Testing associations between diet and premolar size in four African colobine monkeys

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Introduction

- Folivorous primates are hypothesized to have relatively larger premolars than frugivores due to the mechanical and energetic challenges of leaf eating (Kay, 1975; Lucas et al., 1986; Scott et al., 2018).
- More specifically, it is reasoned that as folivory increases, so do the mechanical demands of mastication, resulting in more frequent premolar loading (Scott et al., 2018).
- Given extensive variation in folivory among colobines and extensive variation in leaf material properties (cf. Coiner-Collier et al., 2016) a strictly linear association between folivory and premolar size is unlikely.
- Here, we investigated the relationship between premolar size and diet in four African colobine species for which skeletons and feeding data are available from single source populations, testing the hypothesis that variation in folivory *within* colobines is reflected in premolar size.

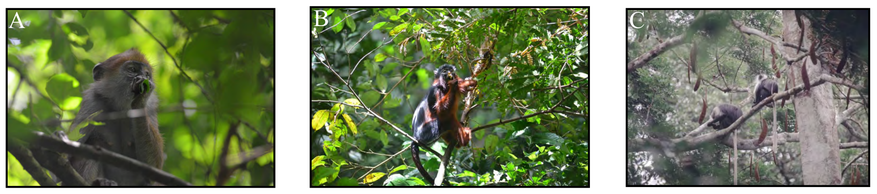

Fig. 1: Dietary diversity in colobines living in the same forest (Taï); A: An olive colobus (*Procolobus verus*) eating young leaves; B: A red colobus (*Piliocolobus badius*) eating young leaves; C: A King colobus (*Colobus polykomos*) eating *Pentaclethra macrophylla* seedpods.

Methods

- Sample: Skeletons of *Colobus polykomos*, *Piliocolobus badius* and *Procolobus verus* from the Taï Forest, Ivory Coast and *Colobus angolensis* from Kenya's Diani Forest.
- *Cercopithecus diana* used as a functional 'frugivorous' outgroup for comparisons.
- Four measurements of premolar area: P^3 area; P^4 area; UP_{total} (P^3 + P^4 areas) and LP_4 area.
- Four size scalars for each measurement: mandibular length, M^1 area, palate area and body size.
- 16 shape ratios were compared between the five species.
- Inter-observer error: 4.6%.

Fig. 2A – 2C: Caliper measurements taken in this study: **A**: P^4 area ($L*W$); **B**: P^3 area ($L*W$); **C**: M^1 area ($L*W$); **D**: Palate Area ($L*W$); **E**: P_4 area ($L*W$); **F**: Mandibular length

Table 1: Dietary information for the four colobines studied (+ 'frugivorous' Diana monkey outgroup). Body mass data from McGraw and Daegling (2019) (Taï) and Dunham (2013) (Diani); Dietary data from Dunham (2017) (*C. angolensis*), McGraw et al. (2016) (*C. polykomos* and *P. badius*) , McGraw and Daegling (2019) (*P. verus*) and Kane and McGraw (2017) (*C. diana*). Chewing data from Dunham and Lambert (2016) (*C. angolensis*), McGraw and Daegling (2019) (*C. diana*, *C. polykomos* and *P. badius*) and Traff et al., 2017 (*P .verus*).

Species	Male, Female body weight (kg)	Dietary Composition*	% Total Foliage in Diet	Av. Chews per masticatory bout
Cercopithecus diana	5.2 / 3.9	56% FR; 38% IN; 5.2%ML; 1.1% YL	6.3%	10
Colobus angolensis	8.9 / 7.1	58% YL; 14% FL; 14% FR; 13% ML; 10% S; 1% O	71%	14
Colobus polykomos	9.9 / 8.3	28% YL; 27% S; 21% FR; 20% ML; 3% FL; 1% O	48%	20.4
Piliocolobus badius	8.3 / 8.2	46% YL; 29% FR; 20% FL; 4% ML; 1% O	50%	17.5
Procolobus verus	4.7 / 4.4	91% L; 9% FR	91%	11

*** FR: Fruit; IN: Invertebrates; FL: Flowers; S: Seeds; ML: Mature leaves; YL: Young leaves; O: Other**

Fig. 3: Study species: A) *Colobus polykomos*; B) *Procolobus verus*; C*) Colobus angolensis;* D*) Piliocolobus badius*

• Results

- **Premolar Area to Mandibular Length**
  - Among colobines, *C. polykomos* tended to have the largest premolars relative to mandibular length, even though they are not the most folivorous (Table 1). *P. verus* have the relatively smallest premolars (lower than *C. diana*), even with their high degree of folivory (91%).

