsus than is usual in *T. spectrum*; and the incisor and canine differences have already been mentioned. The number of taxa is small enough to be run using MacClade 3.1. The shortest tree (length 87, consistency index 0.75) is shown in Figure 6a. Making *T. pumilus*, rather than Salayar, the most
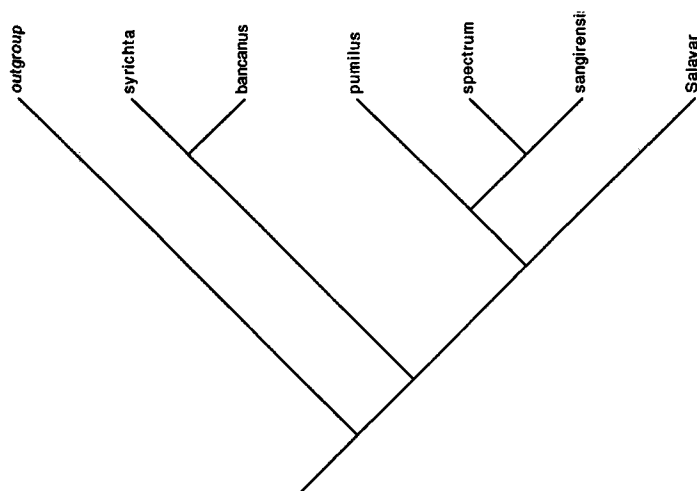

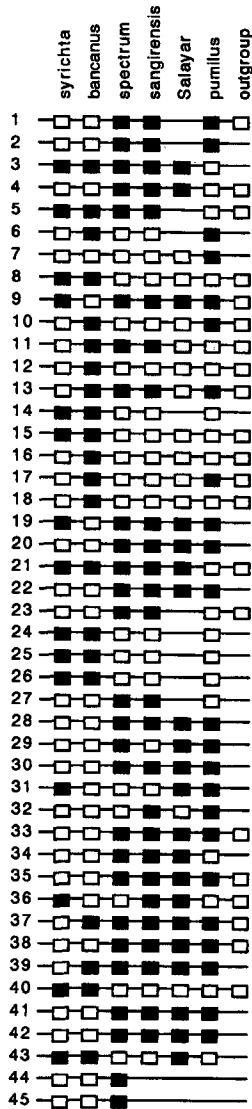**Fig. 6a.** Shortest cladogram of *Tarsius* spp. Length 87, C. I. 0.75.

Fig. 6b. Distribution of derived (dark) character states among *Tarsius* spp.

divergent of the Sulawesi group adds one to the tree length and reduces the consistency index to 0.74. The distribution of primitive and derived conditions is shown in Figure 6b, and the distinguishing features, both polarized and unpolarized, of the two species groups are shown in Table 2.

DISCUSSION

MUSSER and DAGOSTO (1987) are correct in seeing the living tarsiers as split into two very distinct groups: the *bancanus-syrichta* group and the *spectrum-pumilus* group. These differ as listed in Table 2. It could be maintained that the two groups represent different genera; the type species of *Tarsius* STORR, 1780 and of *Macrotarsius* LINK, 1794 is *T. syrichta*; *Cephalopachus*

Table 2. Derived characters of the two species-groups in *Tarsius*.

T. spectrum group	*T. bancanus* group
M3 hypoconulid shortened	Lower incisors spaced cervically, slope medially
Diastema between I^2 and canine	Strong lateral orbital flare
Black paranasal spot	Bulla enlarged anterior to carotid foramen
Postauricular bare patch	Eyes larger
Tail scaly on ventral surface	Tail hair greatly reduced

