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Tooth chipping patterns and dental caries suggest a soft fruit diet in early anthropoids

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Abstract

Objectives: Fossils from the Fayum Depression, Egypt, are crucial for understanding anthropoid evolution due to the abundance of taxa and the time interval they represent (late Eocene to early Oligocene). Dietary and foraging behavioral interpretations suggest fruits were their dominant food source, although hard foods (e.g., seeds and nuts) and leaves could have been important dietary components for particular groups. In this study, we compare dental chipping patterns in five Fayum primate genera with chipping data for extant primates, to assess potential hard object feeding in early anthropoids.

Materials and Methods: Original specimens were studied (*Aegyptopithecus*: $n = 100$ teeth; *Parapithecus*: $n = 72$, *Propliopithecus*: $n = 99$, *Apidium*: $n = 82$; *Catopithecus*: $n = 68$); with the number, severity, and position of chips recorded. Dental caries was also recorded, due to its association with soft fruit consumption in extant primates.

Results: Tooth chipping was low across all five genera studied, with a pooled chipping prevalence of 5% (21/421). When split into the three anthropoid families represented, chipping prevalence ranged from 2.6% (4/154) in Parapithecidae, 6% (12/199) in Propliopithecidae, and 7.4% (5/68) in Oligopithecidae. Three carious lesions were identified in Propliopithecidae.

Discussion: The chipping prevalence is low when compared to extant anthropoids (range from 4% to 40%) and is consistent with a predominantly soft fruit diet, but not with habitual hard food mastication. The presence of caries supports consumption of soft, sugary fruits, at least in Propliopithecidae. Our results add support for low dietary diversity in early anthropoids, with soft fruits as likely dominant food sources.

KEYWORDS
dental caries, Egyptian Fayum, primate evolution, Propliopithecidae, tooth fractures

1 | INTRODUCTION

At least 21 genera of primates have been described from the Fayum Depression of Egypt, including 12 anthropoids (Seiffert, 2012). Five of these anthropoid genera are included in this study: *Aegyptopithecus*, *Apidium*, *Parapithecus*, *Propliopithecus*, and *Catopithecus*. These genera range from the late Eocene through the early Oligocene epochs (between 34 and 29 Ma; Simons et al., 1999; Seiffert, 2006). Due to the relatively large sample size available and the crucial evolutionary timing (i.e., close to the divergence of several key anthropoid clades/families, including Cercopithecidae-Hominoidea, and Catarrhini-Platyrrhini), anthropoid fossils from the Fayum offer the opportunity to study how diet and behavior may have shaped the evolution and dispersal of anthropoid primates.

Aegyptopithecus, *Apidium*, *Parapithecus*, *Propliopithecus*, and *Catopithecus* are anthropoids, being more closely related to living platyrrhines and catarrhines than to *Tarsius* (Kay et al., 1997). There is debate around the placement of different specimens into particular taxa, and how genera and families should be placed within the anthropoid phylogenetic tree, especially in relation to extant groups (e.g., Gingerich, 1978; Harrison, 2013; Jaeger et al., 2019; Seiffert et al., 2010; Simons, 1995; Szalay & Delson, 1979). *Aegyptopithecus* and *Propliopithecus* are closely related, both belonging to the Propliopithecidae superfamily. Some researchers suggest they should be placed within the same genus, in which case all material referred to *Aegyptopithecus* would be placed under *Propliopithecus*, although this is still debated (Andrews, 1985; Harrison, 1987; Harrison, 2013; Seiffert et al., 2010). Propliopithecidae includes taxa considered as some of the earliest catarrhine relatives, with included genera falling in basal or stem positions relative to Catarrhini (Ankel-Simons et al., 1998; Fleagle & Kay, 1987; Kay et al., 1981; Seiffert et al., 2020; Seiffert & Simons, 2001). *Apidium* and *Parapithecus* are part of the family Parapithecidae, and although some researchers consider them stem catarrhines (e.g., Jaeger et al., 1998), others suggested a stem anthropoid placement for the clade (Fleagle & Kay, 1987; Harrison, 2013; Ross et al., 1998; Seiffert et al., 2005; Seiffert et al., 2020; Simons, 2001). *Catopithecus*, in the family Oligopithecidae, has also been considered both a catarrhine (Rasmussen, 2002; Seiffert et al., 2005, 2010, 2020) and stem anthropoid (Harrison, 2013; Kay et al., 1997; Ross et al., 1998).

