



Jaw Morphology and Function in Living and Fossil Old World Monkeys

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This allometric investigation on a sample of 29 cercopithecine and 22 colobine taxa augments the data and implications of prior work on subfamilial variation in mandibular form and function in recent Cercopithecidae. To increase the size range encompassed by living cercopithecines and colobines, I included many of the larger-bodied fossil specimens. These analyses serve to fill a gap in our understanding of size-related changes in masticatory function and symphyseal morphology and curvature in extant and extinct Old World monkeys. Results of subfamilial scaling comparisons indicate that for a given jaw length, colobines possess significantly more robust corpora and symphyses than those of cercopithecines, especially at smaller sizes. Following from previous work, the most plausible explanation for why the subfamilies differ in relative corporeal and symphyseal dimensions is that colobine mandibles experience elevated loads and greater repetitive loading during mastication due, on average, to processing a diet of tough leaves and/or seeds. Although colobines have relatively larger symphyses, subfamilial analyses of symphyseal curvature demonstrate that they evince less symphyseal curvature vis-à-vis cercopithecines of a common size. Moreover, both subfamilies exhibit similar allometric changes in the degree of curvature, such that larger-bodied Old World monkeys have more curved symphyses than those of smaller taxa. Subfamilial scaling analyses also indicate that colobines possess a shorter M^2 bite-point length relative to masseter lever-arm length, but not versus temporalis lever-arm length. Thus, as compared to cercopithecines, colobines can recruit

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less masseter-muscle force to produce similar bite forces during mastication. In both clades, M^2 bite-point length scales with positive allometry relative to masseter lever-arm length, such that larger species are less efficient at generating molar bite forces. This seems especially important due to the lack of subfamily difference in M^2 bite-point:temporalis lever-arm scaling (which is isometric across cercopithecids). A consideration of extinct cercopithecids indicates that many of the large-bodied papionins have more robust corpora, due perhaps to a diet which was of similar toughness to that of extant and extinct colobines. However, the biomechanical arrangements of the masseter and temporalis in all but one fossil cercopithecine and all of the fossil colobine specimens are much as predicted for a subfamilial member of its skull size. That most large-bodied papionins with tougher diets nonetheless maintain a less efficient jaw-muscle configuration may be due to stronger offsetting selection for increased relative canine size and gape.

KEY WORDS: skull form, masticatory biomechanics, allometry, scaling, fossils

INTRODUCTION

Over the past two decades, there has been a vast increase in the amount of comparative, experimental and systematic research on the craniofacial skull of Old World monkeys (Ravosa and Profant, 1996). Given the presence of differences in craniodental form between cercopithecines and colobines, this natural experiment has attracted considerable interest in the functional and evolutionary significance of subfamilial patterns of variation (Delson, 1975; Hylander, 1975, 1979b; Walker and Murray, 1975; Kay, 1978; Kay and Hylander, 1978; Bouvier, 1986a,b; Happel, 1988; Ravosa, 1988, 1990, 1991b; Lucas and Teaford, 1994; Ravosa and Shea, 1994). Of the various morphological approaches, *in vivo* analyses have been especially important for characterizing dynamic functional determinants of skull form in cercopithecids and other primates (Luschei and Goodwin, 1974; Hylander, 1979a,b, 1981, 1984, 1985; Hylander and Johnson, 1985, 1994; Hylander *et al.*, 1987, 1992, 1996; Ravosa, 1996c). To provide an experimental context for interpreting masticatory biomechanics and mandibular form in Cercopithecidae, I summarize *in vivo* data on primate jaw-loading regimes during unilateral mastication.

Primate bone-strain data demonstrate that the balancing-side mandibular corpus experiences sagittal bending during unilateral mastication (Hylander, 1979a,b, 1981, 1984; Hylander *et al.*, 1996). Sagittal bending of the corpus, in turn, causes dorsoventral shear stress at the mandibular symphysis. Both these jaw-loading regimes are proportional to the force generated by the balancing-side jaw adductors (Hylander, 1979a,b, 1981, 1984; Hylander *et al.*, 1996; Ravosa, 1996c).

Experimental analyses also indicate that the anthropoid mandibular symphysis and corpus experience lateral transverse bending—wishboning—during mastication (Hylander, 1984, 1985). This wishboning stress is due to a laterally directed component of jaw-muscle force on the balancing side and a laterally directed component of bite force, and perhaps muscle force, on the working side. Anthropoid mandibular wishboning is due mainly to pronounced activity of the balancing-side deep-masseter muscle at the terminus of the masticatory power stroke (Hylander *et al.*, 1987, 1996; Hylander and Johnson, 1994; Ravosa, 1996c).

Theoretical, interspecific, and ontogenetic work in cercopithecines shows that allometric changes between mandibular length and breadth importantly affect the degree of symphyseal curvature and thus the distribution and amount of wishboning stress at the symphysis (Hylander, 1984, 1985; Vinyard, 1996). As wishboning results in high strain levels along the inner surface of the symphysis, increased wishboning stress is best resisted by increasing the labiolingual width of the symphysis, *i.e.*, the inferior transverse torus (Hylander, 1984, 1985). Moreover, as the symphysis functions as a curved beam during such lateral transverse bending, its inner or lingual surface experiences high stress concentrations.

Given that jaw length is positively allometric relative to jaw breadth in cercopithecines, and assuming that all such monkeys experience wishboning, symphyseal width scales positively to counter size-related increases in wishboning due to greater symphyseal curvature in larger taxa with relatively narrow and elongate jaws (Hylander, 1985). In fact, allometric changes in wishboning stresses due to greater symphyseal curvature may be quite pervasive, as jaw length scales positively versus jaw breadth in interspecific and ontogenetic analyses of a wide variety of primate and non-primate mammals (Radinsky, 1981, 1984; Shea, 1983; Greaves, 1985; Hylander, 1985; Shea *et al.*, 1990; Ravosa, 1991a,b, 1992, 1996a, this study; Ravosa and Ross, 1994; Ravosa and Profant, 1996; Vinyard, 1996).

Primate *in vivo* studies further demonstrate that both halves of the mandibular corpus are twisted about their long axes during unilateral mastication (Hylander, 1979a, 1981). Axial torsion of the corporeal elements is due to the overall jaw-muscle force resultants, both of which lie lateral to the mandible on each side, as well as the working-side bite force. Axial twisting everts the lower borders and inverts the upper borders of both corporeal components, such that the symphysis is bent vertically (Hylander, 1979b, 1981). This symphyseal bending, in turn, causes compression along the alveolar surface of the symphysis and tension along its basal aspect.