Unpolarized differences between the two species-groups

	T. spectrum group	*T. bancanus* group
Molar talonids	Broad	Narrow
Dentition in general	Smaller	Larger
Maxillary incisor/canine cingulum	Poorly developed	Prominent
Pyriform aperture	Wide	Narrow
Palate	Narrow	Wide
Inion, in lateral view	Not prominent	Very prominent
Sides of rostrum	Pinched in	Converge evenly
Occipital condyles	More knob-shaped	Rim-like
Cranial vault	Flattened	Arched
Jaw angle	Not prominent	Produced backward
Ears	Longer	Shorter
Nails on fingers and toes	Better developed	Very small
Fingers and toes	Less elongated	Very elongated

SWAINSON, 1835 and *Hypsicebus* LESSON, 1840 (type species *T. bancanus*) would be synonyms. The name *Rabienus* GRAY, 1821 (type species *T. spectrum*) would appear to be available for the Sulawesian group if generic separation is required. The enormous degree of separation in the morphometric analyses would fully support generic separation between Sulawesi and other tarsiers, and might raise questions about the separateness of Bornean and Philippine taxa as well.

Within the Sulawesian group, differences between the Sangihe tarsier and the rest are absolute and clear-cut, and following FEILER (1990), but for different reasons (the cranial features listed by FEILER turn out, on larger samples, to be variable), I propose to recognize *Tarsius sangirensis* MEYER, 1897, as a distinct species.

The single available specimen from Salayar is even more distinct. I do not propose to name a new species at this time, given the availability of only one preserved specimen.

The northern and central populations of *T. spectrum* are distinct at least at subspecific level. The rich material in the American Museum of Natural History must be taken into account before formalizing this taxonomy. The Peleng population is distinct, more than the two mainland samples but less than that from Sangihe, and could perhaps equally well be recognized as a subspecies (*T. spectrum pelengensis*) or as a full species. As far as *T. dianae* is concerned, all that can be said at present is that a specimen showing similarities in external features to those described for this taxon by NIEMITZ et al. (1991) does seem to differ in cranial characters from other Central Sulawesi tarsiers. The status of this putative species remains in doubt.

GENUS *Loris*

Introduction

Ever since HILL (1933, 1952), all members of the genus *Loris* have been ascribed to a single species, *L. tardigradus*, with six subspecies:

L. t. tardigradus: southwestern lowland Sri Lankan "wet zone." Small, red-coloured above when adult (grey when newborn), with grey-white "frosting" on loins; yellowish below.

L. t. grandis: submontane zone of central Sri Lanka. Larger and greyer or grey-fawn with little frosting; white below, also on throat and cheeks.

L. t. nycticeboides: central high plains of Sri Lanka. Distinguished by its exceedingly thick, woolly brown coat.

L. t. nordicus: "dry zone" of rest of Sri Lankan lowlands. Large and grey, often with lumbar "frosting"; white below, and on cheeks.

L. t. lydekkerianus: dry forests of southern India. Grey like *nordicus*, but with heavier pelage on limbs.

L. t. malabaricus: wet forests of southwestern India. More reddish (but not like *tardigradus*), and large in size.

All these lorises have a pattern of dark forks on the crown, leading to dark eye-rings and laterally to the ears; there is also a dark dorsal stripe of varying definition (best developed in *nordicus*). The six seem homogeneous, and no reason has been found to separate subsamples within any of them.

Results

Principal Component (PC) 1 was, as is usually the case, dependant largely on absolute size: the loadings of all the raw measurements on PC1 were greater than 0.9, except for Bicanine breadth (0.87) and Palate breadth (0.75). Figure 7 shows PC2 on the horizontal axis, PC3 on the vertical. *L. t. tardigradus* is well separated from the others, which form a graded series *malabaricus-nordicus-lydekkerianus*, with the single available specimens of *grandis* and *nycticeboides* close to *malabaricus*. PC2 contrasts palate breadth and bicanine breadth with biorbital breadth and the cranial length measurements; PC3 contrasts greatest skull length and palate breadth with bicanine breadth and palate length.

