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Comparative gastrointestinal organ lengths among Amazonian primates (Primates: Platyrrhini)

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Abstract

Objectives: The morphological features of the gastrointestinal tract (GIT) in mammals reflect a species' food niche breadth and dietary adaptations. For many wild mammals, the relationship between the structure of the GIT and diet is still poorly understood, for example, the GIT for frugivorous primates is usually classified as unspecialized and homogeneous. Here, we compare the GIT structure of 13 primate species from the three families of extant platyrrhines (Atelidae, Pitheciidae, and Cebidae) in Amazonia, and discuss possible evolutionary adaptations to different diets and trophic niches.

Methods: We measured the length of the esophagus, stomach, small intestine, large intestine, cecum, colon, and rectum of the digestive tracts of 289 primate specimens. We determined the allometric relationships of the different tubular organs with the total length of the GIT as a proxy of specimen body size. Allometric parameters were used to establish the quotients of differentiation of every organ for each primate specimen.

Results: There was a high differentiation in structure of the digestive organs among genera. *Alouatta* specimens clearly separated from the other genera based on dissimilarities in gastric, colonic, and rectal quotients, likely linked to the fermentation of plant contents. In contrast, all cebines (*Sapajus*, *Cebus*, and *Saimiri*) and *Cacajao* species had similar small intestine quotients, which is expected due to their high rates of animal matter consumed.

Conclusions: We show that diverse adaptations in digestive structure exist among frugivorous primates, which in turn reflect different dietary patterns within this group that may enable the geographic coexistence of different primate species.

KEYWORDS
biometry, dietary adaptations, digestive morphology, digestive organs, platyrrhines

1 | INTRODUCTION

The vertebrate gastrointestinal tract (GIT) is composed of tubular organs through which food and liquids travel when they are swallowed, digested, absorbed, and leave the body as feces. Comparisons of GIT from several animal species has been used to explain their dietary adaptations (Stevens & Hume, 2004) and to describe species trophic niche breadth (e.g., in birds, Martínez del Rio & Restrepo, 1994). The relative size of each organ, that is, esophagus, stomach, small intestine, large intestine, cecum, colon, and rectum, reflect feeding adaptations among different taxonomic groups (Chivers & Hladik, 1980; Hoppe et al., 2021). For domestic and laboratory mammals the association between morphology and functionality of the organs in the GIT is well understood (Langer, 2002; Stevens & Hume, 2004), but this has been less explored in wild species (but see Duque-Correa et al., 2021; McGrosky, Codron, et al., 2019; McGrosky et al., 2016). However, some general patterns have emerged.

Faunivorous mammals have a simple and short GIT (and a lack of a cecum) linked to the high digestibility of animal matter (McGrosky et al., 2016; Pinheiro et al., 2018). In contrast, mammals consuming low-digestibility diets, largely composed of structural plant fiber, require gut adaptations for bacterial fermentation to degrade cell walls and/or detoxify plant chemical compounds to improve nutrient extraction (Alexander, 1994; McDowell et al., 2005; McGrosky, Codron, et al., 2019). Fiber fermentation can take place in the foregut, as in ruminants, colobine monkeys, and also in birds, such as the hoatzin (Godoy-Vitorino et al., 2012). However, in mammals such as carnivores, horses, pigs and rabbits, which possess a simple stomach (monogastric), fiber fermentation takes place in the large intestine; these species are categorized as hindgut or cecocolic fermenters (Lambert, 1998; Stevens & Hume, 2004).

Gut adaptations of frugivorous primates are considered intermediate between faunivorous and herbivorous, although they consume a variety of foods other than fruit (Hawes & Peres, 2014a). Fruits, although energy-rich, have a low protein content and therefore do not provide an adequate daily supply of amino acids for frugivorous primates (Janson & Chapman, 1999). To compensate for the low protein in fruits, frugivorous primates consume arthropods and/or leaves to a varying degree (Chapman et al., 2012); this fact may explain differences found in GIT structure (Chivers & Hladik, 1980; Langer & Clauss, 2018). Despite a strong phylogenetic signal for GIT morphology in the Primates, where related species may share similar gastrointestinal morphologies, until now there has been no clear demonstration of an association between diet and digestive morphology within this group (Duque-Correa et al., 2021; McGrosky, Meloro, et al., 2019), especially at lower taxonomic levels, that is, species or genus.

The wide diversity of diets and body sizes, despite all being considered frugivores, in the parvorder Platyrrhini make this an ideal primate group to investigate the association between diet and digestive morphological features (Fleagle, 2013; Lambert, 1998; Norconk et al., 2009). Most of our knowledge of the digestive structure of platyrrhines is derived from a limited number of studies of low sample sizes (e.g., Fooden, 1964; McGrosky, Meloro, et al., 2019). These have involved only representatives of a few taxonomic groups (e.g., Ferrari, 1995; Ferrari et al., 1993; Ferrari & Martins, 1992) whose diets have been broadly classified as frugivory, folivory or faunivory (Chivers & Hladik, 1980).

Here, we compare GITs of a variety of Amazonian platyrrhines from a large sample of digestive tract lengths measured from hunted animals voluntarily donated by Amazonian local people as part of their normal subsistence activities. We calculated the differentiation quotients (Q) determined from the allometric relationship between the length of digestive organs and the total length of the GIT as a proxy for the specimens' body size. Finally, we discuss how the digestive morphology of this group of primates may relate to possible evolutionary adaptations to different diets and trophic niches.

2 | MATERIALS AND METHODS

2.1 | Sample collection

We examined the GITs of 289 adult specimens of 13 species of 11 platyrrhine genera (Table 1) of three separate families (Atelidae, Cebidae, and Pitheciidae; Wang et al., 2019). All specimens were stored in the scientific collection of the Instituto Veterinario de Investigaciones de Trópico y de Altura de la Universidad Nacional Mayor de San Marcos, in Peru, and at the Mammal Collection of the Mamirauá Institute for Sustainable Development, in Brazil. Specimens were obtained from one community in the upland forest in the Yavarí-Mirin River basin (YMR; 04°S, 71°W) in Western Amazonia, North-eastern Peru, during 2009–2015; from five communities in the white-water flooded forest of the Mamirauá Sustainable Development Reserve (MSDR; 2°S, 65°W), Central Amazonia, Northern Brazil during 2002–2017; and from three communities in the upland forest of the Amanã Sustainable Development Reserve (ASDR; 01°S, 64°W), between 2002 and 2018, Central Amazonia, Northern Brazil. All locations have a typical equatorial climate, with relative humidity of 80%–100%,

TABLE 1 Taxonomic categories, sample size (*n*), body mass (kg), average of GIT sections' length measurement in cm (*X*), average of representativeness of each GIT section in percentage (%) and their respective standard deviations (±SD) from the sampled platyrrhine species.