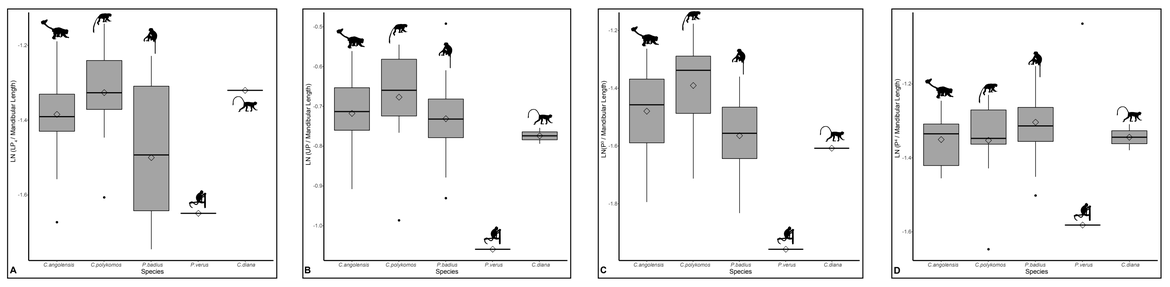

Figure 4 – Premolar measurements scaled to mandibular length (ML; Fig. 2C); A: LP_4 / ML; B: UP_{total} / ML; C: P^3 / ML; D: P^4 / ML. All indices are ln-transformed.

- **Premolar Area to M^1 Area**
  - Among colobines, *C. polykomos* tend to have relatively larger premolars, even though they are not the most folivorous (Table 1). By contrast, *P. verus* is the most folivorous (91%), yet has the relatively smallest premolars. *C. angolensis* (71%) did have relatively larger premolars than less folivorous *P. badius* (50%).

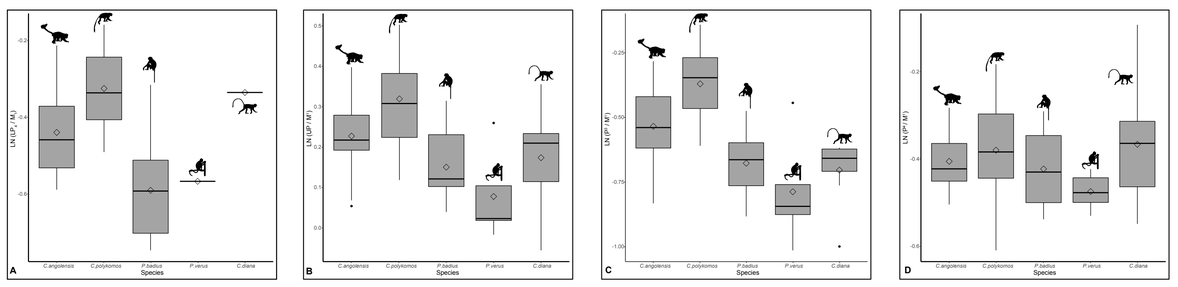

Figure 5 – Premolar measurements scaled to M^1 area (M^1; Fig. 2A); A: LP_4 / M^1; B: UP_{total} / M^1; C: P^3 / M^1; D: P^4 / M^1. All indices are ln-transformed.

- **Premolar Area to Palate Area**
  - All colobines tended to have relatively larger premolars than *C. diana* (6% folivory). But among colobines, relative premolar size was not a strong predictor of folivory, with *P. badius* (50%) having relatively larger premolars than both *C. angolensis* (71%) and *P. verus* (91%).