L. t. tardigradus is very small but has a long jaw body and relatively broad bicanine and bizygomatic width. The two Indian taxa agree in being longer in jaw body than *nordicus*, though they are not overall larger in size. Two young skulls of the Indian taxa (specimens 3 and 4) approach *L. t. tardigradus*; one is of *lydekkerianus*, the other (no. 4), from Trivandrum, is presumably of *malabaricus*, although there is no skin to confirm this.

Discussion

The sharp separation of *tardigradus* from all other taxa is noteworthy; it is markedly smaller, but differs in some skull proportions as well, and its colour is unique.

Of the other Sri Lankan forms, I cannot distinguish *grandis* from *nordicus* externally, and the single skull is but marginally distinguishable. I propose to synonymize them: the prior name is *grandis*. *L. t. nycticeboides* is likewise represented by only a single skull, but this is more distinct (and it is very different externally as well).

The two Indian forms differ from each other. The grey, dry-country *lydekkerianus* is quite close to the grey, dry-country *grandis* (=*nordicus*) from Sri Lanka; but the redder, wet-zone *malabaricus* is quite different from its Sri Lankan representative *tardigradus*.

It is worth noting that, although $2n=62$ has been recorded for all slow lorises karyotyped thus far, there are differences in chromosome morphology (GOONAN et al., 1995). Two *grandis* have 16:18:26 and 18:18:24 (large submetacentric, small submetacentric, and acrocentric auto-
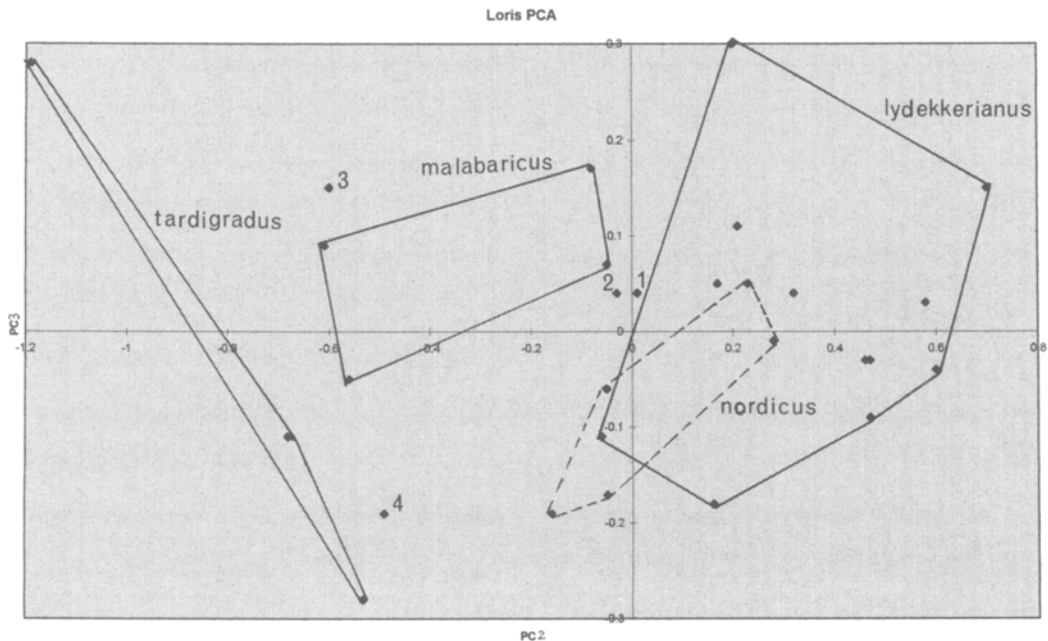
Fig. 7. *Loris*, cranial variables: Principal Components 2 and 3. The polygons enclose samples of *tardigradus, malabaricus, lydekkerianus,* and *nordicus*, as indicated. The numbered specimens are as follows: 1: type of *grandis*; 2: type of *nycticeboides*; 3: a juvenile specimen of *lydekkerianus*; 4: a juvenile skull from Trivandrum, presumably *malabaricus*.

somes, respectively), while a *tardigradus* has 18:16:26, and one from India was reported by MANNA and TALUKDAR (1968) to have 22:16:22.