Investigations of jaw-muscle activity in papionins indicate that chewing and biting of tougher foods are accompanied by absolutely greater jaw-muscle electromyographic (EMG) activity (both longer duration and higher

force amplitudes) and relatively higher levels of balancing-side jaw-muscle force recruitment (Luschei and Goodwin, 1974; Hylander and Johnson, 1985, 1994; Hylander *et al.*, 1992). A more obdurate diet also increases the likelihood of fatigue failure of the cortical bone along the corpus and symphysis due to greater repetitive or cyclical loading (Hylander, 1979a,b; Bouvier and Hylander, 1981). In terms of the functional relationship between jaw form and jaw-loading regimes, taxa like colobines which routinely masticate a tough diet should possess: (1) vertically deeper corpora due to greater sagittal bending, (2) vertically deeper and labiolingually thicker symphyses to counter increased dorsoventral shear due to greater sagittal bending, (3) labiolingually wider symphyses related to increased wishboning, and (4) buccolingually thicker corpora to resist greater axial torsion due to elevated repetitive loading (Demes *et al.*, 1984; Hylander, 1985, 1988; Bouvier, 1986a,b; Daegling, 1989, 1992, 1993; Ravosa, 1991a,b, 1992, 1996a; Cole, 1992; Daegling *et al.*, 1992; Jablonski, 1993; Ravosa and Hylander, 1994; Ravosa and Ross, 1994; Takahashi and Pan, 1994; Pan *et al.*, 1995; Antón, 1996; Ravosa and Profant, 1996; Vinyard, 1996).

Considered more broadly, as leaf-eating and seed-eating requires elevated jaw-muscle activity and a greater amount of the day processing food, extinct and extant colobines might also have developed a more efficient arrangement between postcanine bite points and jaw-muscle lever arms (Hylander, 1979b; Ravosa, 1988, 1990). Dietary-related variation in musculoskeletal form between close relatives has been noted in diverse primate clades such as archaeolemurines (Tattersall, 1973), australopithecines (DuBrul, 1977), capuchins (Cole, 1992), gelada baboons (Jablonski, 1993), and macaques (Antón, 1996).

Although Bouvier (1986a) provides an especially informative study of subfamilial differences in cercopithecoid corporeal and condylar scaling, similar comparisons of symphyseal allometry are unavailable. Such data are particularly relevant to address issues related to wishboning of the symphysis during molar biting and chewing (Hylander, 1985). While the allometry of cercopithecine symphyseal curvature and wishboning stress are well characterized (Hylander, 1985), this relationship is undescribed for colobines. Additionally, there is no analysis of masticatory function and jaw scaling in any fossil species of the Cercopithecidae. The inclusion of taxa from as early as the Late Miocene facilitates an assessment of the relative antiquity of subfamilial variation in skull form and function. From an allometric standpoint, the larger-bodied extinct taxa broaden the morphospace encompassed by extant subfamilial members. This perspective facilitates an investigation of whether jaw proportions and jaw-muscle efficiency in an extinct species, especially larger-bodied monkeys, are as

predicted for a colobine or cercopithecoine of its size or whether the shape of the maxillomandibular apparatus is specially related to diet.

MATERIALS AND METHODS

Samples

At least one species is included from each subgenus of extant Old World monkey (Table I). This results in perhaps the broadest amount of size variation in each subfamily, ranging from *Miopithecus talapoin* to *Theropithecus brumpti* in the Cercopithecoinae and from *Procolobus verus* to *Paracolobus chemeroni* in the Colobinae. Recent taxa are typically represented by equal numbers of wild-caught adult males and females derived mostly from one subspecies. The cercopithecoine sample consists of 160 adults from 29 species and 13 genera, of which there are 6 extinct papionin taxa. The colobine sample contains 118 adults from 22 species and 15 genera, of which 6 fossil taxa are included.

Measurements

I recorded metric data with digital calipers accurate to 0.1 mm. Based on preservation, I took up to nine linear dimensions on each adult specimen: mandibular corporeal height and width at M_2 , symphyseal height and width, jaw (palate) length, jaw (palate) breadth at M^1 , masseter and temporalis lever-arm lengths, and M^2 bite-point length (cf., Ravosa, 1988, 1990, 1991a, 1996a,b; Ravosa and Hylander, 1994; Ravosa and Profant, 1996). Following Hylander (1985), symphyseal curvature is assessed from the allometry of jaw length versus jaw breadth, such that a higher ratio indicates a narrower and more elongate jaw and, thus presumably, a more curved symphysis. I examined masticatory efficiency via a consideration of the scaling of M^2 bite-point length versus masseter and temporalis lever-arm lengths, such that lower ratios depict more efficient masseter and temporalis arrangements in which larger bite forces are produced for equivalent levels of muscular force (Ravosa, 1988, 1990).

Statistical Analyses

I performed all statistical analyses on natural logs of species means. Least-squares bivariate regressions ($p < 0.01$) are calculated to describe scaling patterns at the subfamilial level; bivariate correlations are figured

as well. I used least-squares regression because variation in jaw length is believed to have a direct influence on mandibular robusticity. In addition, as the correlations are quite high within each subfamily in all but one case, this minimizes the likelihood that scaling results would differ using alternative bivariate regression methods (Table II).

Table I. Old World Monkey Craniomandibular Samples

Cercopithecinae (29 species, 13 genera; $n = 160$)
Cercopithecini (10 species, 4 genera; $n = 60$)
<i>Cercopithecus aethiops</i> ($n = 6$)
<i>Cercopithecus ascanius</i> ($n = 6$)
<i>Cercopithecus campbelli</i> ($n = 6$)
<i>Cercopithecus cephus</i> ($n = 6$)
<i>Cercopithecus lhoesti</i> ($n = 6$)
<i>Cercopithecus mitis</i> ($n = 6$)
<i>Cercopithecus mona</i> ($n = 6$)
<i>Erythrocebus patas</i> ($n = 6$)
<i>Miopithecus talapoin</i> ($n = 6$)
<i>Allenopithecus nigroviridis</i> ($n = 6$)
Papionini (19 species, 9 genera, $n = 100$)
<i>Macaca fascicularis</i> ($n = 12$)
<i>Macaca hecki</i> ($n = 5$)
<i>Macaca nigra</i> ($n = 6$)
<i>Macaca nemestrina</i> ($n = 6$)
<i>Macaca sylvanus</i> ($n = 5$)
<i>Macaca thibetana</i> ($n = 4$)
<i>Paradolichopithecus arvernensis</i> ($n = 2$) ^a
<i>Theropithecus gelada</i> ($n = 8$)
<i>Theropithecus oswaldi</i> ($n = 8$) ^a
<i>Theropithecus brumpti</i> ($n = 3$) ^a
<i>Theropithecus baringensis</i> ($n = 1$) ^a
<i>Cercocebus torquatus</i> ($n = 6$)
<i>Lophocebus albigena</i> ($n = 6$)
<i>Parapapio jonesi</i> ($n = 4$) ^a
<i>Papio anubis</i> ($n = 6$)
<i>Papio hamadryas</i> ($n = 4$)
<i>Dinopithecus ingens</i> ($n = 4$) ^a
<i>Mandrillus leucophaeus</i> ($n = 4$)
<i>Mandrillus sphinx</i> ($n = 6$)
Colobinae (22 species, 15 genera, $n = 118$)
Colobina (8 species, 6 genera, $n = 31$)
<i>Cercopithecoides williamsi</i> ($n = 5$) ^a
<i>Rhinocolobus turkanensis</i> ($n = 1$) ^a
<i>Paracolobus chemeroni</i> ($n = 1$) ^a
Colobine species "A" ($n = 1$) ^a
<i>Colobus guereza</i> ($n = 6$)
<i>Piliocolobus badius</i> ($n = 6$)
<i>Piliocolobus rufomitatus</i> ($n = 6$)
<i>Procolobus verus</i> ($n = 5$)
Presbytina (12 species, 7 genera, $n = 76$)
<i>Presbytis frontata</i> ($n = 6$)