Research reconstructing the diets of Fayum anthropoids has mostly focused on tooth morphology and size (e.g., Cachel, 1983; Fleagle, 1988; Fleagle & Kay, 1985; Kay & Simons, 1980, 1983; Kirk & Simons, 2001). These studies suggest Fayum anthropoids were frugivores, although *Apidium* (*Ap. phiomense*) has been suggested to consume harder foods based on its thicker enamel, and *Parapithecus* (*Par. grangeri*) has been suggested to have had a more folivorous diet based on molar morphology (Fleagle & Kay, 1985; Kay & Simons, 1980). Body size is also important for dietary reconstructions. Based on extant primate body size/diet comparisons with early anthropoids, it has been suggested they likely supplemented their fruit diet with leaves, rather than with insects (Bajpai et al., 2008; Williams et al., 2010). Dental microwear analysis and microstructure of enamel both support a predominantly frugivore diet in Fayum anthropoids, but also suggest *Aegyptopithecus* consumed hard foods, while *Apidium* was less likely to exhibit this behavior (Teaford et al., 1996). A recent study utilizing dental topography metrics in mandibular second molars suggests *Aegyptopithecus* had a Pitheciine-like strategy of seed predation, while *Apidium* likely consumed berry-like compound fruits with hard seeds (Morse et al., 2023).

In this study, we utilize frequencies of antemortem enamel chipping prevalence to evaluate the likelihood of habitual durophagy in Fayum anthropoids. Chipping is suggested to be a reliable indicator of hard object mastication, with hard object feeders showing high rates of chipping (Fannin et al., 2020; Towle et al., 2023a; Towle & Loch, 2021). Dental caries has been associated with soft fruit eating in extant anthropoids (Colyer, 1931; Lovell, 1990; Stoner, 1995; Towle et al., 2022) and therefore would be supportive of soft/sugary fruit consumption if found in association with low rates of tooth fractures in early anthropoids. Based on previous research on Fayum anthropoids, including the studies outlined above, we tested two hypotheses. The first hypothesis suggests that if Fayum anthropoids were habitual durophages, they would display high levels of antemortem chipping, similar to frequencies seen in extant hard object feeding primates. The alternative hypothesis suggests that if Fayum anthropoids were generally frugivorous, with soft fruits the predominant food source, they would display (1) low and uniform enamel chipping frequencies, similar to extant frugivorous analogs and (2) would develop caries since ripe soft fruits contain high concentrations of sugars.

2 | MATERIALS AND METHODS

The sample consists of five genera. These include 21 *Aegyptopithecus* individuals (*A. zeuxis*), 19 *Apidium* (*Ap. phiomense*), 16 *Parapithecus* (*Par. grangeri*), and 11 *Catopithecus* (*C. browni*). All genera are represented by the species mentioned. *Propliopithecus* is represented by two species: *Pro. chirobates* (17 individuals) and *Pro. ankeli* (1 individual). All specimens are curated at the Duke Lemur Center Museum of Natural History at Duke University, Durham, USA (accession code DPC). Information on each specimen (i.e., collection location, age and species identification) is detailed in Table 1. The data that supports the findings of this study are available in the supplementary material.

An overall chipping prevalence (i.e., percentage of chipped permanent teeth) was calculated for each genus. Chipping prevalence was also compared for anterior vs. posterior teeth, with premolars and molars grouped as posterior teeth, and incisor and canines as anterior teeth. However, this split is not convenient for studies that compare species with different dental formulas (e.g., *Parapithecus* does not have permanent lower incisors) (Table 1). Therefore, the study focused on the overall chipping prevalence and comparisons with extant anthropoids. Dental formulae for each species were based on the literature (e.g., Seiffert et al., 2010; Simons, 1986; Simons, 2001). Quarry age is based on age ranges in Seiffert et al. (2020).

