# Comparative Dental Metrics and the Radiation of New World Monkeys: A Preliminary Analysis

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*Very little is known about the quantitative relationships of tooth morphology within New World monkeys as a whole. Previous studies have focused on nonmetric data or have presented basic statistics of individual tooth measurements without comparisons among genera. This study presents selected comparisons of measurements of the upper postcanine dental battery of modern platyrrhines and demonstrates that metric indices are valuable as taxonomic markers for the New World monkey radiation. Callitrichines, pithecines, and atelines show diagnostic patterns and ranges of variation in a number of premolar and molar comparisons. These indices are also useful for interpreting the wealth of fossil teeth being recovered in South America, and should help to fill the void of comparative odontometrics in platyrrhine studies.*

## INTRODUCTION

Living New World monkeys comprise sixteen genera of large, medium and small-bodied arboreal primates. The behavioral ecology of some groups of extant platyrrhines, such as marmosets and tamarins, has been studied extensively (Sussman and Kinzey 1984), while that of other groups, such as uakaris, has not (Fleagle 1988). Platyrrhines have radiated into a wide variety of arboreal habitats and foraging niches which are diagnostic at the subfamily level and in some cases at the generic level. Unfortunately, modern habitats are difficult to recognize in the South American fossil record, which is biased against preservation of the predominant tropical forest ecosystem. Fossil platyrrhine tooth morphology is thus one of the only indicators available for evolutionary analyses. Nonetheless, comparative quantitative data on modern dentitions are conspicuously lacking. This study introduces a few selected metric indices of modern platyrrhine upper teeth in order to illustrate useful diagnostic patterns and ranges of variation. A comprehensive series of dental metric indices will greatly facilitate the systematic study of fossil New World monkeys, as has been done for other primate groups.

## MATERIALS AND METHODS

The dental measurements used in this study were taken on the collections at the Field Museum of Natural History in Chicago, Illinois. The number of specimens for each genus is listed in Table 1. At the time data were collected, no specimens of *Brachyteles* were available. All graphs and statistics were generated from standard mesio-distal (M-D) and bucco-lingual (B-L) tooth measurements taken in the occlusal plane with hand-held digital read-out calipers.

Strict absolute measures of tooth magnitude cannot possibly stand alone as analytical tools, for they cannot represent the qualitative shape differences in cusps within and among genera. This study is an independent analysis of the size patterning in platyrrhine upper postcanine teeth, and in no way encompasses the many other analyses of intra-platyrrhine variation and relationship. Its value lies primarily as a check of hypotheses generated from nonmetric studies and as a means of scoring various dental parameters and indices as taxonomic markers. As noted above, comparative odontometry is practically nonexistent in platyrrhine studies. Ranges of variation are known for only a few genera (Rosenberger *et al.* in press).

## RESULTS

Figures 1-7 illustrate a variety of dental metric parameters and indices. In each case the data points are coded according to genus name (see Table 1 for codes). The most obvious message in these graphs is that tooth size regression in platyrrhines is highly consistent, a result common in primate families as a whole but not superfamilies or suborders. The correlation coefficients and regression values clearly indicate that no platyrrhine genus has departed markedly from any other or away from the expected dependent variable regression. Thus, the adaptive radiation of New World monkeys, while diverse ecologically, has been conservative along the postcanine dental battery.

Table 1. List of genera and the number of each used in this study. The abbreviations refer to the data points in Figures 1-7.

| Genus | Number of specimens | Abbreviation |
|---|---|---|
| Alouatta | 34 | A |
| Aotus | 13 | O |
| Ateles | 24 | T |
| Cacajao | 7 | J |
| Callicebus | 12 | C |
| Callimico | 7 | M |
| Callithrix | 74 | X |
| Cebuella | 6 | U |
| Cebus | 11 | B |
| Chiropotes | 6 | H |
| Lagothrix | 7 | L |
| Leontopithecus | 12 | R |
| Pithecia | 10 | P |
| Saguinus | 74 | G |
| Saimiri | 2 | S |

Figure 1 plots the summed area of $P^3$ and $P^4$ against the summed area of $M^1$ and $M^2$. $M^3$ is excluded in order to compare callitrichines, which do not have third molars, with other platyrrhines. Figure 2 is an expanded reproduction of this comparison which excludes *Alouatta* in order to compare the smaller genera more clearly. This comparison cleanly separates the platyrrhine genera into subfamily groupings. Callitrichines, the smallest in size, naturally are grouped at the bottom of the regression. Two genera, *Leonto-pithecus* and *Callimico*, grade into the cebine and pithecine range, while the large-bodied atelines complete the top of the regression.