Presbytis melalophos (n = 6)
Presbytis potenziani (n = 6)
Presbytis rubicunda (n = 6)
Semnopithecus entellus (n = 6)
Trachypithecus johnii (n = 6)
Trachypithecus cristata (n = 6)
Trachypithecus obscura (n = 5)
Nasalis larvatus (n = 10)
Simias concolor (n = 6)
Pygathrix nemaus (n = 7)
Rhinopithecus roxellana (n = 6)
 Incertae Sedis (2 species, 2 genera, n = 11)
Mesopithecus pentelici (n = 10)^a
Dolichopithecus ruscinensis (n = 1)^a

^aExtinct.

Table II. Regression Analyses for Extinct and Extant Cercopithecinae and Colobinae

Versus jaw length ^a	N	y-Intercept	Slope	95% CI	
M ₂ corporeal height ^b	29	-1.148	1.018	±0.057	0.960
	22	1.376	0.741	±0.059	0.942
M ₂ corporeal width ^c	29	-1.135	0.921	±0.054	0.957
	22	0.571	0.736	±0.068	0.924
Symphyseal height ^b	29	-1.329	1.082	±0.031	0.989
	22	1.728	0.734	±0.056	0.947
Symphyseal width ^b	29	-3.393	1.224	±0.062	0.967
	22	-0.373	0.875	±0.083	0.920
Jaw length versus jaw breadth ^d	29	-4.761	1.622	±0.075	0.973
	22	-6.366	1.794	±0.155	0.933
M ² bite-point versus masseter lever arm ^d	29	-1.359	1.183	±0.042	0.983
	19	-1.296	1.162	±0.066	0.973
M ² bite-point versus temporalis lever arm ^e	25	0.758	0.993	±0.083	0.928
	18	2.897	0.712	±0.096	0.881

^aCercopithecine least-squares regression analyses are indicated on the first line, whereas colobine least-squares regression analyses are indicated on the second line.

^bSignificant slope and y-intercept differences between subfamilies (ANCOVA, $p < 0.05$), with colobines possessing a regression line transposed above, and with a lower slope than, the cercopithecine line.

^cSignificant y-intercept difference between subfamilies (ANCOVA, $p < 0.05$), with the colobine regression line transposed above the cercopithecine line.

^dSignificant y-intercept difference between subfamilies (ANCOVA, $p < 0.05$), with the colobine regression line transposed below the cercopithecine line.

^eNo significant slope or y-intercept difference between subfamilies (ANCOVA, $p > 0.05$). In such cases, functional inferences should be based on the familial-level scaling trajectory (N = 43; y-intercept = 1.064, slope = 0.951, CI = ± 0.065, $r = 0.916$). Across cercopithecids, neither the least-squares slope (0.951) nor the reduced major-axis slope (1.038) differs significantly from isometry (1.000).

By necessity, a scaling analysis of mandibular form and function should account for the size of a bony cross section relative to its structural length, which in a bending loading regime approximates the length of the moment arm. Given the potential for taxonomic differences in jaw length:body size scaling patterns (Bouvier, 1986a; Biknevičius and Ruff, 1992), mandibular length is often used as the independent variable in studies of jaw biomechanics and scaling (Hylander, 1979b, 1985, 1988; Demes *et al.*, 1984; Bouvier, 1986a,b; Daegling, 1989, 1992; Biknevičius and Ruff, 1992; Daegling *et al.*, 1992; Vinyard, 1996). In order to analyze jaw robusticity in extinct taxa with fragmentary mandibular remains, palatal length is used as a measure of jaw length (Ravosa, 1991a, 1996a,b; Ravosa and Hylander, 1994; Ravosa and Profant, 1996). In primates, palatal length is a suitable surrogate for mandibular length since both these variables are highly correlated and scale with isometry (Ravosa, 1996b). As I employ allometry primarily as a "criterion of subtraction," analysis of covariance (ANCOVA, $p < 0.05$) is used to test for subfamilial differences in patterns of variation in mandibular size and shape.

RESULTS

In extant and extinct cercopithecines and colobines, correlation coefficients for mandibular corporeal and symphyseal measures versus jaw length are highly significant as are the remaining bivariate comparisons (Table II, Figs. 1–9). In cercopithecines, least-squares slopes of jaw cross-sectional dimensions versus jaw length are positively allometric for symphyseal height and width, isometric for corporeal height, and negatively allometric for corporeal width. In colobines, all corporeal and symphyseal dimensions scale with negative allometry, which means that larger-bodied colobines have relatively diminutive jaws as compared to smaller species. In both subfamilies, jaw length is strongly positively allometric versus jaw breadth (Table II), which indicates that the symphyseal region is more curved in larger taxa because the mandible is narrower and more elongate (Hylander, 1985; Vinyard, 1996). Moreover, in each subfamily, M^2 bite-point length scales positively versus masseter lever-arm length, which means that larger members have less efficient masseter arrangements during mastication. This differs from the family-level pattern of isometry between M^2 bite-point and temporalis lever arm (Table II).