Conclusions

If phenetic difference relates here to phylogenetic separation, then it will be justified to separate *tardigradus* as a species separate from the rest; the prior name for the larger, more diverse species is *L. lydekkerianus*. The similarity between the dry-zone subspecies of Sri Lanka and India suggests that they formed a continuum in the Pleistocene; contrariwise, the strong differences between the two wet-zone taxa indicates that lorises in India have only comparatively recently invaded this habitat.

GENUS *Nycticebus*

Introduction

Though HILL (1952) placed all slow lorises in one species, *Nycticebus coucang*, sympatry of a large and a small form east of the Mekong means that there must be at least two distinct species. GROVES (1971) consequently recognized *N. pygmaeus* as a separate species, and divided *N. coucang* into four subspecies: *N. c. coucang* (Sumatra, Malaya, and North Natuna Is.), *menagensis* (Borneo, Tawitawi, and Bangka), *javanicus* (Java), and *bengalensis* (mainland
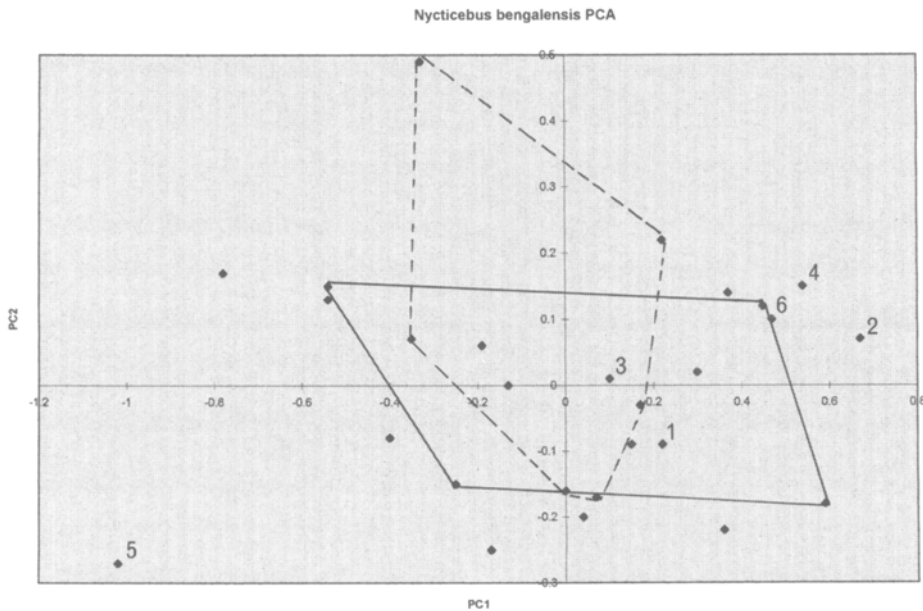
Fig. 8. *Nycticebus bengalensis* cranial variables: Principal Components 1 and 2. The solid line encloses specimens from Hinlaem; the dotted line, 0 specimens from Chiengmai. Numbered specimens are as follows: 1: Chittagong; 2: Chin Hills; 3: Sumprabum (N. Burma); 4: Naga Hills; 5: Bengal (no exact locality); 6: Xieng Khouang (Laos). Unnumbered dots represent specimens from Thailand north of the peninsula.

S. E. Asia north of the Isthmus of Kra). He commented that the distribution of subspecies in Indonesia seems odd, but actually corresponds exactly with the pattern of fossil rivers on the Sunda Shelf; and that there is somewhat of a ring-species effect, *menagensis* being closest to *N. pygmaeus*.

