

1 **Colobine forestomach anatomy and diet**

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22 **Abstract**

23 Colobine monkeys have complex, multi-chambered, foregut-fermenting stomachs with either
24 three ('tripartite') or four ('quadripartite', adding the praesaccus) chambers where a
25 commensal microbiome digests plant cell walls and possibly detoxifies defensive plant
26 chemicals. Though different potential functions for the praesaccus have been suggested, little
27 evidence exists to support any of the proposed functions. To address the issue of the function
28 of the praesaccus, we collated literature data on diet and compared tripartite and quadripartite
29 species. Our results suggest that the praesaccus is an adaptation to a dietary niche, with a
30 particularly high reliance on leaves as fallback foods in colobine clades with quadripartite
31 stomachs, and a higher reliance on fruits/seeds as foods at times of high fruit availability in
32 clades with tripartite stomachs. This supports the notion that a large gut capacity is an
33 important characteristic by which herbivores survive on a high fibre diet, and that this large
34 gut capacity may not be necessary for some species if there are seasonal peaks in fruit
35 availability.

36

37 **Introduction**

38 Colobine monkeys differ from all other primates in having a foregut-fermentation digestive
39 system (Bauchop & Martucci, 1968) with three ('tripartite') or four ('quadripartite')
40 chambers in the forestomach (Chivers, 1994). Quadripartite stomachs are characterised by an
41 additional blind sac or 'pouch'; the praesaccus (Fig. 1), which is lined with a stratified
42 squamous epithelium and has a complete longitudinal muscle coat, representing an additional
43 chamber, prior to the three compartments common to all colobines (Langer, 1988).

44 Compilations of whether individual colobine species have three or four chambers
45 have been published (Caton, 1998; Langer, 1988; Langer, 2017), but no comprehensive
46 overview of the colobine group exists. Notably, the existing evidence does not rule out that

47 there is variation in this trait (whether tripartite or quadripartite forestomach chambers) even
48 within genera. To date, it appears that *Colobus*, *Semnopithecus*, *Trachypithecus*, and
49 *Presbytis* represent taxa with a tripartite stomach, whereas *Procolobus*, *Piliocolobus*,
50 *Rhinopithecus*, *Pygatrix*, and *Nasalis* represent taxa with a quadripartite stomach, with no
51 information on *Simias* (Caton, 1998). Given the taxonomic distribution of this trait, it would
52 seem that the praesaccus evolved in parallel both in some African and some Asian colobine
53 clades. Therefore, it is tempting to assume that the praesaccus represents a functional
54 adaptation that is convergent between the respective species. The alternative scenario would
55 assume the praesaccus is an ancestral trait in both clades and was lost in parallel in some
56 species in each group.

57 Different functions for the praesaccus have been proposed, but as of yet no evidence
58 exists to support one proposal over another. Caton (1998), and subsequently Wright et al.
59 (2008), proposed that the praesaccus functions as a 'gastric mill'. Chivers (1994) suggested it
60 might be an adaptation to seed-eating, without providing a rationale or empirical data. In
61 contrast, Langer (2017) considers the praesaccus an adaptation to folivory, based on the
62 assumption that a large gastrointestinal capacity is a typical adaptation to a diet of low-
63 digestibility items, such as leaves. This last explanation reverberates the finding of Chivers
64 and Hladik (1980) that folivorous mammals generally have more gastrointestinal surface area
65 in relation to metabolic body size than frugivorous and faunivorous mammals. This is
66 because to derive a similar amount of energy from a diet of lower digestibility, more of that
67 diet must be processed. Thus, the objective of our research was to test the prediction that
68 colobines with a quadripartite stomach consume higher proportions of leaves than those with
69 a tripartite stomach.