Intersubfamilial ANCOVAs of extant and fossil cercopithecoid jaw-scaling patterns indicate significant y-intercept differences for all four mandibular cross-sectional measures, with the colobine lines consistently transposed above those for cercopithecines (Table II, Figs. 1–5 and 7). This

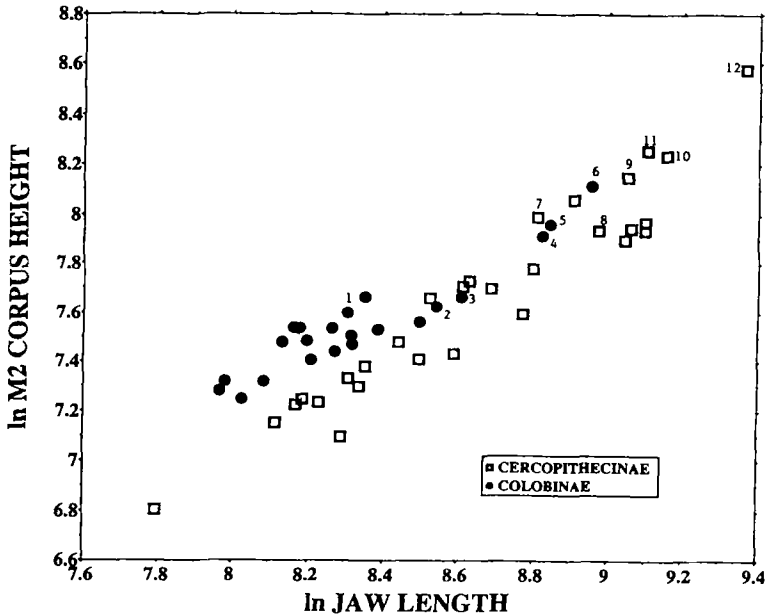


Fig. 1. A plot of $\ln M_2$ corporeal height versus \ln jaw length in 29 cercopithecoidea species (squares) and 22 colobine species (circles). ANCOVA indicates that the colobine regression line for corporeal height is significantly transposed above that for cercopithecoidea. This supports the hypothesis that leaf- and seed-eating primates often possess more robust jaws than frugivorous and omnivorous taxa due to greater sagittal bending of the balancing-side mandibular corpus during unilateral mastication. Note that extinct papionins, all of which have or are inferred to have had tougher diets, also plot at the upper end of the cercopithecoidea scatter much like extant and extinct colobines. 1, *Mesopithecus pentelici*; 2, Colobine species "A"; 3, *Cercopithecoidea williamsi*; 4, *Dolichopithecus ruscinensis*; 5, *Rhinocolobus turkanensis*; 6, *Paracolobus chemeroni*; 7, *Parapapio jonesi*; 8, *Dinopithecus ingens*; 9, *Paradolichopithecus arvernensis*; 10, *Theropithecus baringensis*; 11, *T. oswaldi*; 12, *T. brumpti*.

means that at a common jaw length, colobines have more robust corpora (Bouvier, 1986a) and symphyses than those of cercopithecoidea. In comparisons of symphyseal height and width and corporeal height, the colobine regression lines also evince significantly lower slopes than those for cercopithecoidea, thus subfamilial differences in relative jaw proportions are especially marked between smaller-bodied taxa.

Subfamilial ANCOVAs based on extant taxa indicate a slightly different pattern in terms of regression slope values. Only in subfamilial

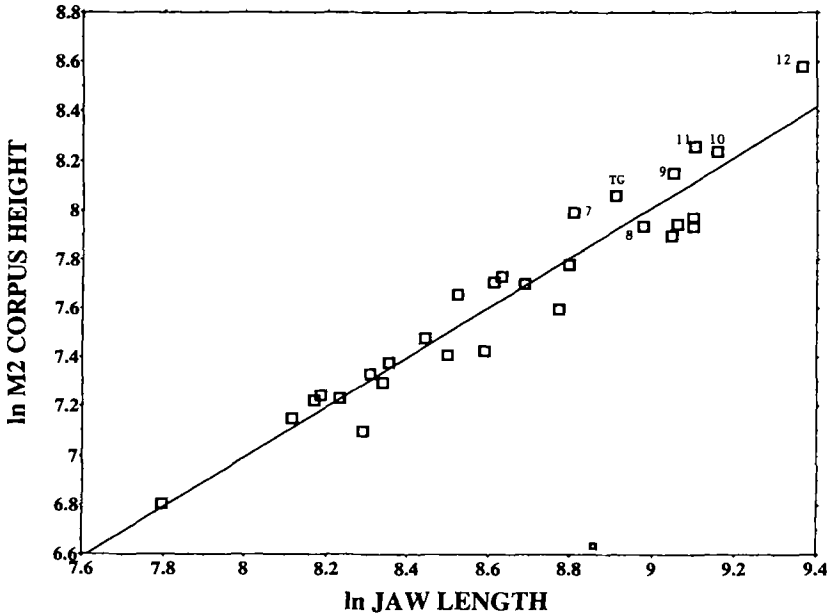


Fig. 2. A plot of $\ln M_2$ corporeal height versus \ln jaw length in 29 cercopithecines. Note, again, that *Parapapio*, *Paradolichopithecus*, and extinct *Papio*, as well as living and fossil *Theropithecus*, all of which have or are inferred to have had tougher diets, fall at the upper end of the cercopithecine species range. This supports the hypothesis that folivorous and grammivorous primates often have more robust jaws than those of frugivorous and omnivorous taxa due to greater sagittal bending of the balancing-side mandibular corpus during mastication. Fossil key as in the legend to Fig. 1. TG, *T. gelada*.

comparisons of symphyseal height are slopes significantly different, with colobines having a lower value. As found in analyses including all taxa (Table II), colobine regression lines for corporeal and symphyseal height and width are significantly transposed above those for cercopithecines. Extant-only ANCOVAs of jaw length versus jaw breadth and M^2 bite-point length versus masseter lever-arm length demonstrate that the cercopithecine regression line is transposed above that for colobines in both cases. As observed with larger samples, there is no subfamilial difference in the scaling of M^2 bite-point length versus temporalis lever-arm length.

In subfamilial comparisons of jaw length versus jaw breadth, the cercopithecine regression line is transposed above that for colobines (Table II, Fig. 6). Therefore, at a similar jaw breadth, cercopithecines have more elongate jaws and, in turn, greater symphyseal curvature than those of colo-