Family				Esophagus	Stomach	Small intestine	Cecum	Colon	Rectum	Total
Subfamily	Genus	*n*	Body mass (kg)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD)
Atelidae										
Alouattinae	*Alouatta juara*	43	6.11[a]	10.9 (±3.1)	31.5 (±6.5)	144.1 (±35.5)	21.1 (±5.4)	84.8 (±18.5)	12.2 (±3.5)	304.6 (±46.9)
				3.7 (±1.3)	10.5 (±2.5)	46.8 (±6.7)	7.0 (±1.7)	27.9 (±4.8)	4.1 (±1.4)	
	A. seniculus	6	5.95[b]	13.3 (±2.3)	36.8 (±8.1)	146.5 (±27.4)	19.8 (±4.8)	97.0 (±7.6)	11.0 (±1.4)	324.5 (±30.4)
				4.1 (±0.7)	11.4 (±2.8)	44.9 (±5.1)	6.2 (±1.6)	30.0 (±1.8)	3.4 (±0.3)	
Atelinae	*Ateles chamek*	8	8.80[b]	15.1 (±2.2)	34.2 (±8.3)	270.5 (±35.7)	27.1 (±8.6)	70.5 (±12.1)	7.7 (±0.3)	425.0 (±34.9)
				3.6 (±0.5)	8.0 (±2.2)	63.6 (±3.9)	6.4 (±1.8)	16.6 (±3.8)	1.8 (±0.2)	
	Lagothrix poeppigii	82	7.10[c]	15.2 (±2.9)	32.1 (±7.5)	228.5 (±55.1)	31.6 (±9.5)	71.8 (±11.7)	7.8 (±2.3)	387.0 (±69.1)
				3.9 (±1.1)	8.3 (±1.8)	59.0 (±4.9)	8.2 (±2.2)	18.6 (±2.9)	2.0 (±0.7)	
Pitheciidae										
Callicebinae	*Plecturocebus cupreus*	4	1.17[d]	9.5 (±2.1)	18.1 (±2.50	99.4 (±6.6)	13.0 (±1.8)	39.6 (±3.6)	5.5 (±1.7)	185.1 (±5.5)
				5.1 (±1.1)	9.8 (±1.3)	53.7 (±2.2)	7.0 (±0.9)	21.4 (±2.5)	3.0 (±0.9)	
Pitheciinae	*Cacajao ouakary*	30	2.70[a]	12.1 (±2.4)	12.4 (±4.6)	187.2 (±10.0)	14.8 (±4.4)	40.9 (±0.9)	5.1 (±0.2)	271.9 (±17.5)
				4.5 (±1.0)	4.5 (±1.4)	68.9 (±0.6)	5.4 (±1.0)	15.1 (±0.7)	1.9 (±0.1)	
	C. ucayali	17	3.16[e]	11.2 (±2.2)	21.9 (±4.0)	236.7 (±34.3)	22.7 (±7.2)	54.6 (±9.7)	5.6 (±1.4)	352.8 (±47.8)
				3.2 (±0.5)	6.3 (±1.1)	67.1 (±3.0)	6.4 (±1.4)	15.5 (±2.0)	1.6 (±0.4)	
	Pithecia monachus	20	2.36[f]	13.2 (±2.1)	21.0 (±3.8)	165.1 (±38.8)	19.1 (±6.8)	59.8 (±10.8)	6.2 (±1.6)	284.4 (±52.3)
				4.6 (±0.9)	7.4 (±1.9)	58.1 (±4.4)	6.7 (±1.8)	21.0 (±3.2)	2.2 (±0.6)	
Cebidae										
Callitrichinae	*Leontocebus nigrifrons*	4	0.35[g]	6.5 (±1.0)	9.4 (±3.0)	63.9 (±13.4)	10.2 (±1.3)	29.0 (±4.6)	3.6 (±1.4)	122.5 (±19.7)
				5.3 (±0.2)	7.7 (±2.1)	52.2 (±4.3)	8.3 (±1.9)	23.7 (±2.5)	2.9 (±0.8)	
	Saguinus inustus	4	0.40[a]	6.5 (±0.0)	12.5 (±6.7)	80.6 (±58.3)	5.8 (±2.5)	23.5 (±5.4)	3.6 (±1.1)	132.5 (±64.5)
				4.9 (±2.2)	9.4 (±6.6)	60.8 (±12.9)	4.4 (±2.4)	17.7 (±5.5)	2.7 (±0.7)	
Cebinae	*Cebus albifrons*	15	2.90[a]	11.9 (±1.5)	19.2 (±3.9)	199.0 (±35.8)	5.6 (±1.3)	31.8 (±4.4)	5.9 (±2.2)	273.4 (±39.0)
				4.4 (±0.8)	7.0 (±1.6)	72.8 (±3.2)	2.0 (±0.5)	11.6 (±1.8)	2.2 (±0.7)	
	Sapajus macrocephalus	53	2.96[a]	12.2 (±1.9)	19.6 (±4.5)	186.8 (±43.6)	5.5 (±2.7)	33.2 (±5.7)	5.6 (±1.0)	263.1 (±48.7)
				4.6 (±1.1)	7.4 (±1.8)	71.0 (±4.9)	2.1 (±0.8)	12.6 (±2.7)	2.1 (±0.6)	

(Continues)

TABLE 1 (Continued)

Family				Esophagus	Stomach	Small intestine	Cecum	Colon	Rectum	Total
Subfamily	Genus	*n*	Body mass (kg)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD) % (±SD)	*X* (±SD)
	Saimiri macrodon	3	0.68[h]	10.0 (±1.7)	11.3 (±1.5)	96 (±5.6)	4.8 (±0.3)	17.0 (±2.6)	5.6 (±0.5)	144.8 (±11.4)
				6.9 (±0.7)	7.8 (±0.4)	66.3 (±1.4)	3.3 (±0.4)	11.7 (±0.9)	3.9 (±0.3)	

[a]This study.
[b]Smith and Jungers (1997).
[c]Lu (1999).
[d]Hershkovitz (1990).
[e]Ford (1994).
[f]Emmons and Feer (1990).
[g]Ravetta (2015).
[h]Jack (2011).

annual precipitation of 1500–3000 mm and temperatures that vary annually between 22 and 36°C.

Subsistence hunters from these three locations in the Amazon rainforest (Figure 1) hunt game species, such as ungulates, caviomorph rodents and primates for wild meat, especially in the high river-water period when fishing is less productive (Endo et al., 2016; Torres et al., 2018). Viscera from hunted animals were collected in these communities as part of long-term projects that aim to guarantee the sustainable management of wildlife and food sovereignty of local human populations. Data are gathered the communal participatory monitoring of the hunting activity. Monitoring by hunters consists of the voluntary provision of information on hunting events and of the donation of thoracic and abdominal organs of all hunted animals for research purposes.