Results

The *bengalensis* PCA (components 1 and 2) is shown in Figure 8; the first component is strongly size-correlated, all loadings being greater than 0.8 except for palate breadth which is only 0.54, and a diagram including the first component adds nothing to the picture. The two sizeable samples, from Hinlaem and Chiengmai, overlap widely; individuals from other localities are scattered haphazardly around them, with no indication of genetic structure. Northerly (Bengal, Chittagong, and Nagaland) specimens do not cluster together; the only skull from east of the Mekong is associated with others from west of it. This analysis confirms the homogeneity of *bengalensis*. Skins from this region are also homogeneous, with white head, neck and foreparts and pale brown hindparts, and poorly expressed dorsal stripe and head-forks.

Discriminant Analysis using cranial and mandibular measurements is shown in Figure 9. A skull from Bangka fell into the Borneo cluster; Malayan and Sumatra samples were indistinguishable, and skulls from the North Natuna Islands and from Tioman fell in this same cluster. The homogeneity of the GROVES (1971) subspecies being confirmed, they were thenceforth taken as the level of analysis. They form a graded series: *pygmaeus—menagensis—coucang—javanicus—bengalensis*: precisely the ring-species effect postulated in the GROVES (1971)

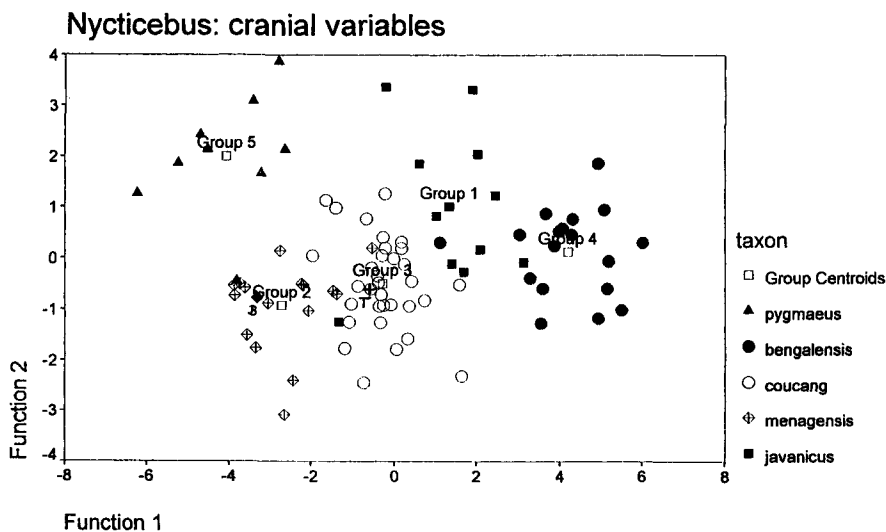## Nycticebus: cranial variables

Fig. 9. *Nycticebus*, cranial variables: Discriminant Functions 1 and 2. Three individual skulls are marked as follows: B: Bangka; T: Tioman and North Natunas Is. (these two skulls occupy the same position).

paper, except that *javanicus*, somewhat unexpectedly, is closest to *bengalensis*. The five taxa overlap; even, a specimen of *pygmaeus* overlaps with *menagensis*. DF1 (83%) is largely size-based, except that cranial breadth and mandibular measurements are not highly correlated with the Function; DF2 (10%) contrasts high ramus and long jaw body with bicanine, biorbital, and bizygomatic breadths. Note that, although the total spread of the diagram is large (not as large as in the *Tarsius* figures), the separation of the taxa is not as great as in the *Tarsius* case, indeed there tend to be overlaps.

