Placing the cranial morphology of a rare endemic colobine, *Presbytis natunae*, within the context of its genus

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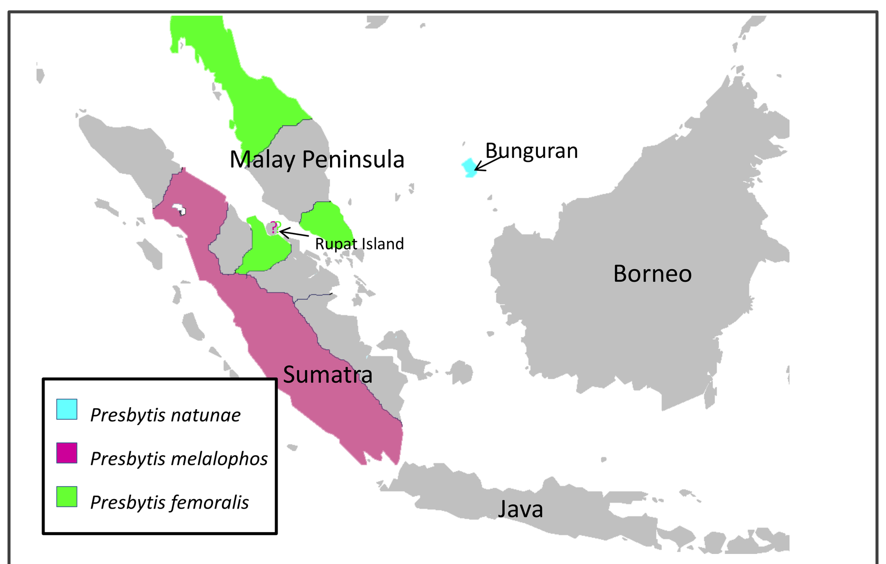
A *Presbytis* leaf monkey.
Photo: 2004 K.W. Chan

Introduction

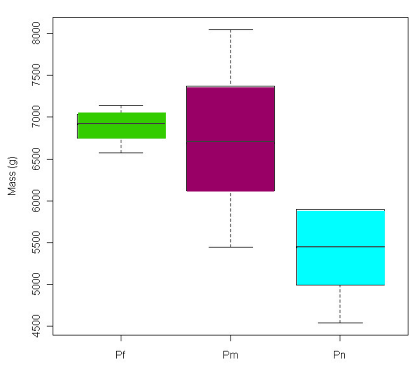
The extant species of Asian colobine monkeys have widespread and often fragmented distribution patterns. Members of the genus *Presbytis* are confined to Sundaland, a region of exceptionally mutable biogeography thanks to frequent tectonic activity, changing sea levels and unstable climatic regimes. The complex biogeography of *Presbytis* implies an evolutionary history that is difficult to reconstruct, and phylogenies that are challenging to resolve (Meijaard and Groves 2004). Furthermore, species-level systematics are based primarily on skin and pelage characters (Groves 2001), hampering attempts to interpret the sparse (sub)fossil material relevant to *Presbytis* evolution. Although debate over the use of quantitative shape traits as "characters" for phylogenetic inference continues (e.g., Felsenstein 2002), modern morphometrics presents a toolkit whose potential in *Presbytis* systematics remains largely unexplored.



Sundaland, illustrating species distributions
The approximate current geographic distribution of the three species of *Presbytis* considered in this study. Distributions based on Groves (2001) and Meijaard and Groves (2004).

Bunguran (Greater Natuna Island)

- Located 475 km E of Malay Peninsula; 225 km NW of Borneo
- Land area: 1700 km^2 (cf. smallest U.S. state, Rhode Island: 2700 km^2)
- Other non-human primate inhabitants: slow loris, long-tailed macaque



Comparative body mass
Mean body mass values (in g) for the three species. Data from museum records of only specimens used in this study (sample sizes in table below).

The present study sets out to better understand evolution within *Presbytis*, particularly with respect to a little-studied population endemic to the small island of Bunguran (a.k.a. Greater Natuna). Given its small body size relative to other *Presbytis*, the Natuna leaf monkey (*Presbytis natunae*) represents one of the few extant primate species permitting the study of cranial morphology in relation to insular body size reduction, or island dwarfing. The purpose of this study is to **evaluate cranial morphology in the Natuna monkey as a putative example of insular dwarfing** in primates and, more generally, **to assess the potential for cranial morphometrics as a tool for systematic and, perhaps, phylogenetic inference in *Presbytis*.**

Hypotheses

(1) The insular species *Presbytis natunae* exhibits a derived cranial shape and size associated with its isolation and body size reduction.