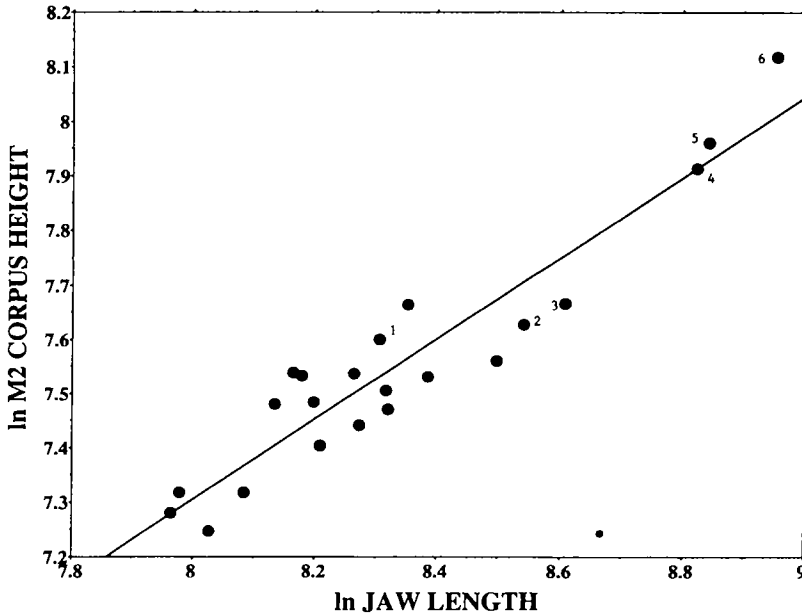


Fig. 3. A plot of $\ln M_2$ corporeal height versus \ln jaw length in 22 colobines. Note that *Mesopithecus* and, especially, *Paracolobus* both fall at the upper end of the colobine scatter, whereas *Cercopithecoides* and Colobine species "A" plot below the scaling trajectory. Fossil key as in the legend to Fig. 1.

bines. Finally, scaling analyses indicate that, as compared to cercopithecines, colobines have shorter M^2 bite-point lengths relative to masseter (Fig. 8), but not temporalis (Fig. 9), lever-arm length (Table II). Thus, colobines can recruit less masseter-muscle force to generate similar bite forces during mastication (Hylander, 1979b; Ravosa, 1990). Fossil species typically follow the allometric trends noted for recent subfamilial members.

Allometric analyses also show that fossil papionins typically possess more robust mandibles much like extant and extinct colobines (Figs. 1, 2, 4, 5, and 7). This suggests that such taxa may have had a similarly obdurate diet. While some fossil colobines have more robust jaws than those of other subfamilial members, this pattern is not characteristic of all such monkeys (Figs. 1, 3–5, and 7). The fact that larger-bodied extinct papionins generally lie above the cercopithecine regression lines may explain why subfamilial jaw-scaling trajectories converge at larger sizes, i.e., there is an uneven distribution of extinct taxa at one end of the size spectrum. As noted earlier, only one slope difference is significant in subfamilial comparisons using ex-

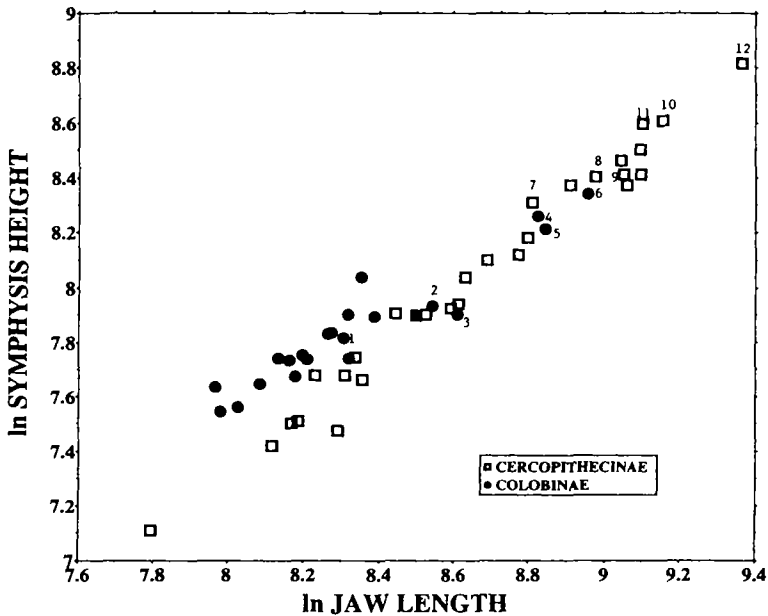


Fig. 4. A plot of \ln symphyseal height versus \ln jaw length in 29 cercopithecines (squares) and 22 colobines (circles). Note that colobine symphyseal dimensions are typically located above those for cercopithecines, thus supporting the hypothesis that folivorous and graminivorous primates like colobines experience greater dorsoventral shear than taxa with softer diets. Fossil key as in the legend to Fig. 1.

tant species (symphyseal height). The distribution of fossil monkeys in analyses of symphyseal curvature and M^2 bite-point:muscle lever-arm scaling normally follows the allometric differences observed for recent clade members (Figs. 6, 8, and 9).

DISCUSSION

In a larger cercopithecoid sample including a dozen fossil species, jaw-scaling analyses indicate that the folivorous and graminivorous colobines have relatively deeper corpora in the molar region than cercopithecines (Table II, Fig. 1). This subfamilial difference corresponds to previous comparative analyses of extant Old World monkeys and is due likely to greater sagittal bending of the colobine balancing-side corpus during the mastication of a tougher diet (Hylander, 1979b; Bouvier, 1986a). Interestingly,

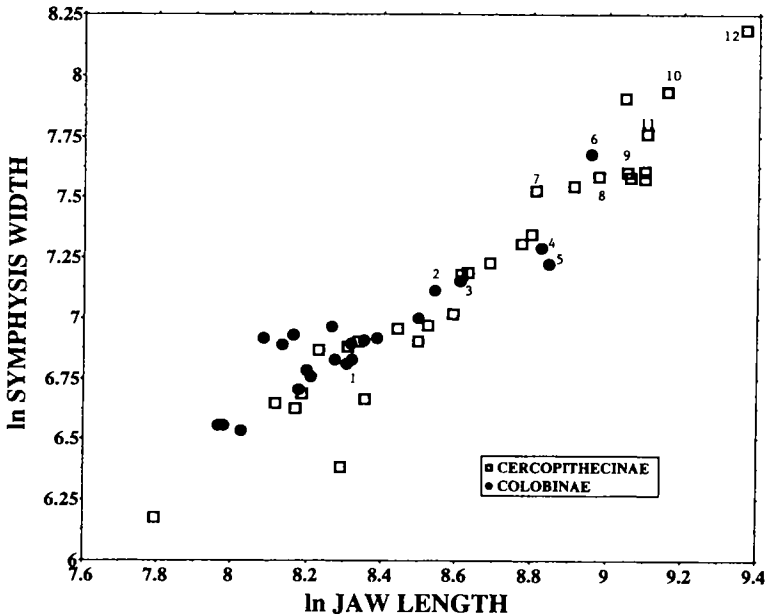


Fig. 5. A plot of ln symphyseal width versus ln jaw length in 29 cercopithecoidea (squares) and 22 colobines (circles). Colobine symphyseal means again tend to plot above those for cercopithecoidea, thus suggesting that, as a group, they likely experience greater wishboning. This pattern is surprising given that colobines show a lesser degree of symphyseal curvature (Fig. 6). Fossil key as in the legend to Fig. 1.

subfamilial differences in mandibular scaling are mirrored by ontogenetic comparisons of jaw allometry in *Nasalis larvatus* and *Macaca fascicularis*, as the more folivorous proboscis monkeys have more robust mandibular corpora and symphyses than those of crab-eating macaques (Ravosa, 1991b).