The use of biological samples donated by subsistence hunters has provided relevant ecological (e.g., Mayor et al., 2015), reproductive (e.g., Andrade et al., 2018; El Bizri et al., 2018; Mayor et al., 2017), feeding (e.g., Jesus, Castilla Torres, et al., 2022; Torres et al., 2022) and parasitic (e.g., Conga et al., 2019; Gomez-Puerta et al., 2020; Jesus, Oliveira-Ramalho, et al., 2022) data affecting wildlife populations in these areas. These results have been transmitted to the participating communities in meetings and via educational materials. All data gathered are used in management decisions of the natural resources within their territories (IDSM, 1995; SEMA, 2020).

In Peru, subsistence hunting is legal, according to Law No 29.763/2011. In Brazil, rural, indigenous, and non-indigenous peoples inhabiting Type VI protected areas (sensu IUCN, as is the case of the reserves where samples were collected), can use their natural resources in accordance with management plans, including subsistence hunting (SNUC, 2000). These villages undertake subsistence activities such as timber extraction and collection of non-timber forest products as well as fishing, hunting, and small-scale agriculture. Primate hunting in our sample locations has been considered sustainable (Mayor et al., 2015; Pereira et al., 2017), even for endangered (*Ateles chamek* and *Lagothrix poeppigii*) and vulnerable (*Cacajao ucayali*) species listed in IUCN Red List (Alves et al., 2021; Aquino et al., 2022; Stevenson et al., 2021).

During specimen preparation, the viscera of hunted animals are usually discarded in the forest, given to domestic animals (e.g., dogs) or thrown into the river. Hunters who participated in our study were trained to remove all thoracic, abdominal, and pelvic organs from hunted primates complete with the perineal region. These were then preserved in large plastic vats containing buffered 4% formaldehyde solution (vol/vol), following Mayor et al. (2017). By training hunters to donate viscera to the project rather than dispose of them it reduced parasitic infections (e.g., dogs are infected by endoparasites when consuming infected viscera, and throwing them in the river can attract piranhas and caimans, which increases the risk of accidents). No animals were killed other than those harvested as part of the local hunters' subsistence activities and no hunter received any incentive to hunt.

The sampling protocol was approved by the Chico Mendes Institute for Biodiversity Conservation in Brazil (License SISBIO no

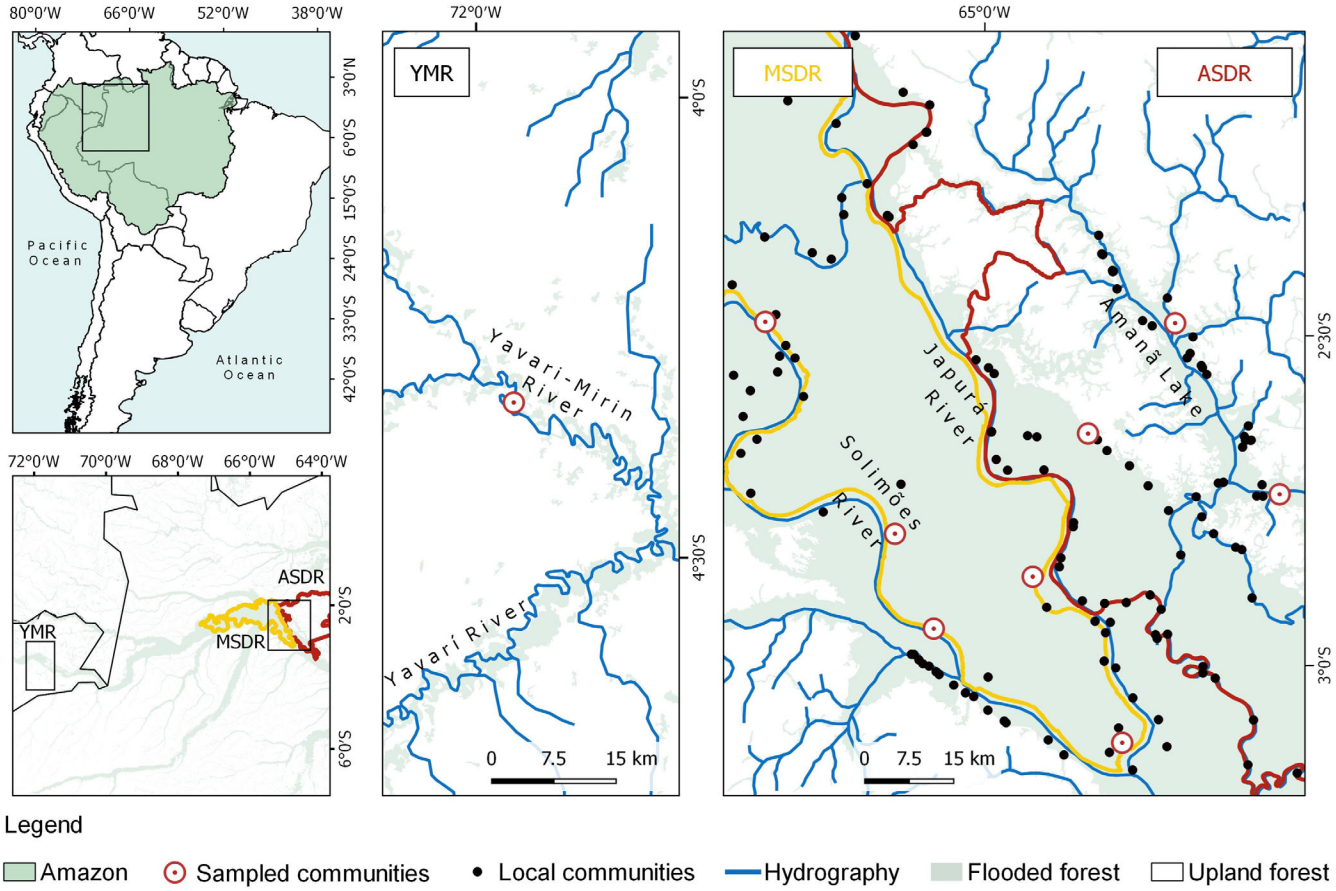

FIGURE 1 Map of the sampling area's locations in Western (Yavarí-Mirin River—YMR) and Central Amazonia (Mamirauá Sustainable Development Reserve—MSDR, and Amanã Sustainable Development Reserve—ASDR).

29092-1) and by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0229-2011-DGFFS-DGEFFS).

2.2 | Biometry of tubular digestive organs

Area and volume of digestive organs can change when these are full. By contrast, the length of the organs is easier to measure with less error. This measurement consistency is especially important here because we have no control over the fullness of the GIT in the specimens. Therefore, the relative length of each digestive organ can provide more precise and reliable information to estimate the relationship between GIT and diets (Duque-Correa et al., 2021).

After removing the mesentery from each GIT, we measured the length (in cm) of the esophagus, stomach, small intestine, cecum, colon, and rectum using a flexible, non-elastic measuring tape. The esophagus length was taken from the pharyngoesophageal junction to its connection with the stomach, the gastroesophageal junction. The stomach was measured at its longest curvature and the intestinal portions at the antimesenteric edge. The length of the small intestine was from the stomach pyloric sphincter to the ileocolic papillae (cecum entry). The cecum at its longest curvature was from the ileocolic papillae to the blind end of the organ. The colon was measured from the ileocolic papillae to the final portion of colon (often sacculated), and the rectum from the final portion of the colon to the anus. The total GIT length of each specimen was the sum of all measurements of each digestive organ.