Figures 3 and 4 illustrate the relative sizes of $P^3$ and $P^4$ against a linear scale of the summed M-D lengths of $P^2$-$M^2$. This scale is used in order to more clearly separate longer from shorter toothrows. The high correlation coefficients are logical; i.e., one would expect premolar area to be highly correlated with the M-D length of the postcanine toothrow, even if $M^3$ is excluded. The more interesting application of these graphs is what they reveal about the relationship between $P^3$ and $P^4$. In all platyrrhines, $P^3$ and $P^4$ have maintained a constant size relationship with one another such that even in genera which show slightly higher (e.g., *Chiropotes* and *Cacajao* among the pithecines, *Leontopithecus* among the callitrichines) or lower (e.g., *Aotus* and *Calli-cebus* among the pithecines) premolar areas compared to the molar area regression (Figures 1-2), it is the $P^3$-$P^4$ complex as a whole which has

changed (or conversely, remained the same as the $M^1$-$M^2$ complex changed). The platyrrhine with the largest teeth, *Alouatta*, has enlarged upper molars but premolariform premolars with areas predicted by this regression. Similarly, the smallest platyrrhine genus, *Cebuella*, tracks consistently along the regression. Its greatly reduced body size, therefore, has not affected the relative size of the postcanine dental battery in any unusual way.