70

71 **Materials and Methods**

72 To address the question of the association between colobine praesaccus and the diets (i.e.,
73 fruit/seed- and leaf-eating), we collated literature data on the natural diet of all colobine
74 species for which the status of the number of forestomach chambers was known [according to
75 Caton (1998) as a starting point for our literature search]. Most authors do not distinguish
76 whether colobines consumed only seeds or fruits and consider both pulp and seed parts
77 together, therefore we defined the amount of consumed seeds as that of consumed fruits and
78 seeds. We obtained data on colobine natural diets, published by Fashing (2011), Kirkpatrick
79 (2011), Sterck (2012) and added recently published literature (Appendix I); these data
80 represent the natural diet in percent of its various components, based on field observations
81 that recorded the time spent feeding. If the values were not represented in the text, but were
82 presented in figures, we measured the values using the Web Plot Digitizer ver. 4.1 (free
83 software: <https://apps.automeris.io/wpd/>). An assessment of dietary variation has been
84 demonstrated to be important for evaluating colobine foraging strategies (Harris & Chapman,
85 2007) and multiple diet descriptions were found for several taxa (Appendix I). For each
86 species, we calculated both the mean and the maximum percentage of fruits/seed and leaves
87 in the diet based on annual averages, and additionally the maximum percentages based on
88 monthly averages to better account for intra-annual variation.

89 In spite of the small number of species and the fact that the species with a quadripartite
90 stomach in our dataset were from the closely related odd-nosed colobine clade except
91 *Piliocolobus* and *Procolobus* (Sturner et al., 2006), we accounted for the phylogenetic
92 structure of the dataset. For this purpose, analyses were performed on species means with
93 Generalized Least Squares (GLS) and with Phylogenetic Generalized Least Squares (PGLS).
94 For PGLS, data were linked to a supertree of extant mammals (Fritz et al., 2009). The
95 phylogenetic signal λ was estimated using maximum likelihood (Revell, 2010). λ can vary
96 between 0 (no phylogenetic signal) and 1 (the observed pattern is predicted by the phylogeny;

97 similarity among species scales in proportion to their shared evolutionary time) (Freckleton et
98 al., 2002; Pagel, 1999). GLS and PGLS regression analyses were performed in R ver. 2.15.0
99 (R-Core-Development-Team, 2011) using the packages *caper* (Orme et al., 2010) and *nlme*
100 (Pinheiro et al., 2011), and the significance level was set to 0.05, and results of $0.05 < P <$
101 0.10 are discussed as trends. Due to the nature of the dataset, with the majority of colobine
102 species not having been classified with respect to their stomach anatomy (and therefore
103 excluded), the analysis should be considered preliminary until more anatomical data becomes
104 available.

105

106 Results

107 Time spent feeding on fruits/seeds by 9 tripartite and 5 quadripartite species, including 33
108 and 25 populations, ranged from 0 to 84% (mean = $34.9 \pm$ standard deviation 20.8) and 6 to
109 50% (mean = 23.6 ± 13.0), respectively (Fig. 1a), while the time spent feeding on leaves
110 ranged from 10 to 88% (mean = 54.0 ± 21.4) and 31 to 88% (mean = 64.5 ± 15.6), respectively
111 (Fig. 1d). The mean maximum percentage of time devoted to feeding varied between
112 tripartite and quadripartite species from 50.7 ± 17.8 to 37.8 ± 14.8 for fruit/seeds and $53.4 \pm$
113 17.4 to 82.8 ± 5.54 for leaves, respectively (Fig. 1b and e). Furthermore, the mean maximum
114 monthly percentage of time devoted to feeding varied between tripartite and quadripartite
115 species from 74.1 ± 14.2 to 54.3 ± 26.4 for fruit/seeds and 73.1 ± 18.8 to 87.3 ± 14.0 for
116 leaves, respectively (Fig. 1c and f).