2.3 | Statistical analyses

We used descriptive statistics to report the mean and SD of the absolute and relative (percentage) length of each digestive organ per species. Since we did not have information on individual body mass for all samples collected, we used the mean body mass recorded by hunters in the ASDR and MSDR, and from the literature for YMR (see Table 1). We performed a Pearson correlation analysis to assess the relationship between mean total GIT length and mean body mass of each genus to validate the use of total GIT length as an alternative for body size. There was an allometric relationship close to geometric scaling ($b \sim 0.33$), although not included in the 95% CI ($b = 0.38$, 95% CI: 0.37; 0.39), there was a strong linear relationship ($r = 0.9309$; Figure 2) indicating the GIT length is a good proxy for body mass among the studied primate genera. In this case, the allometric scaling approximates the general geometric principles expected for

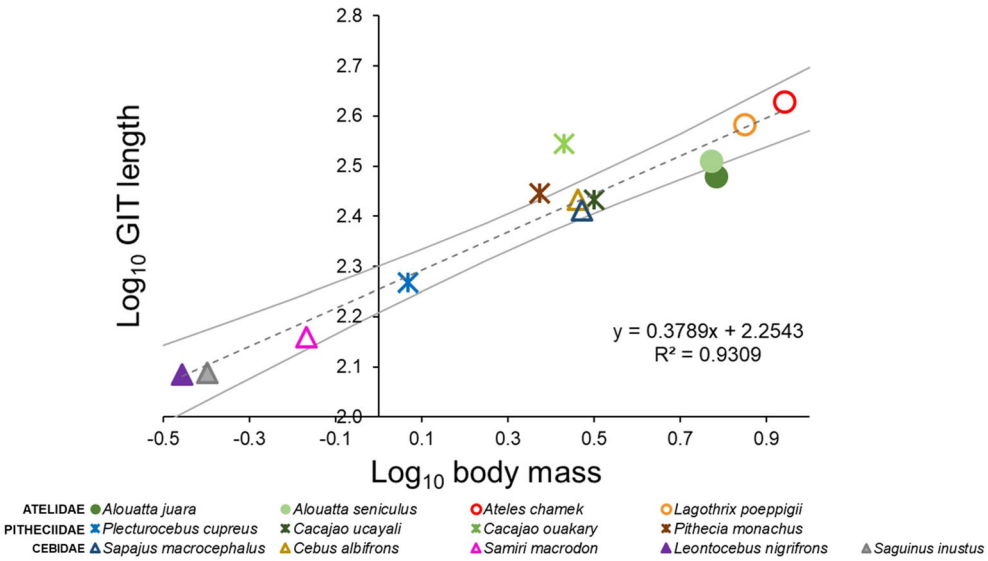

FIGURE 2 Correlation between the log mean total length of the gastrointestinal tract (GIT) and the log mean body mass for each primate genus evaluated. The dotted line is the regression trend line. Light gray lines represent the 95% confidence interval (CI). Circles represent the Family Atelidae (Subfamily Alouattinae: filled circle; Subfamily Atelinae: unfilled circles), asterisks represent the Family Pitheciidae (Subfamily Callicebinae: blue asterisks; Subfamily Pitheciinae: green and brown asterisks), triangles represent the Family Cebidae (Subfamily Cebinae: unfilled triangles; Subfamily Callitrichinae: filled triangles).

relationships between a measure of length and a multi-dimensional measure (such as weight, area, or volume), if primates GIT length scales at a multiple power of one-third of body mass (Calder, 1996; van Soest, 1996).

We analyzed the association between the length of the digestive organs and GIT length by determining the allometric relationships using linear regressions. We used log-transformed data to make the allometric relationships linear, since they are empirically exponential: $\log Y = (b)\log X + \log(a)$, where Y is the dependent variable (i.e., length of a given digestive organ) and X is the independent variable (i.e., total GIT length as a proxy of body size); "a" refers to the intercept point of the relationship and "b" represents the allometric coefficient (i.e., a dimensioning scale for the allometric relationship) (Huxley & Teissier, 1936; Peters & Peters, 1986). For a length-length scaling, a linear relationship, with an isometric scaling ($b = 1$) is expected to be found (Gayon, 2000; Huxley & Teissier, 1936). However, when $b > 1$ the allometry is positive, that is, the organ would be larger than expected for a primate with that given total GIT length. Likewise, if $b < 1$, the allometry is negative and the GIT section is smaller than expected (Gayon, 2000; Huxley & Teissier, 1936). For these analyses, we used the mean values of each digestive organ per genus to avoid biases resulting from different sample sizes for each genus, and to use statistically independent data (see Woodall & Skinner, 1993).

Based on "a" and "b" parameters of the allometric equations of each digestive organ, we calculated the quotients of differentiation (Qs) of each digestive organ for each individual primate following Martin et al. (1985), in which $Q = \text{antilog}\,[\log(\text{digestive organ length}) - ((b) \times \log(\text{GIT total length}) - \log(a))]$. The use of Q eliminates the effect of different body sizes among species, allowing a direct comparison of GIT among genera (Martin et al., 1985; Woodall & Skinner, 1993). We measured the esophageal quotient (EQ), gastric quotient (GQ), small intestine quotient (IQ), cecal quotient (CeQ), colonic quotient (CoQ) and rectal quotient (RQ). A $Q = 1$ indicates that the measurement of the given organ is as predicted by the best fit line of the allometric relationship; $Q > 1$ indicates that the organ is larger than predicted; and $Q < 1$ indicates that the organ is smaller than predicted. Therefore, a higher absolute value of Q means a more specialized structure.

Finally, to analyze the dissimilarities in the GIT among the different species, we first reduced the multidimensionality of the data using a principal coordinates analysis (PCoA), based on Euclidean distances of the Q of each organ for each specimen, using R 3.5.2 (R Core Team, 2019). As a complementary approach, we performed an analysis of similarity (ANOSIM) to test whether the differences observed among species in the PCoA are greater than within each genus.

3 | RESULTS

We found a large variation in the relative length of tubular digestive organs among the studied species. Organs with a greater interspecies variation relative to the overall GIT length were: small intestine, 44.9%–46.8% (*Alouatta* sp.)—72.8% (*Cebus albifrons*); cecum, 2.0% (*C. albifrons*)—8.3% (*Leontocebus nigrifrons*), and colon, 11.6% (*C. albifrons*)—27.9%–30% (*Alouatta*). Absolute and relative biometric measures of the digestive organs for each species are given in Table 1, and images of the GIT for each genus can be seen in Figure 3 (also available in the freely e-book "Amazon Wild Species Anatomy Atlas," Mayor & López-Plana, 2021, kindly provided by the authors).