(1) The various species of *Presbytis* are identifiable based on cranial form (i.e., size and shape).

Although these two hypotheses pertain to the genus as a whole, this study is preliminary in that it restricts its analyses to just three out of approximately one dozen *Presbytis* species. Due to specimen availability, *P. melalophos* forms the primary comparative sample for cranial morphology in *P. natunae*. A small female sample of *P. femoralis* was measured opportunistically, and is included for additional context. Naturally, continued work extending to include all species of *Presbytis* is needed to fully address the above hypotheses.

Materials & Methods

***P. natunae* (L) and *P. melalophos* (R) crania**
In lateral (left panel) and superior (right panel) views.
Adult female specimens. Scale bar = 1 cm.

Sample sizes used in this study
Values in parentheses () indicate number of specimens with accompanying body mass data.

Species	Sample size	
	Male	Female
Presbytis natunae	4 (2)	10 (4)
Presbytis melalophos	31 (8)	29 (5)
Presbytis femoralis	0 (0)	7 (4)

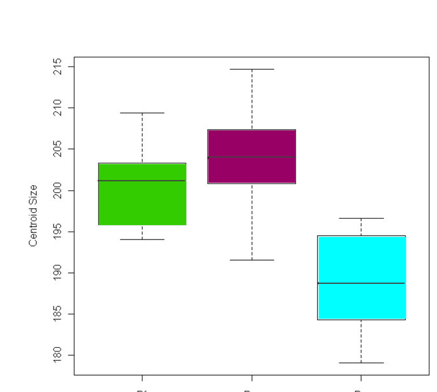
Three-dimensional cranial landmark data were collected from museum specimens using a MicroScribe G2X digitizer. Forty-five bilateral landmarks were subjected to geometric morphometric analysis using two primary methodologies, Generalized Procrustes Analysis (GPA) and Euclidean Distance Matrix Analysis (EDMA). Procrustes-based analyses were performed in MorphoJ (Klingenberg 2011); EDMA analyses in WinEDMA (Cole 2002).

Hypothesis (1) was addressed by pairwise comparisons of cranial size and shape in the three species. Males and females were pooled when comparing *P. natunae* with *P. melalophos*, as cranial sexual dimorphism is minimal in these species. However, because the sample of *P. femoralis* includes only female specimens, only female cranial data of *natunae* and *melalophos* were used in pairwise comparisons with *femoralis*. Visualizations of mean shape differences were made in AMIRA using surface reconstructions of a male *P. natunae* cranium and a female *P. melalophos* cranium.

Hypothesis (2) was addressed by considering the principal components of cranial shape variation across the three species, paying particular attention to biogeographic information from individual specimen records. Discriminant function analysis of cranial shape variables (following GPA) was performed to assess to what extent cranial morphology indicates species membership in pairwise species comparisons.

Results

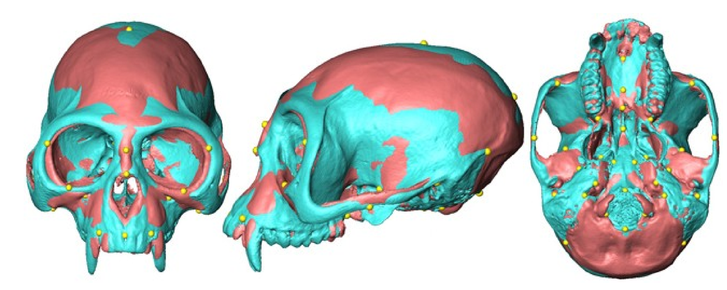
Size. Cranial landmark data confirm that overall cranial size is reduced in *P. natunae* compared to the other two species, albeit with some overlap in size distributions. *P. melalophos* and *P. femoralis* do not differ significantly from each other in cranial size (keeping in mind that only a small, all-female sample of *P. femoralis* was considered here). Thus, cranial size can be a useful indicator in predicting species affiliation within *Presbytis* when used in conjunction with other data, but cannot by itself discriminate between species in most cases.