Figures 5 and 6 document one of the few diagnostic indices for the dental radiation of platyrrhines as a whole. The vertical axis is an index calculated by dividing the M-D length of $P^2$-$M^2$ by the area of $M^1$ plus $M^2$ (Figure 5) or by the area of $P^3$ plus $P^4$ (Figure 6). The horizontal axis is used as a scale for increasing toothrow length. The indices reflect the range of variation in molar (Figure 5) or premolar (Figure 6) battery size across taxa, and document two trends. First, callitrichines are much more variable than other platyrrhines in this relationship, as indicated by their more vertical distribution. While the range of variation in their postcanine toothrow length is absolutely low, relative widths of $P^3$-$M^2$ are not. Second, larger platyrrhines are progressively less variable in these indices than smaller platyrrhines, which suggests a tighter allometric relationship between increase in tooth length and area. As toothrow length increases, the area indices and range of variation decrease, especially for molars (Figure 5). Platyrrhine upper postcanines widen at least as much as they
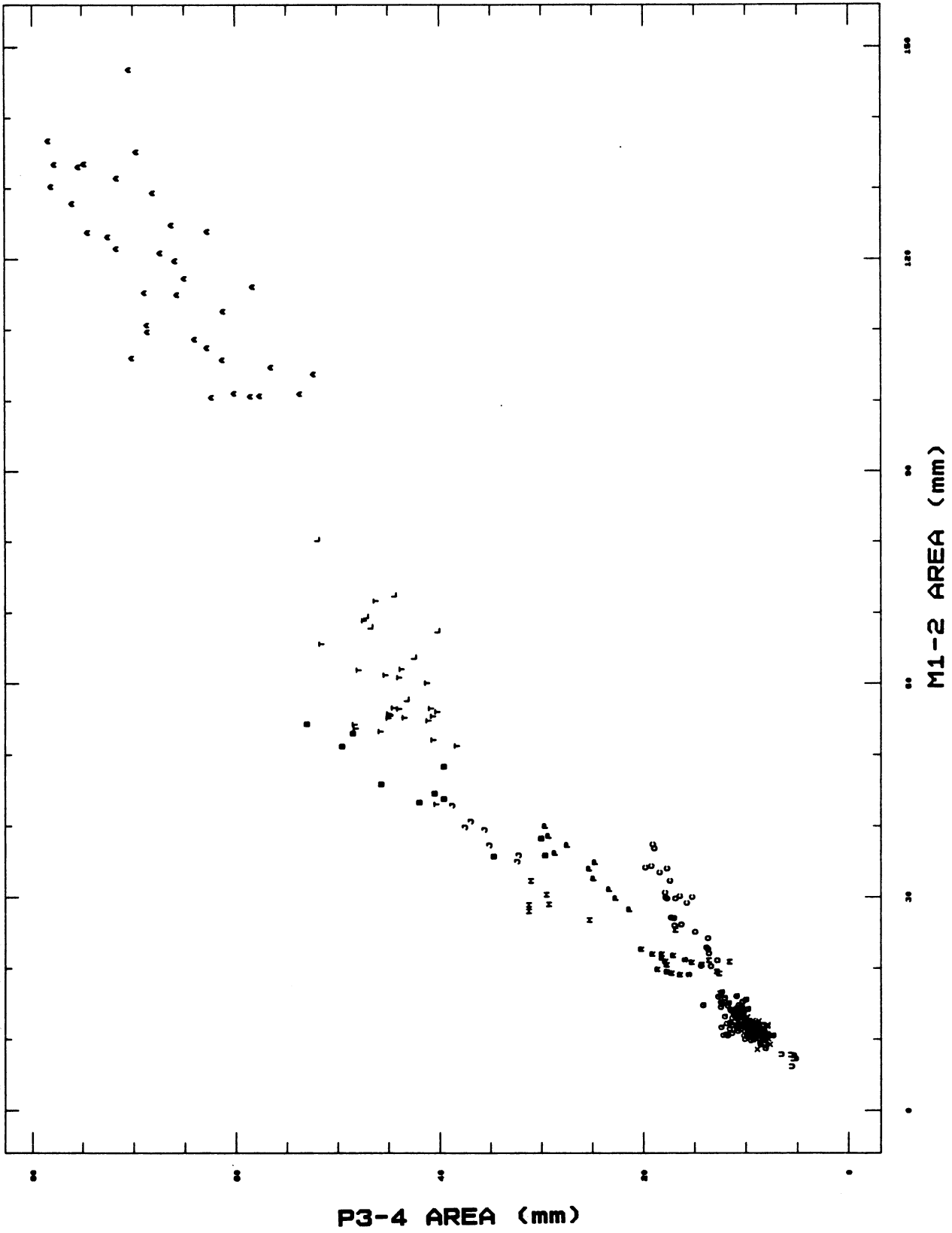
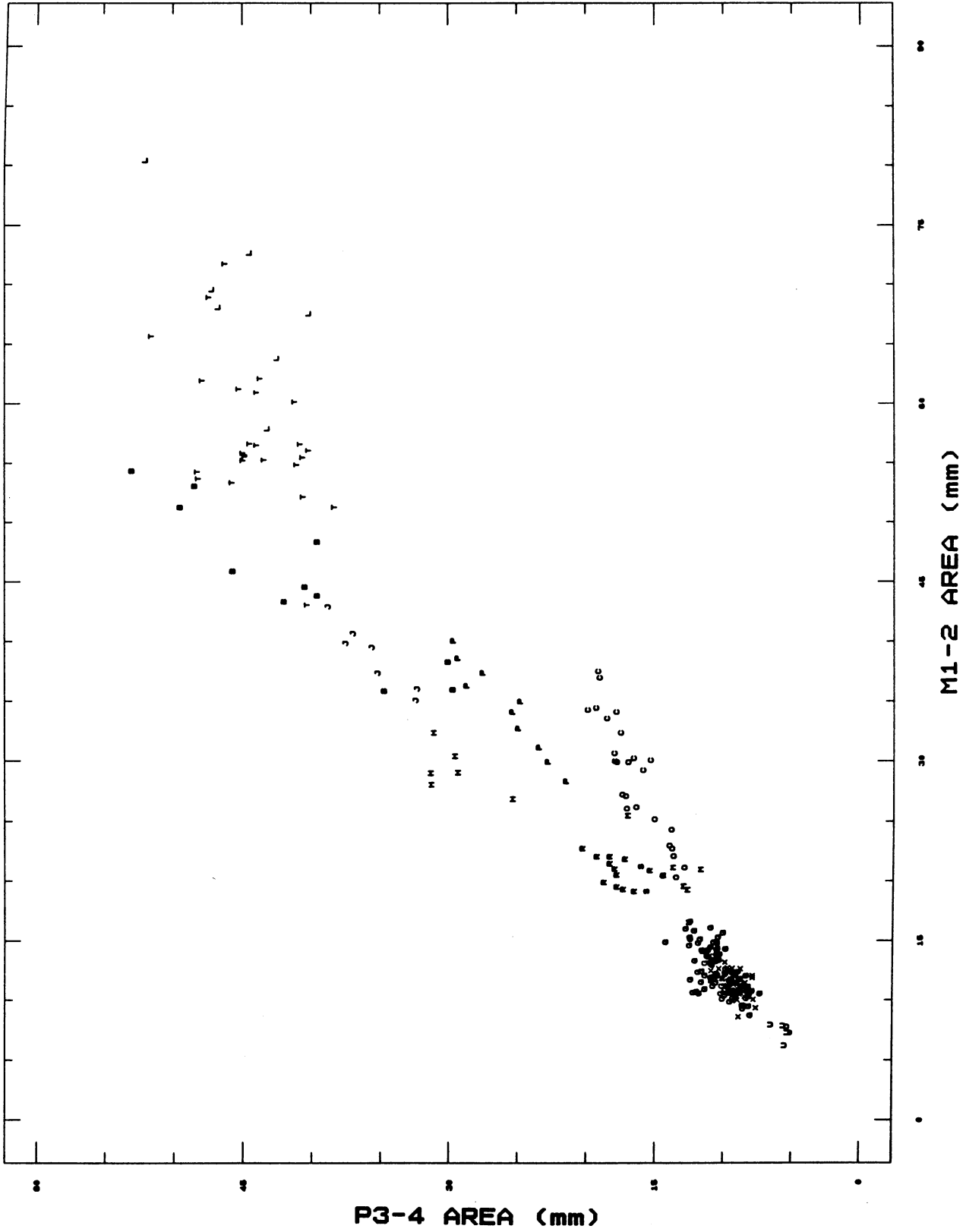Figure 1. Occlusal area for indicated teeth in all platyrrhine genera. r = .97