A consideration of large-bodied, fossil cercopithecoidea shows that all but *Dinopithecus ingens* are similar to geladas and living and extinct colobines in possessing relatively deep jaws (Figs. 1 and 2) (see also Jolly, 1970a,b; Hylander, 1979b; Bouvier, 1986a). Among fossil colobines, *Mesopithecus pentelici* and, especially, *Paracolobus chemeroni* possess deeper corpora, whereas Colobine species "A" and *Cercopithecoides williamsi* have relatively shallow jaws (Figs. 1 and 3). As most larger-bodied extinct papionins are inferred to have had more obdurate diets (Benefit and McCrossin, 1990; Delson and Dean, 1993; Jablonski, 1993; Teaford, 1993; Lucas and Teaford, 1994), the presence of deeper jaws in them may be

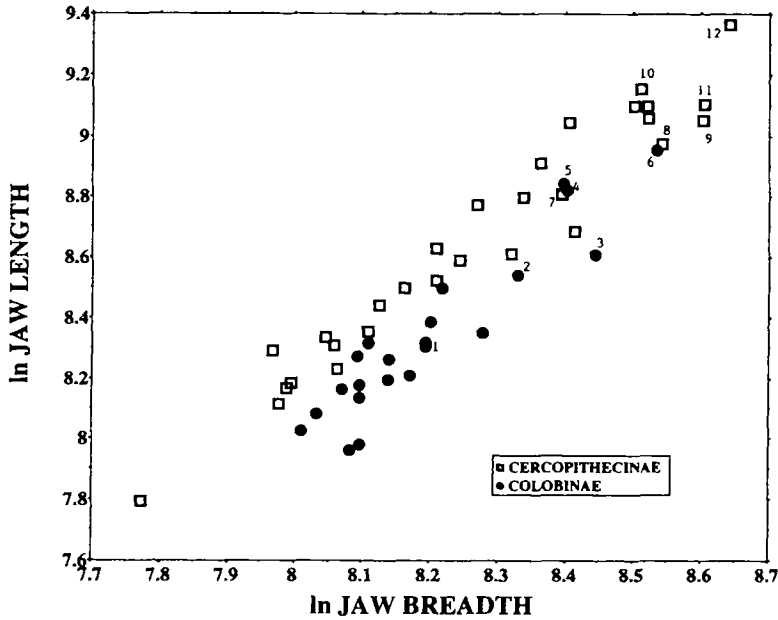


Fig. 6. A plot of ln jaw length versus ln jaw breadth in 29 cercopithecinines (squares) and 22 colobines (circles). This indicates that, at a given jaw length, cercopithecinines exhibit increased symphyseal curvature relative to colobines. In each group, the degree of curvature also increases with size, such that larger taxa have more curved symphyses, and presumably more wishboning, than those of smaller species. Fossil key as in the legend to Fig. 1.

due to greater balancing-side muscle-force recruitment during frequent, powerful mastication (Luschei and Goodwin, 1974; Hylander *et al.*, 1992). Apart from certain papionins and most colobines, an association between mandibular robusticity and dietary toughness has been noted for other primates (Bouvier, 1986b; Hylander, 1988; Daegling, 1989, 1992; Ravosa, 1991a, 1992; Cole, 1992; Ravosa and Hylander, 1994; Ravosa and Ross, 1994), chiropterans (Freeman, 1979, 1981, 1984, 1988), carnivorans (Biknevicius and Ruff, 1992; Ravosa, nd), and bovids (Spencer, 1995).

In this regard, subfamilial comparisons of symphyseal allometry demonstrate that, primarily at smaller sizes, the colobines exhibit larger symphyses than those of cercopithecinines (Table II, Figs. 4 and 5). This is due perhaps to increased dorsoventral shear of the symphyseal during molar biting and chewing. However, the presence of these scaling differences could also be inferred to mean that colobines experience elevated wish-

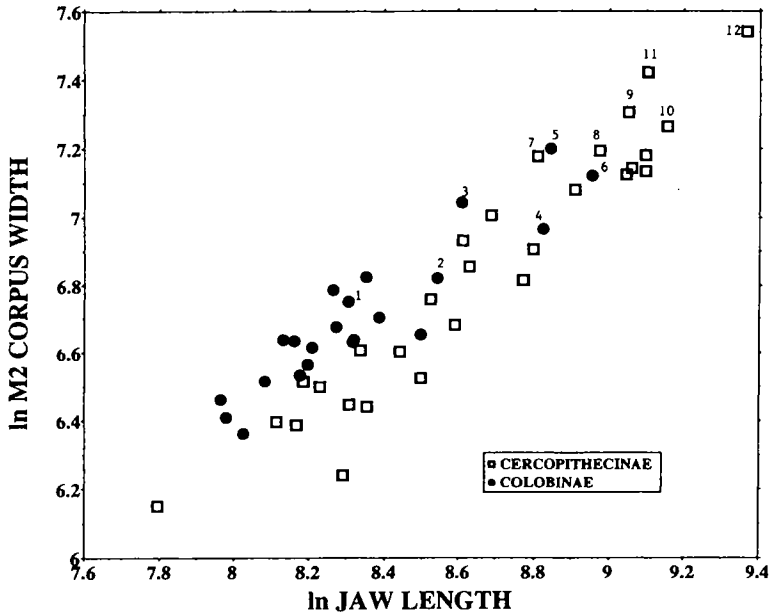


Fig. 7. A plot of $\ln M_2$ corporeal width versus \ln jaw length in 29 cercopithecines (squares) and 22 colobines (circles). Colobine corporeal measures are located above those for cercopithecines. Once more, this supports claims that primate folivores and graminivores exhibit relatively larger mandibles. Note that many extinct cercopithecines have wider corpora than other subfamilial members, which likely indicates the presence of elevated axial torsion. Fossil key as in the legend to Fig. 1.

boning levels due to a tougher diet requiring greater balancing-side muscular force recruitment during mastication. Irrespective of the possible explanation(s) for the transposition at smaller sizes, it is interesting that the colobine and cercopithecine data scatters converge at larger sizes, such that subfamilial differences in symphyseal robusticity are less marked for many larger taxa.