117 In the dataset comprising all 14 species listed in the Appendix, the average percentage
118 of fruits/seeds showed a negative relationship in GLS ($t = -2.687$, $P = 0.020$), with a similar
119 trend in PGLS ($\lambda = 0.00$, $t = -2.065$, $P = 0.069$). The maximum percentage of fruits/seeds
120 tended towards a significant, negative relationship with the number of stomach compartments
121 in GLS ($t = -1.930$, $P = 0.078$), without an evident trend in PGLS ($\lambda = 0.00$, $t = -1.665$, $P =$

122 0.130). By contrast, the average percentage of leaves showed a positive relationship in GLS (t
123 = 2.966, $P = 0.012$) as well as in PGLS ($\lambda = 0.37$, $t = 2.524$, $P = 0.033$). The maximum
124 percentage of leaves also showed a significant, positive relationship in GLS ($t = 3.614$, $P =$
125 0.004), indicating that quadripartite species had a higher maximum percentage of leaves in
126 their diet. This relationship was also significant in PGLS ($\lambda = 0.03$, $t = 2.945$, $P = 0.016$),
127 indicating that the pattern occurred in parallel, or convergently, in the different colobine
128 lineages. When using the more reduced dataset (studies reporting monthly data, with 3
129 species less, i.e., a total of 11 species only) for data on the maximum percentage of
130 fruits/seeds or leaves on the basis of monthly data, considering the effects of intra-annual
131 variation, there was again a negative relationship with the percentage of fruits/seeds in GLS (t
132 = -2.424, $P = 0.038$) and a corresponding trend in PGLS ($\lambda = 1.00$, $t = -2.027$, $P = 0.073$). For
133 the percentage of leaves, however, no significant relationship with the number of stomach
134 compartments could be ascertained in this reduced dataset (GLS: $t = 1.586$, $P = 0.147$; PGLS:
135 $\lambda = 1.00$, $t = 1.380$, $P = 0.201$).

136

137 Discussion

138 Our results indicate that the extremes of the natural diet might be more important in
139 understanding morphophysiological adaptations than the averages, and the term ‘fallback
140 food’ has been used to explain such patterns (Lambert & Rothman, 2015; Marshall et al.,
141 2009; Marshall & Wrangham, 2007). Our similar results from both GLS and PGLS analyses,
142 the general patterns of a positive relationship between consumption of leaves and the number
143 of chambers, but a negative relationship with fruits/seeds, suggest that the praesaccus is an
144 adaptation to a dietary niche with a particularly high reliance on leaves as a fallback food in
145 certain colobine clades. A higher reliance on fruits/seeds as foods at times of high fruit
146 availability in clades that do not have a praesaccus suggests that a praesaccus may not be

147 required for this niche. The difference between tripartite and quadripartite stomachs and diet
148 niches apparently evolved in both the African and the Asian colobine lineages, if our small
149 sample is considered representative. However, the scope of the datasets submitted to
150 statistical testing in this study – either 14 or 11 species – is limited. Until the anatomy of a
151 larger number of colobine species has been described, these results must be considered
152 preliminary.

153 The preliminary findings support the notion that a large gut capacity is an important
154 characteristic by which herbivores survive on a leafy, high fibre diet (Müller et al., 2013),
155 and that it may not be necessary for some species if there are strong seasonal peaks in fruit
156 availability. A logical extension of our results is the prediction that the presaccus will allow a
157 higher food intake per feeding bout. Female tripartite and quadripartite colobines monkeys
158 may not differ much in body mass (i.e., < ca. 10kg), though some male quadripartite species
159 are substantially larger than tripartite ones (Appendix I). Therefore, gut size relative to body
160 mass might be greater in colobines with quadripartite stomachs, especially in females. This
161 prediction needs to be tested with behavioural observations of colobines with quadripartite
162 and tripartite stomachs. If our prediction is correct, this would suggest that species with a
163 tripartite stomach would be constrained by the fact that they cannot ingest relatively large
164 amounts, which would preclude them from occupying leaf-only niches. There are few
165 examples that properly analysed the fallback feeding behaviour in species with a tripartite
166 stomach, accounting for diet quality, abundance and preference as recommended by Marshall
167 et al. (2009). Hanya and Bernard (2012) describe young leaves of specific plant species as
168 fallback foods for red leaf monkeys (*Presbytis rubicunda*) at Danum Valley, but they
169 nevertheless rarely represent more than 60% of their diets. A further test of this relationship
170 would involve examining if taxa with quadripartite stomachs are found in regions with a less
171 reliable year-round supply of young leaves or fruits than species with tripartite stomachs, and

172 whether tripartite species occur in habitats where mature leaves represent the only food
173 source for a certain part of the year.