M1-2 AREA (mm)

P3-4 AREA (mm)

Figure 2. Same as Figure 1 but excluding *Alouatta*. Note the increase in premolar area for pithecine genera of equal molar size (*Pithecia, Chiropotes, Cacajao, Aotus, Callicebus*).

Figure 3. The x-axis is the total of the M-D lengths of $P^2$-$M^2$. The high correlation (r = .989) is expected because the variables are partially dependent upon one another. Deviations from this regression are therefore informative, such as the relatively greater premolar area of *Cebus* compared to other platyrrhines of similar toothrow lengths.
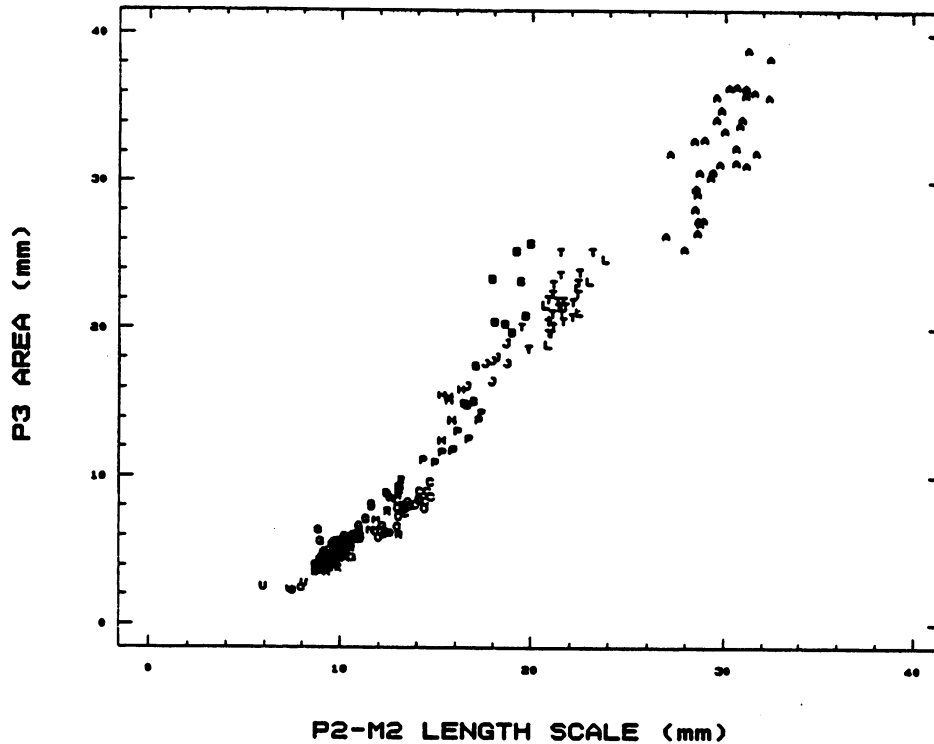