Tooth chipping was recorded following Towle and Loch (2021). A fracture was only recorded if there was further attrition evident on the chipped surface (i.e., the chip scar), to rule out postmortem damage. This meant smoothed occlusal edges and uniform coloration of the fractured surface with other parts of the observed crown. A 10X hand lens was used in some cases to help determine whether a chip formed ante- or postmortem. Chip position was recorded as mesial, buccal, lingual, or distal, and the total number of chips per tooth was also recorded. Chipping size was recorded on an intensity grade scale of 1–3, following Towle and Loch (2021):

1. Small enamel chip (crescent-shaped) in the outer edge of the enamel. Dentine is not exposed, and the chip is restricted to the outer rim of the occlusal surface;
2. Larger chip that extends near to the enamel-dentine junction. A small area of dentine might be exposed;
3. Large irregular fracture in which a significant area of dentine is exposed. More dentine than enamel was removed by the fracture.

Statistical analysis was undertaken to test whether the prevalence of chipping varied between anterior and posterior and maxillary and mandibular teeth. Additional comparisons were made between chipping frequencies in Fayum anthropoids with values from extant primates (using data from Towle & Loch, 2021). Statistical significance was tested between tooth groups using a chi-squared test, with significance set at the 0.05 alpha level. Due to limited sample size for chipped teeth in Fayum anthropoids, comparisons were made based on combined frequencies for all five genera.

Tooth wear was examined and scored to elucidate the potential influence of wear on chipping patterns. Molars were scored following Scott (1979), who proposed dividing teeth into quadrants, each given a score of 1–10: a value of 1 means a tooth is unworn or has negligible wear facets, while 10 describes complete loss of enamel. The average quadrant value was calculated for each genus. Anterior teeth were scored on a scale from 1 to 8, following Smith (1984), with an average score calculated for each genus.

Dental caries was recorded following Towle et al. (2022). Caries position on the crown was recorded as buccal, occlusal, distal, lingual, or mesial. Whether lesions were primarily affecting the crown or root was also noted. Micro-CT scans of the lesions were used to assess the shape and depth of lesions and to observe evidence of mineralization changes. Given that such changes are typically masked by taphonomy in fossil specimens, micro-CT scans were predominantly used for visualization and description purposes. Micro-CT scans of all specimens examined in this study are accessioned on MorphoSource as part of the Duke Lemur Center Museum of Natural History's online digital collection. Since it can be difficult to identify carious lesions in fossils, a differential diagnosis was conducted for each lesion. Each diagnosis involved ruling out other possible antemortem effects (e.g., enamel defects, non-carious cervical lesions, and acidic erosion), and postmortem damage or alterations, based on the macroscopic inspection of the lesions.

3 | RESULTS

Tooth chipping was low in the five genera studied, with a pooled chipping prevalence of 5% of teeth displaying chipping (21/421) in the

FIGURE 1 *Propliopithecus chirobates* specimen (DPC 10700) showing an antemortem chip on the distal surface of the mandibular left third molar (white arrow). White stars indicate postmortem damage. Scale bar 5 mm.

TABLE 1 Information on each species studied.

Taxon	N	Dental formula	Clade	Fayum quarry	Geological age	Absolute age (ma)
Aegyptopithecus zeuxis	21	2.1.2.3/2.1.2.3	Propliopithecidae	M&I	early Oligocene	30.0–29.2
Apidium phiomense	19	2.1.3.3/2.1.3.3	Parapithecidae	M&I	early Oligocene	30.0–29.2
Catopithecus browni	11	2.1.2.3/2.1.2.3	Oligopithecidae	L-41	latest Eocene	35–33.9
Parapithecus grangeri	16	2.1.3.3/0.1.3.3	Parapithecidae	M&I	early Oligocene	30.0–29.2
Propliopithecus ankeli	1	?0.1.2.3/2.1.2.3	Propliopithecidae	V	early Oligocene	31–30.6
Propliopithecus chirobates	17	?0.1.2.3/2.1.2.3	Propliopithecidae	M&I	early Oligocene	30.0–29.2

TABLE 2 Chipping prevalence (% of teeth) for each species studied, split by anterior/posterior and maxilla/mandible.