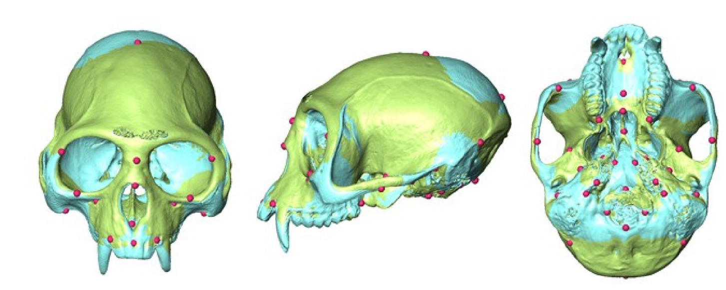
Comparative cranial size
Distribution of centroid size for specimens used in this study (45-landmark configurations).

Shape in the Natuna monkey

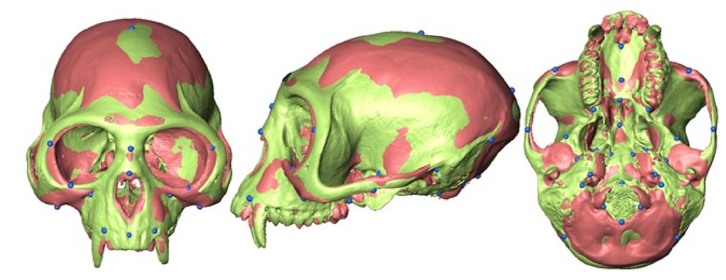
Sample mean shapes were visualized by warping the surface reconstruction of a "holotype" specimen to each group mean landmark configuration. Mean shapes were then superimposed to show shape differences between groups. Note that three of the most prominent shape differences distinguishing the Natuna monkey from *P. melalophos* also distinguish *P. femoralis* from *P. melalophos* (gray text), whereas two features are unique to *P. natunae* relative to the other groups (**bold** text). Blue = *P. natunae*, red = *P. melalophos*, green= *P. femoralis*.



P. natunae shape vs. *P. melalophos*:
-Broader cranium at level of EAM
-Wider biorbital distance
-More projecting premaxilla
-Less vertical nasal bones
-Shorter palate



P. natunae shape vs. *P. femoralis*:*
-Less projecting nasion
-Taller facial aspect of zygoma
-Narrower zygomatic arches
-Less vertical nasal bones
-Shorter palate
* Only females considered

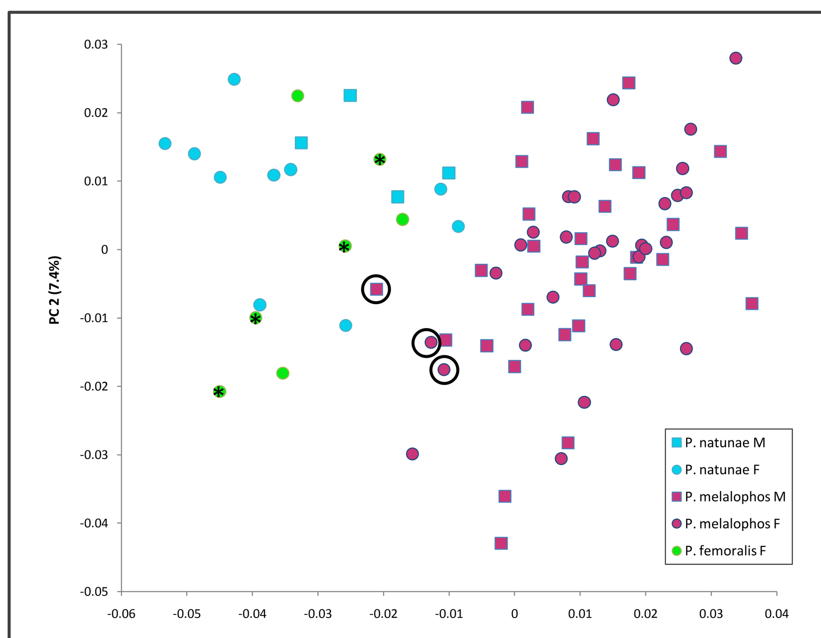


P. femoralis shape vs. *P. melalophos*:*
-Broader cranium at level of EAM
-Wider biorbital distance
-More projecting premaxilla
-Shorter nasal bones
* Only females considered