Figure 4. Same as Figure 3 but using $P^4$ area instead of $P^3$. The graph does not appear to be informative since the area of a tooth should be closely related to the length of the toothrow (r = .986). Comparison with Figure 2 indicates, however, that this simple regression reveals differences in molar widths between *Aotus/Callicebus* and *Pithecia/Chiropotes*.
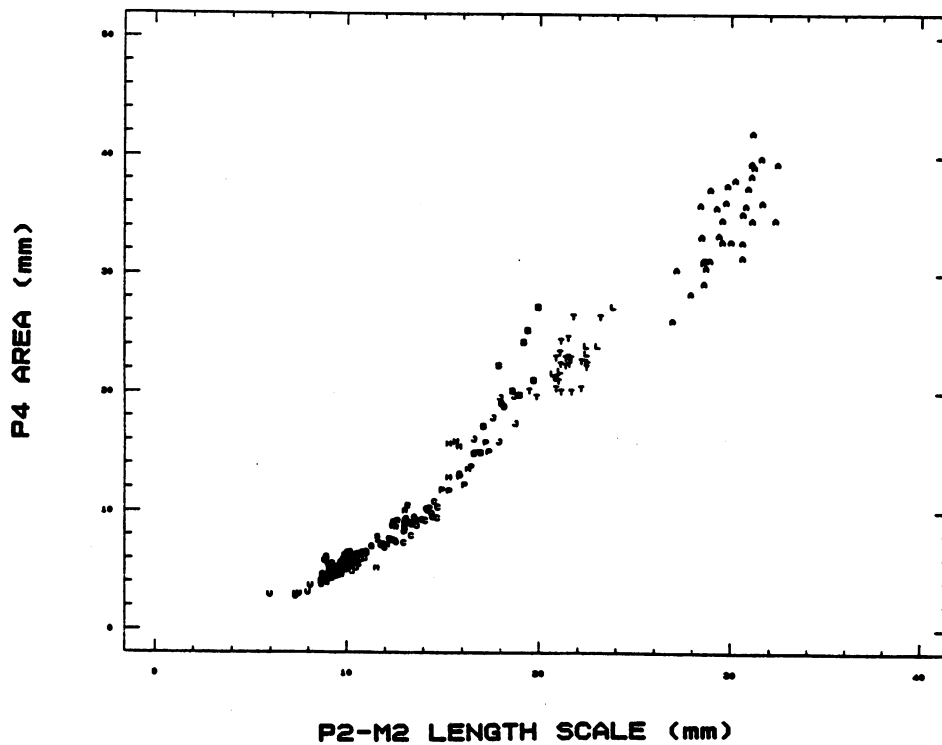
Figure 5. The y-axis represents the M-D lengths of $P^2$-$M^2$ divided by the occlusal area of $M^1$-$M^2$. The logarithmic profile indicates decreased variation in this index from callitrichines through atelines, especially *Alouatta*.
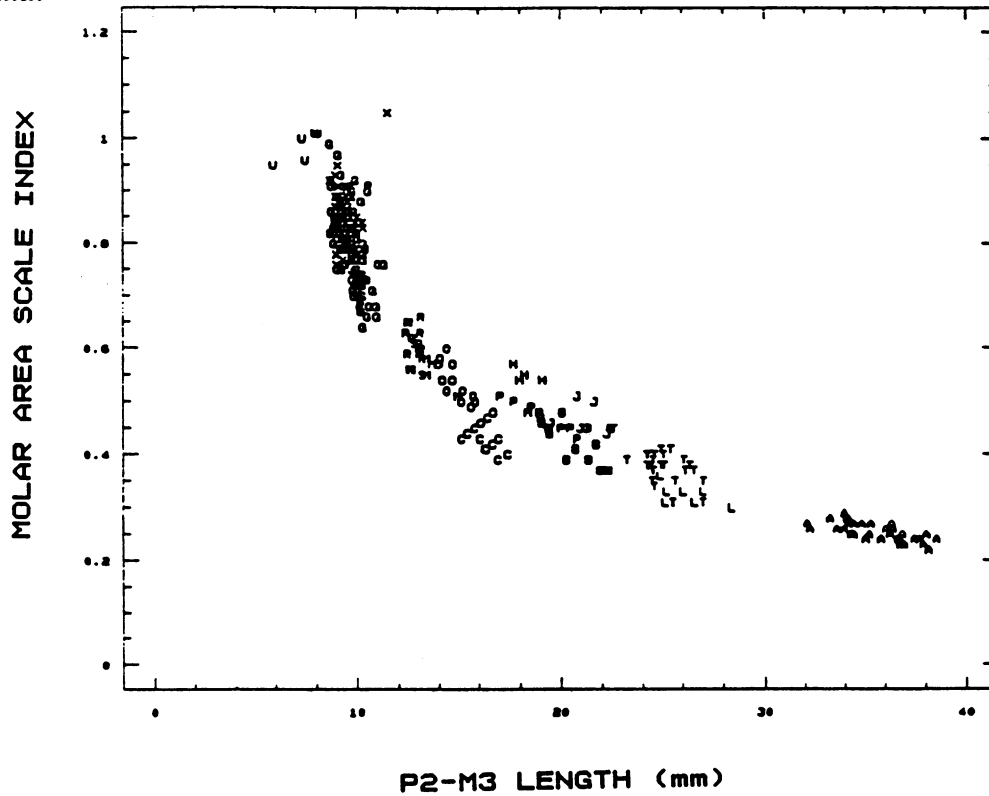