Perhaps the reason why jaw-scaling trajectories for cercopithecines often converge on the colobine scatter at larger sizes is that many large, extinct papionins are inferred to have had more obdurate diets, much like geladas and Tibetan macaques (Benefit and McCrossin, 1990; Delson and Dean, 1993; Jablonski, 1993; Teaford, 1993; Lucas and Teaford, 1994; Takahashi and Pan, 1994). This pattern may represent another example wherein larger mammals within a clade ingest tougher, lower-quality foods

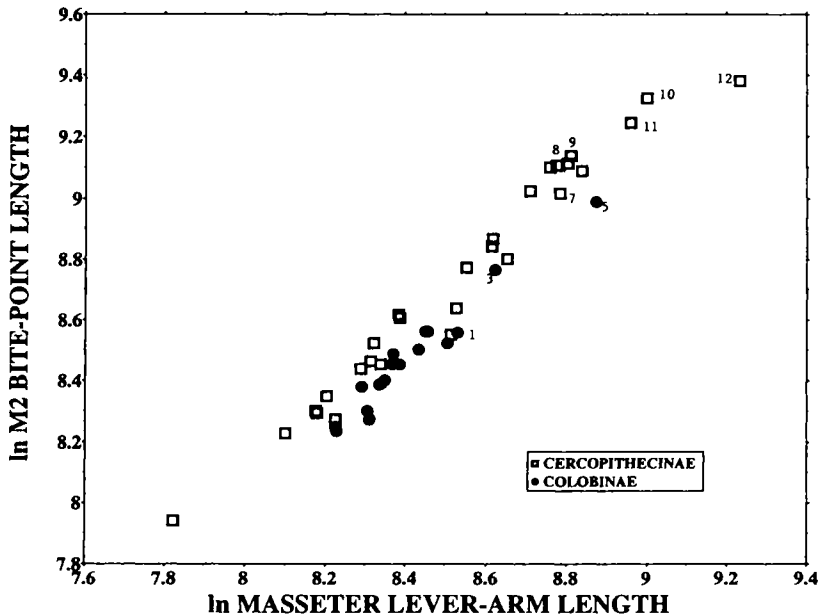


Fig. 8. A plot of $\ln M^2$ bite-point length versus \ln masseter lever-arm length in 29 cercopithecines (squares) and 19 colobines (circles). Colobine M^2 bite-point measures are located below those for cercopithecines. This indicates that living and fossil colobines are able to produce similar molar bite forces using less masseter force. In each subfamily, the degree of masseter efficiency decreases with size, such that larger-bodied species have less advantageous muscle arrangements than those of smaller taxa. Fossil key as in the legend to Fig. 1.

(Janis, 1976; Scapino, 1981; Demment and van Soest, 1985; Sailer *et al.*, 1985; McNaughton and Georgiadis, 1986; Ravosa, 1991a).

It is noteworthy that the distribution of living and fossil cercopithecines does not vary much about the scaling trajectory for symphyseal height; scatter about the colobine regression line is greater (Fig. 4). In colobines, *Paracolobus chemeroni* and *Dolichopithecus rusciniensis* have deeper symphyses, while *Cercopithecoides williamsi* and Colobine species "A" evince relatively shallow symphyses (Fig. 4). Based on intrasubfamilial comparisons of symphyseal width, *Theropithecus brumpti*, *Theropithecus baringensis*, and *Paracolobus chemeroni* all have relatively thick symphyses, whereas *Mesopithecus pentelici*, *Dolichopithecus rusciniensis*, and *Rhinopithecus turkanensis* exhibit labiolingually thinner symphyses (Fig. 5).

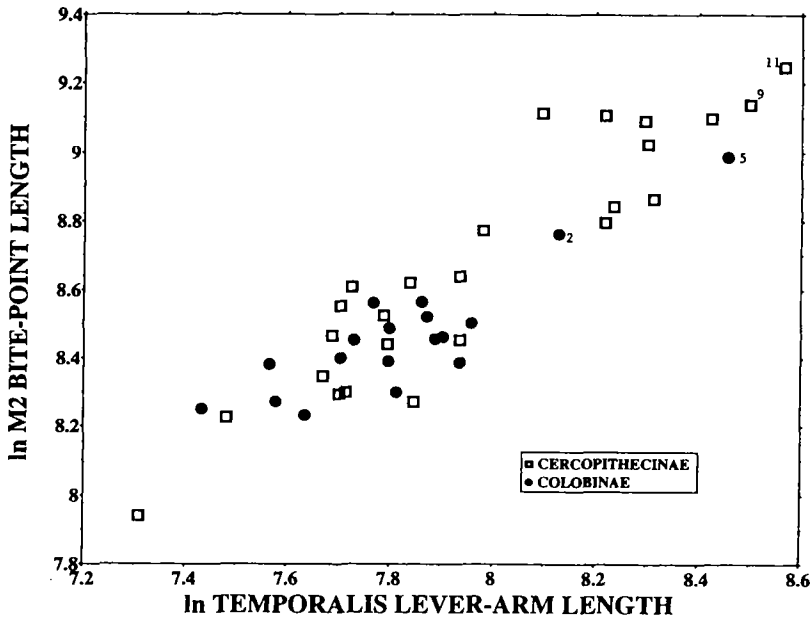


Fig. 9. A plot of $\ln M^2$ bite-point length versus \ln temporalis lever-arm length in 25 cercopithecines (squares) and 18 colobines (circles). Extant and extinct cercopithecines and colobines share similar M^2 bite-point:temporalis lever-arm scaling relationships. Therefore, when considered at the familial level, the degree of temporalis efficiency is isometric, such that molar:muscle arrangements remain constant with size. Fossil key as in the legend to Fig. 1.

Further examination of factors influencing wishboning indicate that colobines have a lesser degree of symphyseal curvature than comparably sized cercopithecines, i.e., colobines have shorter jaw lengths at a common jaw breadth (Table II, Fig. 6). Moreover, colobines exhibit similar levels of positive allometry of jaw length versus jaw breadth (slope of 1.794, versus 1.622 for cercopithecines), but do not show the cercopithecine pattern of positive allometry of symphyseal width (slope of 1.224, versus 0.875 for colobines). Thus, although colobines exhibit allometric increases in symphyseal curvature, inferred wishboning stress levels do not appear to increase proportionally as they do in cercopithecines (Hylander, 1985; Vinyard, 1996). Nonetheless, colobines possess more robust symphyses than those of cercopithecines (Table II, Figs. 4 and 5). Therefore, if the wishboning loading regime characterizes all catarrhines, the jaw-muscle activity pattern underlying colobine wishboning may become less pronounced with

size, which is opposite to that inferred for cercopithecines (Hylander, 1984, 1985; Vinyard, 1996; Ravosa, this study). An alternative explanation for this pattern could be that there is subfamilial variation in wishboning and dorsoventral shear levels at different sizes, both of which may differentially influence symphyseal morphology.