Genera	Anterior	Posterior	Maxilla	Mandible	All teeth
Aegyptopithecus	16.67 (1/6)	2.13 (2/94)	2.50 (1/40)	3.33 (2/60)	3.00 (3/100)
Propliopithecus	16.67 (3/18)	7.41 (6/81)	5.88 (1/17)	9.76 (8/82)	9.09 (9/99)
Parapithecus	0.00 (0/1)	2.82 (2/71)	0.00 (0/18)	3.7 (2/54)	2.78 (2/72)
Apidium	11.11 (1/9)	1.37 (1/73)	4.17 (1/24)	1.72 (1/58)	2.44 (2/82)
Catopithecus	10.00 (1/10)	6.90 (4/58)	8.70 (2/23)	6.67 (3/45)	7.35 (5/68)

Note: Anterior refers to incisors and canines and posterior to premolars and molars.

anthropoids sampled. There is little variance in chipping frequency among genera, ranging from 2.4% (2/82) in *Apidium*; 2.8% (2/72) in *Parapithecus*; 3% (3/100) in *Aegyptopithecus*; 7.4% (5/68) in *Catopithecus*; to 9.1% (9/99) in *Propliopithecus*. When split into the three families studied, chipping prevalence varied from 6% (12/199) in Propliopithecidae to 2.6% (4/154) in Parapithecidae and 7.4% (5/68) in Oligopithecidae. Assessing chipping frequency variation across the dentition is difficult due to small sample sizes for anterior teeth (Table 2). Only one of the 21 chipped teeth had multiple fractures (DPC 6313, *Parapithecus grangeri*, lower left third molar); all other specimens displayed a single chip (Figure 1). In anterior teeth, all but two chips were on the labial edge. Chipping on posterior teeth was similar among positions, although the limited sample size makes inferences difficult (mesial: 2 chips; lingual: 4; distal: 5; buccal: 5). Most of the fractures were small, with fourteen recorded as grade 1 (66.7%), six as grade 2 (28.6%), and one as grade 3 (4.8%).

When all species are combined, anterior teeth have a significantly higher prevalence of tooth chipping than posterior teeth (X^2 (1) = 7.75, p = 0.005). There is no significant difference between maxilla and mandible tooth chipping prevalence in Fayum anthropoid primates (X^2 (1) = 0.29, p = 0.592). The combined chipping prevalence in Fayum anthropoids is significantly lower than all but two extant primate species studied with comparable methods (*Pan troglodytes* and *Hylobates klossii*; Table 3). Average tooth wear scores for Fayum anthropoids vary among genera, but the range of variation is low, and there is no clear association between tooth wear and chipping (Table 4).

Three potential carious lesions were identified in the specimens studied, and a differential diagnosis of each lesion was conducted. Two caries were from the same individual in adjacent teeth (specimen DPC 1108), on the maxillary left first and second molars. The other lesion was observed on the upper right fourth premolar of DPC 1087. All three lesions affected the lingual root surface (Figure 2) and were diagnosed in two specimens of *Propliopithecus* (*P. chirobates*). The smoothed outer edges of the lesions, with no apparent rough or sharp edges common in postmortem damage, suggest they were formed when the animals were alive. The shape of the lesions and their position are also consistent with an antemortem diagnosis. The lesions have a classic "root caries" morphology, when the gum likely receded to expose the underlying root dentine. Because dentine is weaker than enamel, a cup-shaped carious lesion can form. The lesion was restricted by the enamel above and the gum tissue below, leading to an elongated oval shape. This presentation was observed in each case (Figure 2). The only other potential antemortem explanation for these lesions would be non-carious cervical lesions (NCCLs). Although NCCLs cannot be ruled out, the darker coloration of the interior of the lesion may relate either to genuine coloration changes due to carious demineralization or postmortem coloration that was facilitated by the rougher surface of the lesions. The shape and characteristics of the lesions also do not fit with NCCLs, including abfraction and abrasion lesions. Micro-CT shows the loss of dentine tissue; however,

TABLE 4 Average wear score for each species studied, split by anterior and posterior teeth.