Figure 6. The y-axis represents the M-D lengths of $P^2$-$M^2$ divided by the occlusal area of $P^3$-$P^4$. The logarithmic profile is similar but not as uniform as in Figure 5.
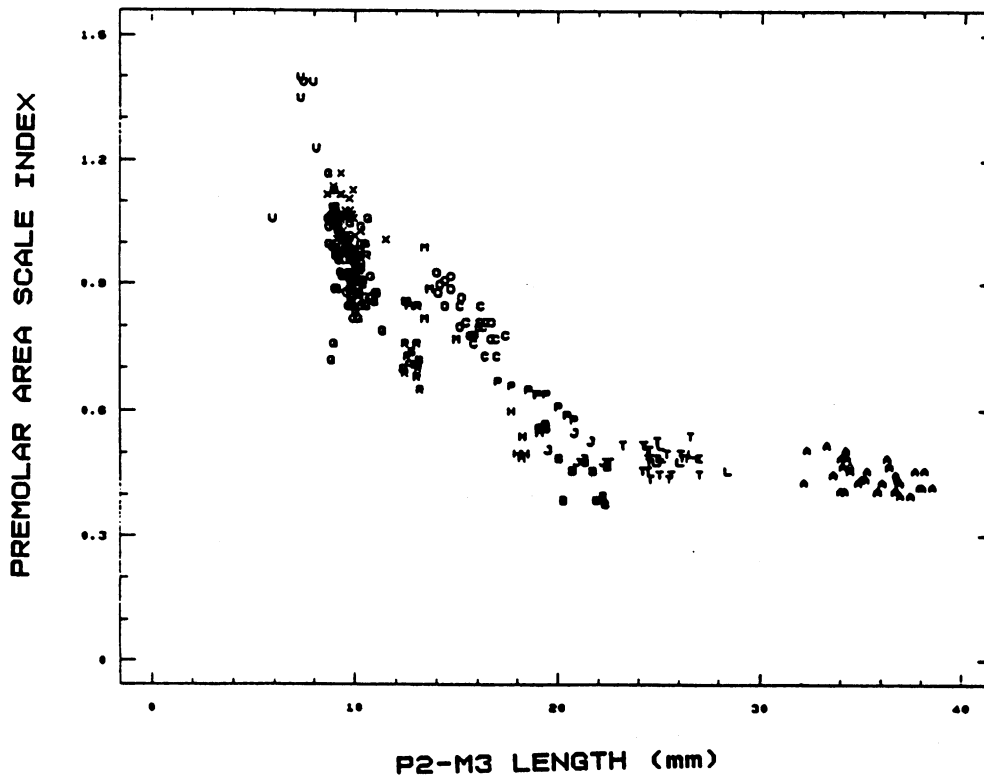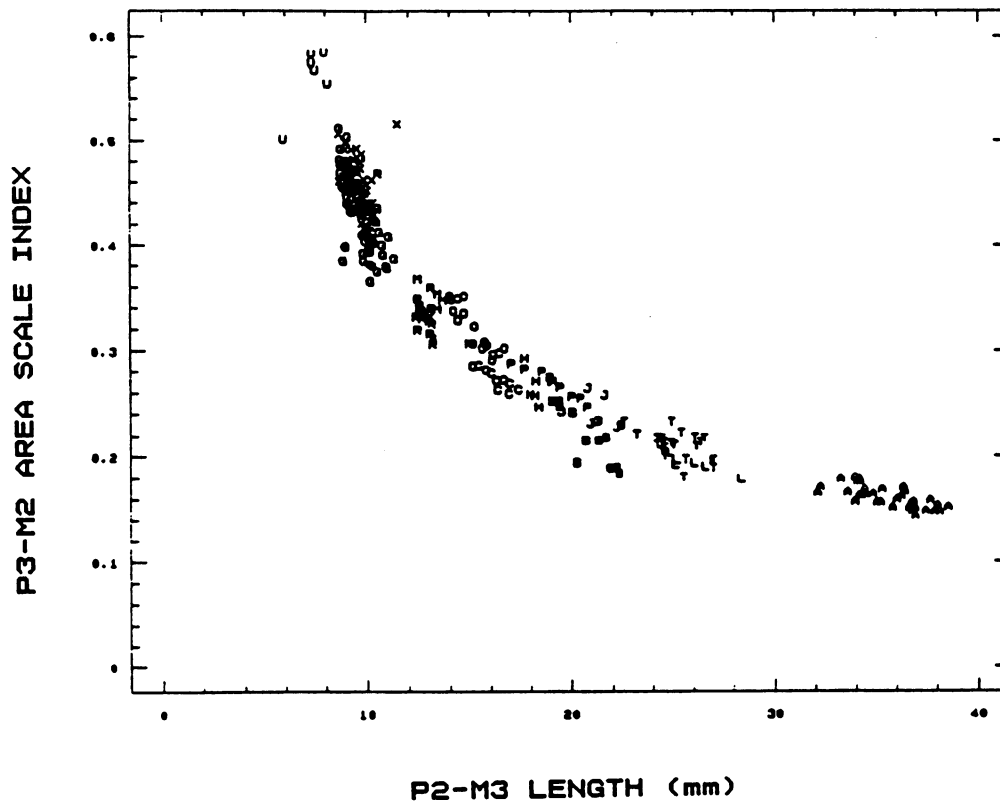
Figure 7. This regression combines the indices of Figures 5 and 6 and demonstrates their independence from one another by maintaining the same logarithmic profile.