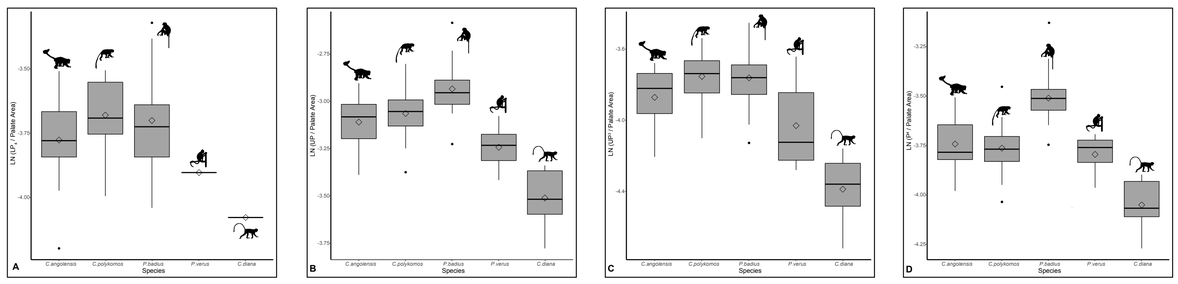

Figure 6 – Premolar measurements scaled to palate area (PA; Fig. 2A); A: LP_4 / PA; B: UP_{total} / PA; C: P^3 / PA; D: P^4 / PA. All indices are ln-transformed.

- **Premolar Area to Body Size**
  - Contrasts between folivores and frugivores in relative premolar size are not in line with energetic predictions (Kay, 1975). However, within colobines, there is a trend towards relatively larger premolars in several of the more folivorous taxa (e.g. *P. verus*, *C. angolensis*).

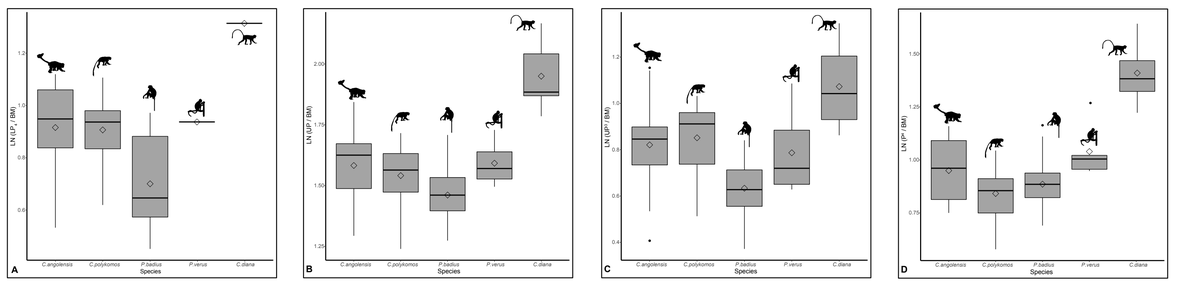

Figure 7 – Premolar measurements scaled to average body mass (BM); A: LP_4 / BM; B: UP_{total} / BM; C: P^3 / BM; D: P^4 / BM. All indices are ln-transformed.

Discussion

The three colobine species have larger premolars, when scaled to palate area, than the highly frugivorous *C. diana* outgroup. This result is consistent with the physics of food breakdown, as a diet of non-bolus-forming leaves, compared to fruit, requires increased tooth size, relative to the area of the oral cavity, to increase the probability of food particle contact (and breakdown) per chew. (Lucas et al., 1986).

Yet *within* colobines, relative premolar size is not strongly associated with degree of folivory. *C. polykomos* tends to have larger premolars than other taxa, even though it consumes less total leaf matter overall. We suspect that the challenges of consuming woody, tough *Pentaclethra macrophylla* seedpods have selected for increased premolar size relative to other taxa to accommodate both greater masticatory stresses and longer sustained bouts of chewing (Table 1) (McGraw et al., 2016).

Conclusions

- Among broad taxonomic groups, folivorous colobines have larger relative premolar sizes, when scaled to palate area, than the frugivorous cercopithecine outgroup. This result is consistent with predictions derived from food material properties (Lucas et al., 1986; Scott et al., 2018), supporting this metric's utility for determining broad dietary differences between taxa in the primate fossil record.
- Yet within the four colobines, comparisons of indices indicate that there is little support for the hypothesis that relative premolar size in African colobines is positively and consistently associated with degree of folivory.
- Departures from dietary hypotheses are likely more interpretable in terms of food mechanical property variation (Scott et al., 2018) and/or scaling effects (Scott, 2011), which will be integrated into future analyses. *****See supplemental pages below for references, acknowledgements, more stats and extra copies of the poster.**