Genera	Anterior teeth	Posterior teeth
Aegyptopithecus	2.90	4.51
Propliopithecus	2.35	4.06
Parapithecus	3.33	4.88
Apidium	2.43	3.54
Catopithecus	2.25	3.07

Note: Posterior teeth (here defined as just molars) are recorded fowling Scott (1979), and anterior teeth (here defined as incisors, canines and premolars) were scored following Smith (1984).

TABLE 3 Number of teeth with and without chips for a range of extant primates (data from Towle & Loch, 2021) and for the combined total values for Fayum anthropoids.

Primate species/group	Teeth with chips	Teeth with no chips	Statistical analysis
Fayum anthropoids	21	400	-
Pan troglodytes	98	2141	X^2 (1) = 0.31, p = 0.578
Hylobates klossii	23	293	X^2 (1) = 1.69, p = 0.194
Gorilla gorilla gorilla	169	1612	**X^2 (1) = 8.75, p = 0.003**
Cercopithecus mitis	37	205	**X^2 (1) = 20.43, p < 0.001**
Simias concolor	72	337	**X^2 (1) = 33.19, p < 0.001**
Lagothrix lagothricha	42	185	**X^2 (1) = 30.69, p < 0.001**
Presbytis potenziani	44	183	**X^2 (1) = 33.86, p < 0.001**
Cercopithecus denti	52	213	**X^2 (1) = 36.63, p < 0.001**
Papio hamadryas	107	411	**X^2 (1) = 48.43, p < 0.001**
Macaca fuscata	215	765	**X^2 (1) = 60.41, p < 0.001**
Pithecia spp.	68	172	**X^2 (1) = 71.50, p < 0.001**
Presbytis femoralis	84	158	**X^2 (1) = 101.85, p < 0.001**
Mandrillus spp.	47	81	**X^2 (1) = 91.07, p < 0.001**

Note: Statistical analysis comparing each extant species with the Fayum anthropoids was conducted using a chi-squared test (significance set at the 0.05 alpha level). Significant differences in chipping rate are highlighted in bold.

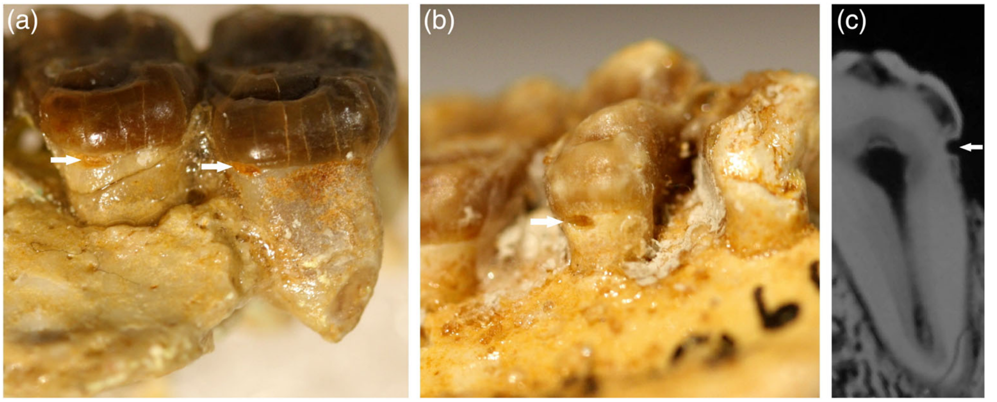

FIGURE 2 Three potential carious lesions in *Propliopithecus chirobates*: (a) Lesions on the lingual root surface of the left maxillary first and second molars of specimen DPC 1108 (white arrows); (b) Lesion on the lingual root surface of the right maxillary fourth premolar of specimen DPC 1087 (white arrow); (c) a Micro-CT longitudinal slice showing root lesion (white arrow) in DPC 1087. Both scale bars 5 mm.

changes in mineral density could not be confirmed (Figure 2c). The shape, position, and surface texture of these lesions are suggestive of dental caries, which in turn suggests an antemortem etiology.