Shape trends in genus *Presbytis*

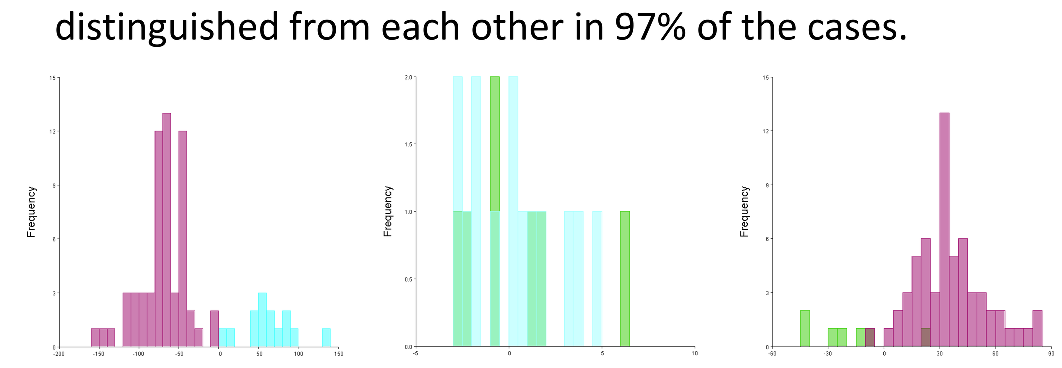
In the first principal component (PC1) of cranial shape variation, the Natuna monkey is more similar to the *P. femoralis* sample than to *P. melalophos*. Notable shape features associated with the "*natunae-femoralis*" (negative) end of PC1 are relatively broad cranium at the level of the external auditory meatus (EAM), wider biorbital distance, and more projecting premaxilla. These features also distinguish both *P. natunae* and *P. femoralis* from *P. melalophos* in the pairwise shape comparisons (above).

Further inspection of the PC analysis of all individuals suggests interesting geographic patterns in the craniometric data. The three *P. melalophos* individuals circled in the plot (right) are from localities in the "Rupat Strait" or "Rupat Island" area, just adjacent the range of *P. femoralis* (see map). Although these specimens are classified in museum (NMNH) records as *P. melalophos*, their position in the plot demonstrates some *P. femoralis* shape affinities. Notably, Miller (1934) assigned these three specimens to *Presbytis percura*—a taxon that was later subsumed as a subspecies of *P. femoralis*. By chance, *P. femoralis percura* is represented in the present study by four of the seven female *femoralis* specimens (marked with a * at right).



PCs 1 & 2 of cranial shape variation
The three circled individuals were collected on or near Rupat Island, Sumatra. The four individuals marked with a * are classified in the subspecies *P. f. percura*.

Classification using cranial morphometrics. The efficacy of classifying individual specimens based on landmark configurations was explored using cross-validation tests on discriminant function analyses of species pairs (plots below). Using a 'leave-one-out' cross-validation algorithm, we see that *P. natunae* individuals from this sample were correctly distinguished from *P. melalophos* 100% of the time. *P. natunae* and *P. femoralis* were poorly distinguished from one another using only cranial shape data, with a 43% misclassification rate. Members of the *P. femoralis* and *P. melalophos* samples were successfully distinguished from each other in 97% of the cases.



Discriminant function cross-validation tests
Cross-validation tests the accuracy of the linear discriminant function to predict species membership by leaving out one specimen in each iteration. High efficacy is indicated by no overlap in discriminant scores (x-axis) between the two species, as in the first panel (far left).

Summary points

- The Natuna monkey and *P. femoralis* share major cranial shape features distinguishing them from *P. melalophos*.
- Few cranial shape features (less vertical nasal bones, shorter palate) were identified that could potentially be uniquely derived in the dwarf species, *P. natunae*.
- Cranial 3D geometric morphometrics may prove useful in distinguishing species-level and/or geographic affinities within *Presbytis*.

Conclusions

These results provide minimal support for hypothesis (1), in that the major cranial shape differences between the Natuna monkey and *P. melalophos* are not due to unique features of the dwarf species. Nevertheless, some aspects of shape in *P. natunae* could be related to its isolation and dwarfing, pending comparison with a broader sample of cranial shape variation in *Presbytis*. Although this study examines only a subset of species variation in the genus, it provides preliminary support for hypothesis (2): these findings suggest that continued investigation of 3D cranial morphometrics as a tool for constructing and testing systematic and evolutionary hypotheses in *Presbytis* is warranted. This corroborates results obtained using more traditional cranial metrics across *Presbytis* by Meijaard and Groves (2004).

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Acknowledgments

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