In a recent discussion of cranial morphology among living and extinct *Theropithecus*, Delson and Dean (1993) claim that stronger development of the inferior transverse torus, which can increase symphyseal width, likely indicates the presence of greater wishboning relative to that in other large-bodied papionins. However, a consideration of cercopithecine symphyseal scaling indicates that symphyseal form in living and fossil baboons is due largely to allometric variation in jaw length (Figs. 4 and 5). Therefore, while Delson and Dean (1993) may be correct in claiming that greater development of the inferior transverse torus is uniquely characteristic of all *Theropithecus*, this morphology does not necessarily result in a relatively thicker symphyseal able to resist greater wishboning than other large-bodied papionins.

Subfamilial comparisons of mandibular allometry in living and fossil Old World monkeys demonstrate that, in addition to having deeper corpora, colobines also possess relatively thick corpora (Table II, Fig. 7). This is similar to the results of Bouvier's (1986a) analysis using a sample of modern forms. Subfamilial differences in corporeal width likely result from greater axial torsion produced during mastication of higher percentages of fibrous leaves and/or seeds among colobine monkeys (Bouvier, 1986a).

A consideration of extinct cercopithecines indicates that all except *Theropithecus baringensis* have relatively wide corpora as compared to other subfamilial members (Fig. 7). Among fossil colobines, *Rhinopithecus turkanensis* and, particularly, *Cercopithecoides williamsi* exhibit wider corpora, while *Dolichopithecus rusciniensis* possesses fairly narrow corpora. Macaques that ingest tougher foods than other congeners also have relatively wide corpora [*Macaca thibetana* (Takahashi and Pan, 1994), *M. fuscata* (Antón, 1996)]. In fossil and extant *Theropithecus*, and perhaps in other folivorous Old World monkeys, this pattern may reflect a larger and more laterally displaced masseter muscle combined with greater emphasis on the masseter/medial pterygoid complex during unilateral mastication of a tough, leafy diet (Ravosa, 1990; Jablonski, 1993; Antón, 1996).

Subfamilial scaling analyses indicate that living and fossil colobines have a shorter M^2 bite-point length relative to masseter lever-arm length (Table I, Fig. 8). On the other hand, cercopithecines and colobines exhibit similar scaling patterns between M^2 bite-point and temporalis lever-arm lengths (Fig. 9). Therefore, another way colobines differ from cercopithecines is that they can recruit less masseter force to generate similar bite forces during masti-

cation (Hylander, 1979b; Ravosa, 1990). Similar subfamilial differences in masticatory biomechanics are noted in ontogenetic analyses of the folivorous proboscis monkey and the crab-eating macaque (Ravosa, 1991b). Likewise, Antón (1996) notes several parallels in the way masticatory efficiency in *M. fuscata* differs from other *Macaca* and the way maxillomandibular morphology differs between colobines and cercopithecines.

Within each subfamily, M^2 bite point scales with positive allometry versus masseter lever arm, suggesting that larger monkeys have less efficient masseter arrangements. This seems especially significant due to the lack of subfamilial difference in temporalis lever-arm scaling, which is isometric across cercopithecids.

It would be interesting to assess how other masticatory parameters scale within and across cercopithecoid subfamilies. Assuming interspecific isometry of the chewing muscles (Cachel, 1984), decreased masseter efficiency at larger sizes could be countered by positive allometry of relative balancing-side muscle-force recruitment (Hylander, 1985; Ravosa and Hylander, 1994), or by positive allometry of muscle pinnation to increase the physiological cross-section, or by both factors.

It is surprising that, although many of the larger-bodied cercopithecines have, or are inferred to have, more folivorous and/or graminivorous proclivities than smaller-bodied taxa, only one (*Theropithecus brumpti*) has a colobine-like degree of masseter efficiency (Fig. 8) (also Jablonski, 1993). The presence in *T. brumpti* of a relatively longer masseter lever arm for a given M^2 bite-point length appears due to the unique development of robust maxillary processes which position the masseter more anteriorly along the facial skull. Moreover, it is possible that selection for increased masseter efficiency in large extinct papionins with tougher diets is offset by selection for increased relative canine size and gape used in agonistic displays (Ravosa, 1990; Jablonski, 1993; Ravosa and Profant, 1996).

CONCLUSIONS

Hylander (1979b) suggested that among the Cercopithecidae, craniomandibular variation appears to be linked to the folivorous adaptations of the Colobinae and to adaptations for gape and canine displays in the Cercopithecinae. Since then, numerous analyses have detailed the specific effects of these selective pressures. My study contributes to this body of theoretical and comparative analyses by determining subfamilial differences in symphyseal allometry and the scaling of symphyseal curvature in colobines. By incorporating fossil Old World monkeys, many of which were larger than living subfamilial members, masticatory biomechanics and

mandibular scaling are more fully evaluated. In using a comparative, integrative approach to masticatory scaling phenomena, this study increases our ability to understand the functional significance of skull form in living and fossil taxa of disparate sizes and shapes. Moreover, the inclusion of taxa from the Late Miocene allows a determination of the relative antiquity of functional variation in skull form between cercopithecines and colobines.

Scaling comparisons in extant and extinct Old World monkeys demonstrate significant subfamilial differences in mandibular robusticity, with colobines having relatively larger corpora (Bouvier, 1986a) and symphyses than those of cercopithecines. This pattern is more distinct at smaller size ranges. The most likely cause of such variation in corporeal and symphyseal robusticity is that the colobine mandible experiences increased repetitive loading during mastication related to ingesting a folivorous and/or graminivorous diet (Hylander, 1979b; Bouvier, 1986a; Happel, 1988; Teaford, 1993; Lucas and Teaford, 1994). Though colobine monkeys have relatively large symphyses, subfamilial comparisons of symphyseal curvature indicate that they exhibit less curvature than similarly sized cercopithecines. In addition, both subfamilies show similar allometric changes in the degree of curvature, such that larger species evince more curved symphyses than those of smaller-bodied monkeys (Hylander, 1985; Vinyard, 1996).

Subfamilial scaling analyses also indicate that extant and extinct colobines have a more efficient biomechanical arrangement as they possess shorter M^2 bite-point lengths relative to masseter, but not temporalis, lever-arm length. Thus, colobines can recruit less masseter-muscular force to produce similar molar bite forces than those of cercopithecines. Presumably, this configuration is important for primates which spend a greater proportion of each day processing larger percentages of tougher, lower-quality forage and seeds.

Allometric analyses indicate that many of the large-bodied fossil papionins have more robust corpora much like those of extant and extinct colobines. This suggests that such taxa may have had a similarly obdurate diet. Interestingly, most of these papionins do not possess a colobine-like degree of jaw-muscle efficiency. In terms of molar bite-point:muscle lever-arm configurations, the extinct cercopithecine and colobine specimens are much as predicted for a subfamilial member of its size.

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