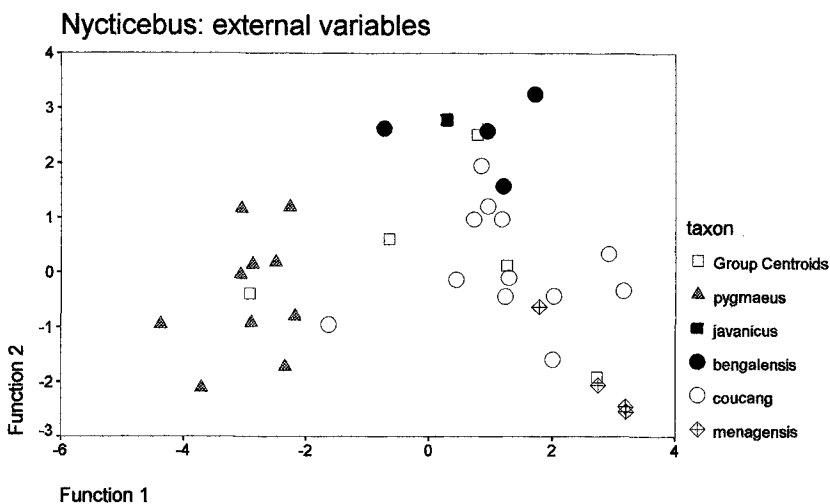Figure 10 shows a discriminant analysis based on external measurements, as recorded on

Nycticebus: external variables

Fig. 10. *Nycticebus*, external variables: Discriminant Functions 1 and 2.

labels, and incorporating some from the literature. Again, *N. pygmaeus* and *bengalensis* are separated from the others. A specimen from Koh Lak, 11°50'N, on the peninsula south of the main range of *bengalensis*, assorts with *bengalensis*. DF1 (77%) contrasts head and body, and hindfoot lengths with ear length; DF2 (23%) is a size function, with all measurements positive especially head and body, and ear. A noteworthy feature is the wide spread of each of the taxa (I thank Prof. CHARLES OXNARD for this observation); provisionally, I put this down to the inherent inaccuracy of flesh measurements, but further investigation, using larger samples if and when these become available, does seem warranted.

Discussion

As expected, *Nycticebus pygmaeus* is distinct; hardly more so, however, than is *bengalensis*. The ring-species effect is as predicted, but not precisely: *coucang*, geographically closest to *bengalensis*, is not phenetically closest, but is in fact clearly separated from it (the two are also very distinct externally: *coucang* is entirely gingery-brown, with well-developed dorsal stripe and head-forks). It is worth considering whether *bengalensis* should not be separated at species level from the Sundaland cluster.

A few specimens are available from localities in peninsular Thailand, between the main ranges of *coucang* and *bengalensis*. Four of these are in the Thai National Collection; time did not permit the full range of skull measurements to be taken, but because of the dramatic differences in size and external appearance a preliminary assessment of them is possible.

Skull length in *bengalensis* averages 65.25mm (s.d. 2.05, $n=28$); in *coucang*, 58.55 (s.d. 2.13, $n=44$). Specimens from Satun (6°30'N) and Koh Terutau (7°35'N), an offshore island, are precisely like *N. c. coucang* externally, and probably cranially (skull lengths 61 and 59mm respectively; above the mean, but well within the range, and >2 s.d.s from *bengalensis*). Two from Ranong (9°55'N) are somewhat intermediate in the pale but gingery tone of the head and neck, and have an intermediate expression of the head-forks; skull length is also intermediate at 62.75mm. Two from Koh Lak (11°50'N) resemble *bengalensis*; as noted above, the external measurements of one of them is placed in the *bengalensis* cluster in the DFA, but two skulls average only 61mm in length. Finally a skin (no skull) from King's Island (12°30'N) is coloured like *coucang* but the dorsal stripe and head-forks are very faint. The total evidence suggests a narrow zone of interbreeding in the peninsula between these two very distinct taxa.

Conclusions

A three-species model of slow loris taxonomy seems to express the position best, given the distinctiveness of *bengalensis* and the ring-species effect: *N. pygmaeus, N. coucang* (with its three subspecies), and *N. bengalensis*. There is a narrow zone of interbreeding between these two in the northern part of the Thai/Burmese peninsula.

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