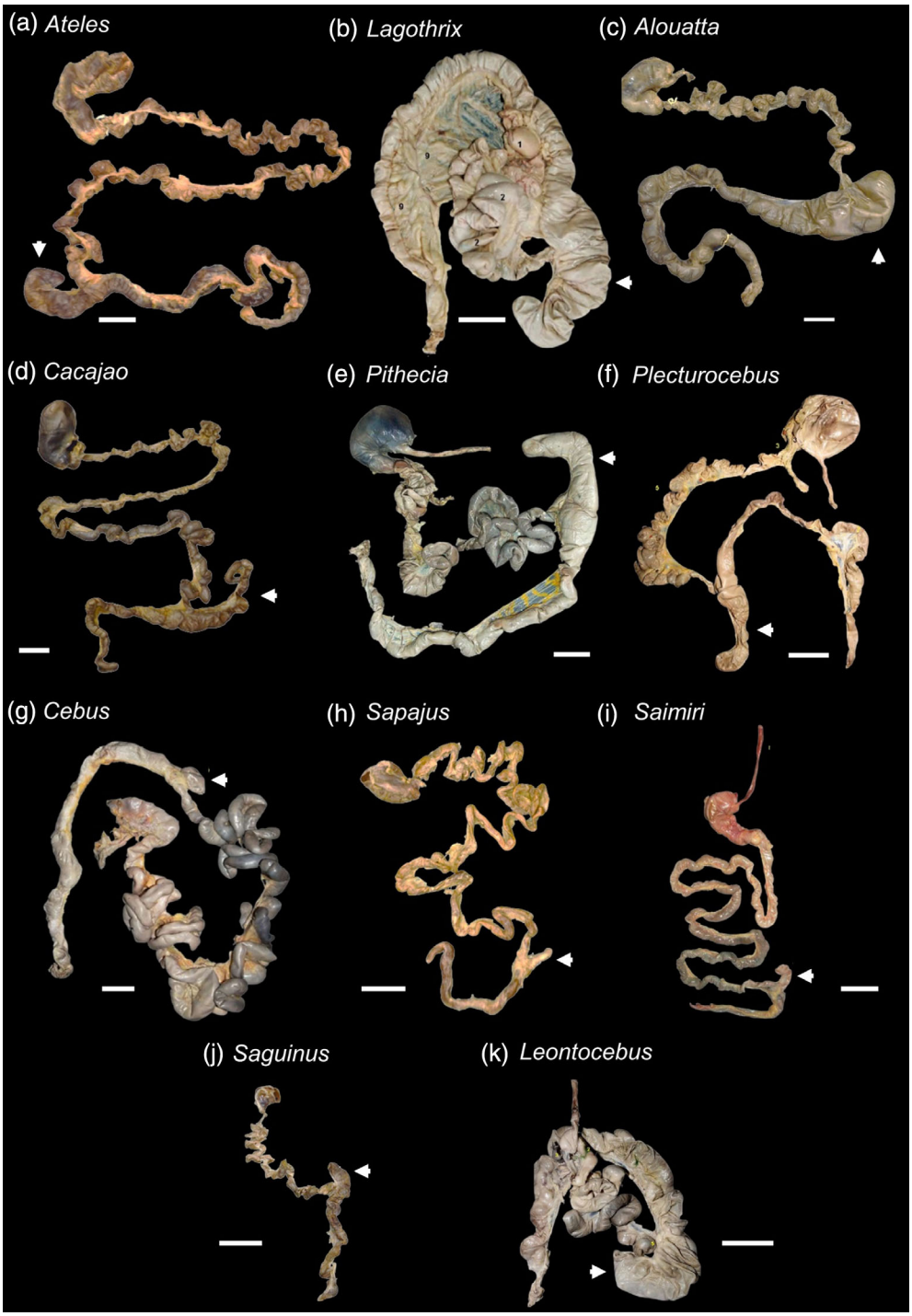

FIGURE 3 The gastrointestinal tracts (GITs) of the 11 frugivorous primates. All images show the complete GIT, except image G (*Cebus*) in which the image was taken after the stomach was removed. The cecum is indicated by arrowhead as a reference. The white scale bars represent 5 cm. Images B, E, F, G, I, and K are also available in the freely available e-book "Amazon Wild Species Anatomy Atlas" (Mayor & López-Plana, 2021), and have been kindly authorized by the authors for inclusion in this panel.

Allometric scaling coefficients were highly variable across all digestive organs ($b = 0.58–1.11$) (Figure 4). The allometry of esophagus, rectum and stomach were negative, scaling at a ratio smaller than total GIT length ($b < 1$), whereas for the small intestine, cecum and colon it was isometric ($b \sim 1$), that is, the scaling of these digestive organs was proportional to the scaling of total GIT length.

Differentiation quotient means (±SD) of the digestive organs are given in Table 2. The EQ ranged from 0.8 (*C. ucayali*) to 1.3 (*Saimiri macrodon*). *Cacajao* sp. also presented the lowest GQs (GQ = 0.6 and 0.8 to *C. ouakary* and *C. ucayali*, respectively) and *Alouatta* the highest (GQ = 1.3 and 1.5 to *Alouatta juara* and *A. seniculus*, respectively). Quotients of the small intestine (IQ) presented the lowest range of differentiation among primates, from 0.8 (*Alouatta* sp.) to 1.2 (*C. albifrons*, *Sapajus macrocephalus* and *C. ouakary*), while all three components of the large intestine had the greatest differentiation. The lowest value of the CeQ was for *C. albifrons* and *S. macrocephalus* (CeQ = 0.4) while the highest was from *L. nigrifrons* (CeQ = 1.8). The CoQ ranged from 0.7 for cebines (*C. albifrons*, *S. macrocephalus*, and *S. macrodon*) to 1.6 for *Alouatta*. Finally, *Cacajao* had the lowest RQ