## DISCUSSION

The evolutionary study of fossil and living New World monkeys is experiencing strong growth and development (see Fleagle and Rosenberger 1990). A remarkable diversity of fossil platyrrhines has been recovered in the last five years (Setoguchi and Rosenberger 1985, 1987; Luchterhand *et al.* 1986; Fleagle *et al.* 1987; Kay *et al.* 1987; Kay 1989; Hartwig *et al.* 1990). Until recently, documentary work on dentition (Orlosky and Swindler 1975; Swindler 1976; Hershkovitz 1977) has been largely descriptive rather than comparative, and comparative studies (Rosenberger 1979) have been largely nonmetric. This is because size based metric analyses can say nothing about morphology and very little about function, the two principal variables in dental studies today. As demonstrated here, however, metric analyses can illustrate important trends in the masticatory apparatus and in some cases serve as taxonomic indicators.

The correlation between premolar ($P^{3-4}$) and

lengthen, but a threshold appears to have been reached in large-bodied atelines (*Alouatta, Ateles*).

molar ($M^{1-2}$) area is strong for platyrrhines as a whole (r = .97), as expected. Along this regression (Figure 1), pithecines *(Aotus, Callicebus, Pithecia, Chiropotes, Cacajao)* with broadly similar molar areas are diagnostically separated by different premolar areas. Hypotheses of a close *Aotus - Callicebus* phylogenetic relationship (Rosenberger 1981) are strengthened by the overlapping ranges and similar regressions of these two genera (Figures 1 and 2).

Callitrichines lack hypocones on upper molars, so areal calculations based on (M-D) x (B-L) dimensions are consequently higher than the actual occlusal surface area. This increases the r-value for platyrrhine-wide comparisons, but the slope of the regression for callitrichines would be the same in either case because all callitrichines would lose roughly the same amount of relative occlusal area. One conclusion to draw from the metric indices as they are presented here is that dental reduction in callitrichines has been primarily nonmetric in distinction (Plavcan and Gomez 1990). In premolar comparisons (Figures 3 and 4), which are free of the problems associated with hypocone loss, callitrichines, including *Cebuella, Callimico* and *Leontopithecus*, fall consistently along the platyrrhine regression. As Figures 5 and 6 suggest, there may in fact be no

metrically diagnostic postcanine features of the callitrichine radiation.