4 | DISCUSSION/CONCLUSION

The findings of this study indicate that Fayum anthropoids had a limited dietary intake of hard foods. Consequently, we can reject the initial hypothesis laid out in this study, while the alternative hypothesis finds support. The prevalence of enamel chipping suggests that the mastication of hard objects, such as hard fruits, seeds, and nuts, was rare across all groups. The evidence for a soft fruit-dominated diet is further substantiated by the identification of three carious lesions, although it is noteworthy that all carious lesions were observed in a single species, *P. chirobates*. The results support previous work on early anthropoid primates, which suggested soft fruits and a variable amount of leaves were their predominant food sources.

Extant anthropoids that regularly eat hard foods (e.g., sakis, mandrills, sooty mangabeys, and Raffles' banded langurs) show high overall chipping prevalence, with over 25% of teeth showing at least one chip, and some tooth types approaching 50% (Fannin et al., 2020; Towle, Constantino, et al., 2023; Towle & Loch, 2021). Species that consume hard foods as part of their diet but only at certain times of the year (e.g., brown woolly monkeys) have intermediate chipping frequencies of 15%–20%, and species in which hard foods do not make up a significant amount of the diet at any time of the year have the lowest chipping frequencies of under 10% (e.g., gibbons, chimpanzees, western red colobus, and Western lowland gorilla; Fannin et al., 2020; Towle & Loch, 2021). Fayum anthropoids fit within the latter group and present one of lowest overall tooth chipping prevalence of any primate yet studied. Therefore, the prevalence of chipping does not support habitual durophagy in these early anthropoids, including *Apidium* and *Aegyptopithecus*, for which hard food consumption has been previously proposed.

It should be noted that most studies that mention potential hard-object feeding in *Apidium* and *Aegyptopithecus* stress that the predominant food source was likely softer fruits (Fleagle & Kay, 1985; Kay & Simons, 1980; Teaford et al., 1996). One character that has been key to hypothesized hard-objects feeding in these early anthropoids is the relatively thick enamel in *Apidium*. However, the thicker enamel of *Apidium* may not relate to hard-object feeding, but instead be an indicator of wear resistance (Pampush et al., 2013; Towle et al., 2020). Mechanisms of fracture resistance for hard object feeding are complex and involve more than increased enamel thickness. The size of the tooth, cusp morphology, and variation in structure and mechanical properties of enamel and dentine also playing a role in fracture resistance (e.g., Lucas et al., 2008; Maas & Dumont, 1999; Towle et al., 2023c; Yang et al., 2022). Teaford et al. (1996) investigated both microwear and enamel microstructure in anthropoids, but were inconclusive in regard to hard object feeding. The presence of decussating enamel (e.g., HSB, Hunter-Schreger bands) is common in anthropoids, found in folivores, frugivores, and devoted hard object feeders (Maas & Dumont, 1999; Martin et al., 1988; Martin et al., 2003). Therefore, the presence of HSB in early anthropoids cannot provide singular evidence of hard object feeding. Similarly, Teaford et al. (1996) concluded that in the three Fayum taxa studied, microwear patterns were consistent with modern frugivores, although pit size variation was used to suggest *Aegyptopithecus* may have occasionally ingested hard foods. The authors were cautious with this conclusion given the limited sample size. These results are not necessarily contradictory to the chipping patterns, with occasional hard object feeding potentially occurring, just at a much lower frequency than in extant hard object feeding primates.

The results of the present study are not consistent with the conclusions of a recent dental topography study, which suggested that hard object feeding was common in both *Apidium* and *Aegyptopithecus* (Morse et al., 2023). Our study revealed low levels of chipping in these two genera, lower than any extant primate yet studied. Indeed, extant hard-object feeders typically show chipping frequencies that are ten times higher. As discussed in the present study, previous techniques used to infer hard object feeding in early anthropoids (e.g., enamel thickness, enamel decussation, and microwear) should be considered inconclusive until further research is conducted. The apparent contradiction between chipping patterns and specific dental topography metrics therefore needs to be explored in light of our results and those of Morse et al. (2023).