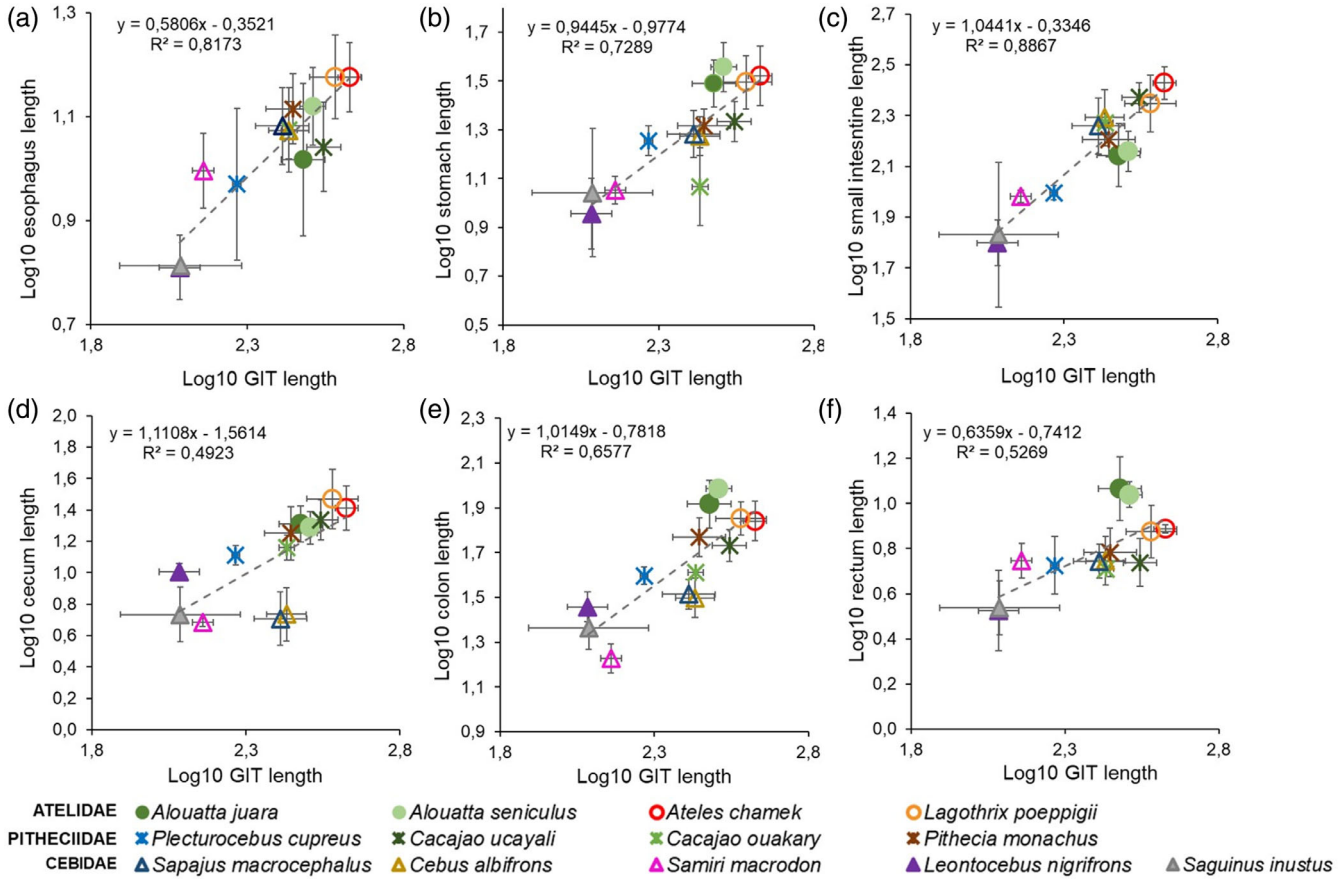

FIGURE 4 Circles represent the Family Atelidae (Subfamily Alouattinae: filled circle; Subfamily Atelinae: unfilled circles), asterisks represent the Family Pitheciidae (Subfamily Callicebinae: blue asterisks; Subfamily Pitheciinae: green and brown asterisks), triangles represent the Family Cebidae (Subfamily Cebinae: unfilled triangles; Subfamily Callitrichinae: filled triangles).

(0.8) and *Alouatta* the highest (RQ = 1.6 and 1.7 to *A. juara* and *A. seniculus*, respectively).

The two first axes of the PCoA explained 77% of the variation in the general GIT structure among primate genera (Figure 5). There was a high differentiation in structure of the digestive organs among genera determined especially by the small intestine, colon, and cecum in axis 1, and cecum in axis 2, and such differences among genera were higher than within genera (ANOSIM $R = 0.537$, $p < 0.001$). *Alouatta* specimens clearly separated from the other genera based on dissimilarities in gastric, colonic, and RQs, and concentrating on the left side of the axis 1. In contrast, all cebines (*Sapajus*, *Cebus*, and *Saimiri*) were grouped together, with *Cacajao* marginally nearby, on the right side of the axis 1 by the similarities in their IQs. The remaining genera are overlapped in relation to the cecum, in the axis 2.

4 | DISCUSSION

The digestive morphology of primates has been characterized by a strong phylogenetic signal, suggesting a high similarity of digestive morphological features among related species (Duque-Correa et al., 2021; McGrosky, Meloro, et al., 2019). Fruit consumption is widespread in platyrrhines (Hawes & Peres, 2014b), and their digestive morphology has been commonly considered unspecialized compared to the more specialized faunivorous or folivorous mammals (to check carnivore GIT images see McGrosky et al., 2016, for ruminant herbivores McGrosky, Codron, et al., 2019, and for primates, McGrosky, Meloro, et al., 2019), usually positioned in an intermediate point between these two dietary patterns at the GIT structure (Chivers, 1998; Chivers & Hladik, 1980; Izawa, 1975). However, our results demonstrate remarkably diverse adaptations in the digestive organs of 11 genera of Amazonian primates, especially in the small intestine, cecum, and colon length. Herein, we discuss in detail the expected relative length similarities and variations among digestive organs in the studied primate genera and explore some possible explanations and implications for such differences.

Cacajao and *Pithecia*, two genera known to be seed predators (Norconk, 2020), presented a longer GIT in relation to the expected given their body sizes, whereas *Alouatta*, the most folivorous platyrrhine (Crockett, 1998), had a shorter GIT. This is unexpected especially because mammals that consume less digestible items (e.g., leaves), as in *Alouatta*, should possess a longer GIT to allow more space for fermentation (Stevens & Hume, 2004). However, it is possible that other dimensions of the GIT not evaluated here, such as

TABLE 2 Mean quotients (esophageal, gastric, small intestine, caecal, colonic, and rectal) and the standard deviations (±SD) of digestive organs per species.