The radiation of large-bodied atelines, such as *Alouatta* and *Ateles,* is characterized by the very trend that is lacking in callitrichines. Figures 5 and 6 indicate that ateline premolar and molar area are tightly related to the length of the postcanine toothrow. More importantly, from a proportional point of view, strict thresholds of .2-.3 apply to the toothrow length/molar area ratio (Figure 5), and .4-.5 to the premolar ratio (Figure 6) as the toothrow length increases. Some of this decreasing variation can be explained as a natural logarithmic consequence of the y-axis index. As tooth area increases in large-bodied platyrrhines, the denominator of the y-axis variable increases and so the difference in the resulting fraction is logarithmically expressed. Nonetheless, for individuals with similar postcanine toothrow lengths, the difference in variation between callitrichines and atelines reflects the nature of selection on body size decrease in the former and tooth size increase in the latter.

Figure 7 represents a combination of Figures 5 and 6, in which the vertical axis now indicates the summed $P^3$-$M^2$ area. The four principal postcanine teeth as a battery logarithmically increase in width as length increases, rather than one variable (length) being directionally dependent upon a component of the other (premolars or molars).

## CONCLUSION

This analysis is part of a larger treatment of platyrrhine morphological variation. No attempts to infer dental function or possible phylogenetic relationships are made here because the comparisons are exclusively size-based. The value of such comparisons lies in their usefulness for discerning trends in adaptive radiations and for tracking patterns within and across taxa. The regressions illustrated in this study show that a number of taxonomic markers can be demonstrated through the use of metric indices, and they underscore the need for further data collection and analyses. A better understanding of the rich diversity of fossil platyrrhines from the Miocene depends upon an understanding of the metric relationships among the living forms.

## ACKNOWLEDGMENTS

## REFERENCES CITED

Fleagle, John G. (1988) *Primate Adaptation and Evolution.* New York: Academic Press.

Fleagle, John G., D.W. Powers, G.C. Conroy and J.P. Watters (1987) New fossil platyrrhines from Santa Cruz Province, Argentina. *Folia Primatologica* 48:65-77.

Fleagle, John G. and A.L. Rosenberger (1990) Paleontology of New World monkeys: Guest editors' introduction. *Journal of Human Evolution* 18:1-7.

Hartwig, Walter C., A.L. Rosenberger and T. Setoguchi (1990) New fossil platyrrhines from the late Oligocene and middle Miocene. *American Journal of Physical Anthropology* 81:237.

Hershkovitz, Phillip K. (1977) *Living New World Monkeys (Platyrrhini), with an Introduction to the Primates,* volume 1. Chicago: University of Chicago Press.

Kay, Richard F. (1989) A new small platyrrhine from the Miocene of Colombia and the phyletic position of the callitrichines. *American Journal of Physical Anthropology* 78:251.

Kay, Richard F., R.H. Madden, J.M. Plavcan, R.L. Cifelli and J.G. Diaz (1987) *Stirtonia victoriae,* a new species of Miocene Colombian primate. *Journal of Human Evolution* 16: 173-196.

Luchterhand, Kubet, R.F. Kay and R.H. Madden (1986) *Mohanamico hershkovitzi,* gen. et. sp. nov., un primate du Miocene moyen d'Amerique du Sud. *Compte Rendus Academie Sciences,* series 3 303:1753-1758.

Orlosky, Frank J. and D.R. Swindler (1975) Origins of New World monkeys. *Journal of Human Evolution* 4:77-83.

Plavcan, J.M. and A.M. Gomez (1990) Dental scaling and callitrichids. *American Journal of Physical Anthropology* 81:282.

Rosenberger, Alfred L. (1979) *Phylogeny, Evolution and Classification of New World Monkeys (Platyrrhini, Primates).* Ann Arbor: University Microfilms.

Rosenberger, Alfred L. (1981) Systematics: The higher taxa. *In* A.F. Coimbra-Filho and R.A. Mittermeir (eds.), *Ecology and Behavior of Neotropical Primates.* Rio de Janeiro: Academia Brasiliera de Ciencias. Pp.9-27.

Rosenberger, Alfred L., M. Takai, W.C. Hartwig, T. Setoguchi and N. Shigehara (in press) Dental variability in *Saimiri* and the taxonomic status of *Neosaimiri,* an early squirrel monkey from La Venta, Colombia. *International Journal of Primatology.*

Setoguchi, Tak and A.L. Rosenberger (1985) Miocene marmosets: First fossil evidence. *International Journal of Primatology* 6:615-625.

Setoguchi, Tak and A.L. Rosenberger (1987) A fossil owl monkey from La Venta, Colombia. *Nature* 326:692-694.

Sussman, Robert W. and W.G. Kinzey (1984) The ecological role of the Callitrichidae. *American Journal of Physical Anthropology* 64(4):419-449.

Swindler, Daris R. (1976) *Dentition of Living Primates.* London: Academic Press.