The tooth chipping results of the present study are supportive of a relatively uniform diet for early anthropoids. All species show low levels of chipping. Extant primates with omnivorous diets show high chipping rates, as do hard object feeders, and species that accidentally ingest environmental grit (Fannin et al., 2020; Towle et al., 2017; Towle & Loch, 2021). Based on body size estimates, it is likely early anthropoids would have supplemented their fruit diet with leaves, though *Catopithecus* – the smallest primate studied here – may have consumed insects alongside soft fruits and leaves (Bajpai et al., 2008; Kirk & Simons, 2001; Williams et al., 2010). There may also have been variation in the types of fruits consumed, with, for example, Propliopithecidae consuming more ripe sugary fruits than the other taxa, based on the presence of dental caries. However, the shared dental traits between earlier anthropoids from Asia and those examined in the present study from Africa may suggest low dietary diversity was a feature of early anthropoids, with frugivory predominating (Kirk & Simons, 2001). In contrast to early anthropoids, late Eocene Fayum prosimians demonstrated remarkable dietary diversity, including specialized insectivory, generalized frugivory, frugivory+insectivory, and strict folivory (Kirk & Simons, 2001). These results support the possibility that dietary changes and diversity were not important selective factors in the origins of anthropoids. These early anthropoids had diets that were likely similar to adapiform and omomyiform taxa (Bajpai et al., 2008; Kirk & Simons, 2001). The anthropoid reliance on tough and hard foods (such as unripe fruit and nuts and leaves) was then a later adaptation in anthropoid evolution (Williams et al., 2010). Low dietary specialization in early anthropoids may also have contributed to the survival and diversification of the group through the Eocene–Oligocene boundary in Africa (de Vries et al., 2021).

The dearth of chipped teeth in Fayum anthropoids also supports an arboreal lifestyle in which foraging on the ground was rare. Extant primates that forage on the ground have an increased likelihood of grit being accidentally ingested, leading to higher chipping prevalence (Towle et al., 2017). These results are consistent with previous research on Fayum primate skeletal morphology (Bown et al., 1982) and environmental reconstructions (Gagnon, 1997) that suggested these species were arboreal. The results of the current study do not support the hypothesis that these primates lived in a semi-arid and largely treeless scrubland (Kortlandt, 1980). In such an environment, grit and other environmental contaminants would likely regularly make it into the oral cavity through a variety of routes, such as being blown on the wind, through grooming, or adhering to foods gathered from the ground. Based on having taller molar crowns and more developed shearing crests, Kay and Simons (1980) suggested *Parapithecus granger* may have been more terrestrial compared to other Fayum anthropoids; however, such a scenario is not supported by chipping patterns.

Dental caries has been described in extant primates that regularly consume sugary fruits, including Cercopithecoidea and Hominoidea taxa (Colyer, 1931; Lovell, 1990; Stoner, 1995; Towle et al., 2022). These lesions are often found on the interproximal region of anterior teeth, relating to food processing behaviors, but can also be found on posterior teeth (Towle et al., 2022). The three carious lesions described here in Propliopithecidae (*P. chirobates*) were present on the same surface: the lingual root surface of posterior teeth. Because this was a small sample (three teeth from two individuals), detailed inferences on etiology and clinical presentation are not warranted. However, it suggests that there must have been gum recession. There is also substantial wear on the teeth of these individuals; thus, age may have played a role in caries formation. Regardless, regular consumption of cariogenic foods over a sustained period must have occurred for these lesions to form. Based on comparisons with extant anthropoids, the carious items were likely ripe, sugary fruits (Colyer, 1931; Lovell, 1990; Stoner, 1995; Towle et al., 2022). Fossil fruits have been described from the Fayum (e.g., Bown et al., 1982), including the genera *Epipremnum*, *Annonaspermum*, and *Canarium*. Some of these species have living representatives whose fruits are consumed by primates (*Canarium*: Sefczek et al., 2012; Federman et al., 2016). It has also been suggested that some of these fruiting plants have co-evolved with primates (e.g., Chen et al., 2020), and therefore the evidence of caries in early anthropoids is supportive of such scenario and suggestive of soft fruits being consumed on a regular basis. It is possible that other Fayum anthropoid taxa studied did not consume sugary fruits to the same extent as *P. chirobates*, as evidenced by the absence of carious lesions. However, it is also plausible that these species processed food slightly differently, or the lack of caries may be due to sampling or taphonomy bias. Future studies on other early anthropoid samples could provide valuable insights into potential variations in the types of fruits consumed by early anthropoids.