174 In captivity, when animals are provided easily digestible diets, such as commercial
175 foods, genera with a quadripartite stomach, such as *Nasalis*, *Pygathrix*, and *Ptilocolobus*
176 (Hollihn, 1973; Matsuda et al., 2018; Struhsaker, 2010), are notoriously difficult to maintain
177 and breed, compared to tripartite species. A potential reason for this could be that the higher
178 intake capacity for species with a quadripartite stomach might be detrimental in the case of
179 highly digestible diets that may lead to malfermentation (Clauss & Dierenfeld, 2008). In
180 comparison, species with a tripartite stomach might be less susceptible to extreme bouts of
181 malfermentation when fed highly digestible diets due to a relatively reduced intake capacity.

182 To date, no physiological data exists that allows speculation on additional functions of
183 the praesaccus. In particular, it is unclear why an additional stomach chamber would be
184 necessary for an increase in capacity, rather than a more voluminous or expandable regular
185 saccus. Unfortunately, the current information on stomach anatomy across colobine species is
186 too limited to further test these predictions with respect to the relevance of the praesaccus
187 with respect to a diet niche. Given our findings, **one** last prediction can be made. Associated
188 with climate change, the fibre concentration in leaves consumed by colobines has increased
189 and protein content has decreased over the past 30 years (Rothman et al., 2015). This leads to
190 the prediction that tripartite species, possibly with a lower fibre tolerance, would be more
191 vulnerable to climate change than quadripartite species.

192

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198

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290

291 **Figure and Appendix legends**

292 **Figure 1** Schematic representation of the colobine stomach, illustrating the tripartite
293 condition (with saccus, tubiform and glandular stomach parts) and the quadripartite condition
294 (with an additional praesaccus). Drawn after Langer (1988; p. 284) for *Colobus verus*. Note
295 that the volumes, and the degree to which the praesaccus can be visually discerned from the
296 saccus, may vary between species: Gl. st. = glandular stomach

297

298 **Figure 2** Boxplots illustrating dietary variation, with each point representing a month, for
299 the percentage of time spent feeding on fruits/seeds (a, b, c) and leaves (d, e, f) (of total
300 feeding time) in natural habitats between colobine monkeys with different forestomach
301 anatomy, being represented by the central line, the extremes of the box representing the upper
302 and lower quartile: annual % in each population (a, d), maximum annual % within species (b,
303 e) and monthly maximum % in each population (c, f). Species with a tripartite forestomach
304 are *Colobus guereza*, *C. polykomos*, *Semnopithecus entellus*, *Trachypithecus vetulus*, *T.*
305 *obscurus*, *Presbytis thomasi*, *P. femoralis*, *P. rubicunda*, *P. melalophos*; species with a
306 quadripartite forestomach are *Ptilocolobus badius* (formerly considered as *Procolobus*
307 *badius*), *Procolobus verus*, *Rhinopithecus roxellana*, *Pygathrix nemaus*, *Nasalis larvatus*.
308 Data from Appendix I (using all available data, i.e. not species averages).

309

310 **Appendix I** Variation in the percentage of natural dietary components (per observed feeding
311 time) in 14 colobine species known forestomach type (i.e., tripartite or quadripartite). ¹*Body
312 mass from Mittermeier et al. (2013). ²*Combining the value of mature, young and unknown
313 leaves and lichen. ³*Maximum values among four seasons.