Family Subfamily	Genera	Esophageal quotient (EQ)	Gastric quotient (GQ)	Small intestinal quotient (IQ)	Cecal quotient (CeQ)	Colonic quotient (CoQ)	Rectal quotient (RQ)
Atelidae							
Alouattinae	*Alouatta juara*	0.9 (±0.3)	1.3 (±0.3)	0.8 (±0.1)	1.4 (±0.3)	1.6 (±0.3)	1.8 (±0.6)
	A. seniculus	1.0 (±0.2)	1.5 (±0.3)	0.8 (±0.1)	1.2 (±0.3)	1.7 (±0.1)	1.5 (±0.2)
Atelinae	*Ateles chamek*	1.0 (±0.1)	1.1 (±0.3)	1.0 (±0.1)	1.2 (±0.4)	1.0 (±0.2)	0.9 (±0.1)
	Lagothrix poeppigii	1.1 (±0.2)	1.1 (±0.3)	0.9 (±0.1)	1.6 (±0.4)	1.1 (±0.2)	1.0 (±0.3)
Pitheciidae							
Callicebinae	*Plecturocebus cupreus*	1.0 (±0.2)	1.2 (±0.2)	0.9 (±0.0)	1.4 (±0.2)	1.2 (±0.1)	1.1 (±0.3)
Pitheciinae	*Cacajao ouakary*	1.0 (±0.2)	0.6 (±0.2)	1.2 (±0.0)	1.1 (±0.2)	0.8 (±0.0)	0.8 (±0.0)
	C. ucayali	0.8 (±0.1)	0.8 (±0.1)	1.1 (±0.1)	1.2 (±0.3)	0.9 (±0.1)	0.7 (±0.2)
	Pithecia monachus	1.1 (±0.2)	1.0 (±0.2)	0.9 (±0.1)	1.3 (±0.3)	1.2 (±0.2)	1.0 (±0.2)
Cebidae							
Callitrichinae	*Leontocebus nigrifrons*	0.9 (±0.1)	0.9 (±0.3)	0.9 (±0.1)	1.8 (±0.4)	1.4 (±0.1)	0.9 (±0.3)
	Saguinus inustus	0.9 (±0.2)	1.2 (±0.8)	1.0 (±0.2)	1.1 (±0.5)	1.1 (±0.3)	0.9 (±0.1)
Cebinae	*Cebus albifrons*	1.0 (±0.1)	0.9 (±0.2)	1.2 (±0.0)	0.4 (±0.1)	0.7 (±0.1)	0.9 (±0.3)
	Sapajus macrocephalus	1.1 (±0.2)	1.0 (±0.2)	1.2 (±0.1)	0.4 (±0.2)	0.7 (±0.2)	0.9 (±0.2)
	Saimiri macrodon	1.3 (±0.2)	0.9 (±0.1)	1.1 (±0.0)	0.7 (±0.1)	0.7 (±0.1)	1.3 (±0.1)

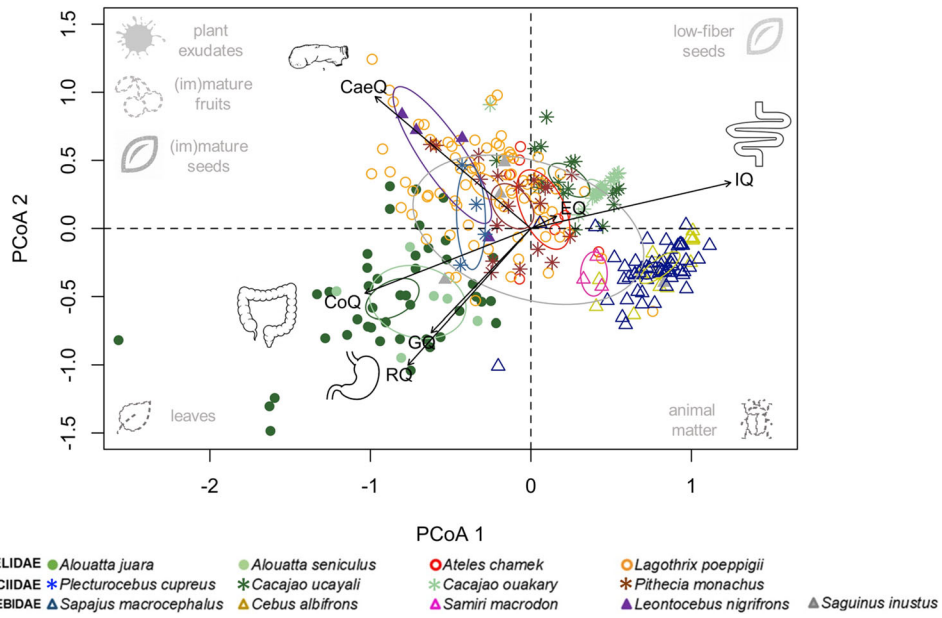

FIGURE 5 Principal Coordinates Analysis (PCoA) comparing the individual gastrointestinal variation based on Euclidean distance (51% of explanation for the axis 1 and 26% of axis 2), where CeQ, cecal quotient; CoQ, colonic quotient; EQ, esophageal quotient; GQ, gastric quotient; IQ, small intestine quotient; RQ, rectal quotient. Ellipses represent 95% confidence intervals and the arrows indicate the direction and intensity of the influence of variables on the ordering of the data, with illustrative images of the organs responsible for the clusters, and in light gray items foods that may be related to the differences in morphological characteristics.

width or expansive capacity, may compensate for the observed difference (e.g., Duque-Correa et al., 2021; Woodall & Skinner, 1993). We suggest this is a potential topic for future investigations.

As reported by McGrosky, Meloro, et al. (2019), we observed a strong positive correlation between total GIT length and body mass, following an allometric scaling that approximates the general geometric relationship between length and weight (Calder, 1996; van Soest, 1996). On the other hand, based on a length-length scaling, the variation found on allometric coefficients indicates that the digestive organs do not follow the same dimension rule relative to total GIT

length. This indicates that although the GIT length is relatively well-conserved in platyrrhines (e.g., McGrosky, Meloro, et al., 2019), different adaptations in the component organs exist among these primates.

In functional terms, the esophagus is responsible for the passage of food and fluids from the pharynx to the stomach (Treuting et al., 2018), while the rectum stores fecal matter and facilitates water absorption and excretion of feces (Washabau & Day, 2013). The biometric variations found in the esophagus and rectum are likely to reflect variations in primates' body size and structure, although the rectum of *Alouatta* was observed to be larger than in the other genera, suggesting a differentiated role in water and nutrient absorption during its post-cecocolic fermentation (McGrosky, Codron, et al., 2019).

The stomach is responsible for storing consumed food and processing easily accessible proteins (Lambert, 1998; Treuting et al., 2018) through the action of pepsinogen in an acidic environment provided by hydrochloric acid production (Stevens & Hume, 2004). Stomach size varies according to the quality and volume of food consumed (Anken-Simons, 2007; Milton, 1984). Lower quality foods tend to be consumed in greater volumes to compensate for their lower energy content (Burini & Leonard, 2018), which in turn influences gastric transit. Gastric emptying time in primates may vary from 2.5 to 7.2 h (Chen et al., 2008). This is compatible with the morphological variations of stomachs detected here. The relatively larger stomach of *Alouatta* can store larger food volumes, consistent with their highly folivorous diet (~50%, Norconk et al., 2009) and longer food transit time (e.g., ~35 h for *A. seniculus*, Crissey et al., 1990). *Cacajao*, by contrast, presents the lowest stomach capacity relative to its body size, suggesting a diet composed mostly of highly digestible items, such as arthropods (e.g., Barnett et al., 2013; Jesus, Castilla Torres, et al., 2022; Torres et al., 2022) and seeds with lower fiber content (Norconk, 2020), and a short transit time (e.g., ~5 h for *C. calvus*, Milton, 1984).