There is no clear association between tooth wear scores and chipping frequencies among the genera studied. The two genera with the highest chipping rates (*Propliopithecus* and *Catopithecus*) overlap with the other genera in the sample in terms of wear (e.g., *Propliopithecus* has a higher average wear score for posterior teeth than *Apidium*, but the relationship is reversed for anterior teeth). Although *Catopithecus* has the lowest mean wear scores for both anterior and posterior teeth, the difference from other groups is small, especially for anterior teeth (i.e., the range of average wear score for anterior teeth is 2.25–3.33). Despite these differences, it is possible that tooth wear could play a role in chipping differences. For example, a higher chipping rate in *Catopithecus* could relate to less wear since there is less attrition to erase previous fractures. However, *Propliopithecus* has a higher chipping prevalence than *Catopithecus*, despite higher average wear in both anterior and posterior teeth. Additionally, teeth with more wear are expected to have been in occlusion longer, and therefore would have had more opportunity to fracture. In extant primates, this is likely a key reason for the higher rate of chipping observed in older individuals with more tooth wear (Towle et al., 2022). Therefore, there is no clear association between wear and chipping, and given the small wear score differences among groups studied, it is unlikely to be a strong contributing factor to the chipping differences observed, or to the overall low rate of fractures in Fayum anthropoids compared to extant primates.

A limitation of the present study is that tooth chipping and wear patterns are influenced by morphological differences among teeth in primates (see Morse et al., 2023, for detailed examples of morphological differences in Fayum anthropoids). This was not addressed in the present study, but has received more attention in the recent literature (e.g., Towle et al., 2023b; Yang et al., 2022). The size of a chip will be influenced by the overall tooth morphology, the thickness of enamel, and the internal structure of enamel and dentine (Constantino et al., 2009; Lee et al., 2011; Schwartz et al., 2020). Differences in prevalence and size of fractures among primates will be influenced by such factors, with species displaying additional adaptations to reduce the occurrence of fractures and to lessen the impact of chips when they do occur (Chai, 2022). It is feasible that chipping differences in early anthropoids may relate, at least partly, to enamel structure or morphological differences, such as decussation of enamel prisms (e.g., high density of Hunter-Schreger Bands) and differences in enamel thickness. Variations in relative enamel thickness, tooth size, and enamel prism decussation have been observed in Fayum anthropoids (Kay & Simons, 1980; Teaford et al., 1996).

Tooth chipping prevalence in early anthropoids was consistently low, aligning with the idea of an arboreal lifestyle focused on the consumption of soft fruits. Our findings do not indicate substantial variations in dietary or foraging behaviors among the genera under study. However, the presence of carious lesions in Propliopithecidae hints at a potential preference for ripe, sugary fruits. Overall, however, this study lends support to the hypothesis that significant dietary changes did not play a pivotal role in early anthropoid evolution. It is more likely that dietary diversification occurred at a later stage during the Paleogene, shaping the evolutionary trajectories of anthropoid lineages.

AUTHOR CONTRIBUTIONS

Ian Towle: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (equal); methodology (equal); project administration (equal); writing – original draft (lead); writing – review and editing (equal). **Matthew R. Borths:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal); writing – original draft (equal); writing – review and editing (equal). **Carolina Loch:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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