The small intestine, the main organ responsible for the absorption of nutrients (Treuting et al., 2018); a larger small intestine produces a greater area for nutrients to be absorbed, especially in diets composed of highly digestible items (Anken-Simons, 2007). Comparatively, cebines have a larger small intestine and a smaller large intestine compared to the remaining groups, suggesting that they have the lowest fermentative capacity among the studied primates. The simplified structure of the digestive morphology of cebines resembles that of carnivorous mammals (e.g., felines, McGrosky et al., 2016) and is compatible with their rapid food transit time (~3.5 h; Milton, 1984) and with a diet composed of high digestible items as indicated by the high arthropod richness and diversity consumed (Torres et al., 2022) which represent 20%–60% of their diets (Ferrari & Lopes, 1995; Norconk et al., 2009). Seed consumption by the largest cebines (~8% of feeding records, Norconk et al., 2009) require cognitive skills (e.g., tool use, Fragaszy et al., 2010) and/or adaptative morphology (robust teeth and strong jaws) for breaking rigid endocarps (e.g., Norconk et al., 2009; Wright, 2005), but there are low requirements for seed digestion.

Highest biometric variations among platyrrhines were observed in the cecum and colon. The increase in size of these organs is related to cecocolic fermentation (Lambert, 1998), where the intestinal microbiome acts to decompose structural carbohydrates and/or detoxify the chemical defenses of the consumed plant matter (Garber et al., 2019; Smodlaka & Henry, 2013). The elongation of the colon accentuates the differentiation of *Alouatta* from other primates in the PCoA compatible with this organ's role in fermentation and absorption of water and nutrients in species with a more folivorous diet (Espinosa-Gómez et al., 2013). As a consequence of cecocolic fermentation, foods with higher fiber contents and/or plant defensive compounds cannot be fully digested beforehand (Murphy & Linhart, 1999), so it is reasonable to expect that the small intestine of these primates is comparatively shorter, especially in more folivorous primates such as *Alouatta*.

In mammals, an enlarged cecum is known to be an adaptation for fermentation in high-fiber diets (Louw, 1993; McGrosky, Codron, et al., 2019), and often associated with coprophagy (e.g., Sakaguchi, 2003). However, in platyrrhines, cecal fermentation also is important in the breakdown of exudates (difficult-to-digest beta-linked polysaccharides, Lambert, 1998; Oftedal, 1991), such as the gum consumed by callithrichines (Ferrari et al., 1993; Ferrari & Martins, 1992), in the detoxification of immature fruits and seeds in pitheciids (Norconk, 2020; Rosenberger, 1992), and in the consumption of ripe fruits by *Ateles* and *Lagothrix* (Kinzey & Norconk, 1993; Stevenson et al., 2015).

All platyrrhine primates analyzed here had important differences in the cecum and colon. As shown in the PCoA, the morphological structure of the GIT in *Cacajao* is closer to that of cebines than other pitheciids, especially by its longer small intestine. This is unexpected, since observational studies in *Cacajao* indicate that 85% of their diet are immature seeds and unripe fruits (Bowler & Bodmer, 2011; Norconk et al., 2009), which would theoretically require cecal detoxification (Ayres, 1989; Rosenberger, 1992). Nonetheless, studies of stomach contents reported the consumption of high diversity of arthropods for *Cacajao*, comparable to the diets of *Cebus* and *Sapajus*, while *Pithecia* consumes comparatively a lower diversity of arthropods (Jesus, Castilla Torres, et al., 2022; Torres et al., 2022). Hence, the unexpected differentiation in the digestive morphology of *Cacajao* and its high similarity with cebines may be explained by the long small intestine related to the digestion of large amounts of animal matter.

Overall, platyrrhines exhibited marked structural differences in their GIT that are most likely to be related to their diet. Diets of platyrrhines can be broad, differing largely in the relative amounts of arthropods, seeds and structural parts of plants consumed by each species (Norconk et al., 2009). Thus, the traditional classification of species into categories such as faunivores, frugivores and folivores may not be appropriate for this group (Anken-Simons, 2007), and may be the reason behind a lack of statistical association between digestive morphology and diet in past studies, which were based mainly on these categories (Duque-Correa et al., 2021; McGrosky, Meloro, et al., 2019).

From an evolutionary perspective, the digestive structure in platyrrhines may have undergone divergent derivations through natural selection, under the influence of multiple factors, such as phylogeny,

competition, body size, diet, and frequency of food consumption (Hladik & Chivers, 1994; Pereira et al., 2016). To the best of our knowledge, the oldest known platyrrhine species is dated to the late Eocene, about 36 million years ago (Wang et al., 2019), and the morphology of its molar teeth indicates it had an insectivorous-frugivorous diet (Bond et al., 2015; Kay, 2015). Based on our results, it is likely that ancestral platyrrhines had a diet of highly digestible items. This suggests they would have a short large intestine and a GIT structure similar to cebines.

Although our data are based solely on comparisons of relative GIT organ length, they may provide insight into primate evolution and coincided with the Eocene angiosperm radiation between 56 and 34 million years ago (Sussman, 1991). For example, the selection of attractive fleshy fruits with high energy content by potential consumers, offset by efficient seed dispersal mechanisms, can lead to high competition among frugivorous primates, especially when the plant-frugivore interaction is not species-specific (Hladik & Chivers, 1994). Thus, the evolution of the physiological, metabolic and cognitive-behavioral strategies of primates, allied with the specialization of cecocolic fermentation in various species which consumed foods of greater digestive difficulty, such as unripe fruits, immature seeds and, finally, vegetative items, plays an important role in reducing the competition for items of greater digestibility such as fruits, and allows the coexistence of the different primate genera (Kay et al., 2013; Lambert, 1998; Rosenberger et al., 2011). Thus, the expanded food niches of ancestral platyrrhines may have promoted the diversification of the three current taxonomic families of platyrrhines in the Oligocene, about 25 million years ago (Wang et al., 2019).

5 | CONCLUSIONS

Our study describes morphological similarities and variations in tubular digestive organs among 11 platyrrhine genera, showing important differences especially in the large intestine. The digestive performance of cebines (Cebidae, Cebinae) is similar to expected for ancestral platyrrhines, with low fermentation capacity, which limits their diets to easily digestible reproductive plant items and animal matter. On the other hand, the greater cecocolic development and symbiosis with cellulolytic and/or detoxifying organisms for genera such as *Alouatta* and *Leontocebus* may expand the consumption of food items, supposedly decreasing food competition among different primate genera and facilitating their coexistence.

AUTHOR CONTRIBUTIONS

Anamélia de Souza Jesus: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (lead); writing – original draft (lead); writing – review and editing (lead). **Hani R. El Bizri:** Conceptualization (supporting); formal analysis (equal); methodology (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal). **Julia E. Fa:** Conceptualization (supporting); methodology (supporting); writing – review and editing (equal). **João Valsecchi:** Conceptualization (supporting); methodology (supporting); supervision (supporting); writing – review and editing (supporting). **Rafael Magalhães Rabelo:** Methodology (supporting); supervision (supporting); writing – review and editing (equal). **Pedro Mayor:** Conceptualization (equal); investigation (equal); methodology (equal); supervision (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

The dataset that supports the findings is available as supplementary material.

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