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BRIEF COMMUNICATION

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The effect of high wear diets on the relative pulp volume of the lower molars

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Abstract

Objectives: One role of dental pulp is in the upkeep and maintenance of dentine. Under wear, odontoblasts in the pulp deposit tertiary dentine to ensure the sensitive internal dental tissues are not exposed and vulnerable to infection. It follows that there may be an adaptive advantage for increasing molar pulp volume in anthropoid primate taxa that are prone to high levels of wear. The relative volume of dental pulp is therefore predicted to covary with dietary abrasiveness (in the sense of including foods that cause high degrees of wear).

Materials and Methods: We examined relatively unworn lower second molars in pairs of species of extant hominoids, cebids, and pitheciids that vary in the abrasiveness of their diet (n = 36). Using micro-CT scans, we measured the percent of tooth that is pulp (PTP) as the ratio of pulp volume to that of the total volume of the tooth.

Results: We found that in each pair of species, the taxa that consume a more abrasive diet had a significantly higher PTP than the closely related taxa that consume a softer diet.

Conclusions: Our results point to an adaptive mechanism in the molars of taxa that consume abrasive diets and are thus subject to higher levels of wear. Our results provide additional understanding of the relationship between dental pulp and diet and may offer insight into the diet of extinct taxa such as *Paranthropus boisei* or into the adaptive context of the taurodont molars of Neanderthals.

KEYWORDS
Cebids, dental tissues proportions, hominoids, pitheciids

1 | INTRODUCTION

The pulp cavity of the tooth houses connective tissue, as well as blood vessels and nerve fibers that enter through the apical or lateral foramina of the roots, playing an important sensory role in the mouth (Schroeder, 1986; Ungar, 2010). However, the part played by the pulp in the formation and upkeep of dentine is equally important. The pulp is formed as the developing dentine surrounds and encloses the dental papilla, and it contains and maintains odontoblasts throughout the life of an individual. The continual presence of odontoblasts and fibroblasts support dentinogenic activity in the pulp, deposit secondary dentine throughout life, and act to repair dentine under wear by depositing tertiary dentine on the roof of the pulp cavity (Smith, 2000). Considering the role pulp plays in the upkeep and protection of arteries and nerves within the teeth, it could be predicted that there may be an adaptive advantage for having a higher pulp volume in animals with more abrasive diets who have teeth that are subject to greater wear. A larger pulp cavity, and consequently larger store of pulp to allow for increased remodeling of the interior of the tooth, may help prevent the pulp cavity from being exposed and becoming vulnerable to infection during life (Blumberg et al., 1971; Coon, 1962; Hamner III et al., 1964; Hillson, 1996). It is well

established that enamel thickness covaries with diet, particularly as animals consume more or less hard or abrasive foodstuffs, as thicker enamel helps to resist fracture and wear, and protect the internal dental organs (e.g., Andrews & Martin, 1991; Daegling et al., 2011; Dumont, 1995; Kono, 2004; Lambert et al., 2004; Pampush et al., 2013; Rabenold & Pearson, 2011; Thiery, Gillet, et al., 2017; Thiery, Guy, & Lazzari, 2017). Pulp volume may also be a covariate of diet as it relates to another means for the tooth to protect those vulnerable soft tissue structures. This would have implications for our understanding of the understudied role of pulp (Ungar, 2010) and for examining dietary adaptations in living and fossil taxa.

It has previously been hypothesized that taurodont molars, like those of Neanderthals, may provide a functional advantage to resist elevated occlusal forces and fracture during the breakdown of hard foods (Benazzi et al., 2015; Kupczik & Dean, 2008; Spencer, 2003). However, using finite element analysis, Benazzi et al. (2015) found that taurodont molars do not provide a direct biomechanical advantage to resisting occlusal loading. They, and others (Blumberg et al., 1971; Hamner III et al., 1964; Hillson, 1996; Kupczik & Hublin, 2010), suggest that an enlarged pulp cavity may provide an advantage to populations consuming a high-wear diet. Previous studies have examined pulp cavity morphology and volumetrics (e.g., Bayle et al., 2009; Bayle et al., 2010; Kupczik, 2003; Kupczik et al., 2019; Kupczik & Hublin, 2010; Olejniczak et al., 2008; Şenyürek, 1939; Zanolli & Mazurier, 2013). However, to date there has been no formal test comparing the pulp volume of closely related animals that consume diets that differ in abrasiveness. Here we examine three pairs of closely related extant primate taxa. Each pair includes one taxon whose teeth are subjected to higher levels of wear and a closely related taxon whose teeth are subjected to lower levels of wear. Using micro-CT scans, we measured the percent of tooth that is pulp (PTP) of the lower second molar, which is the ratio of the volume of the pulp to that of the whole tooth (enamel + dentine + pulp), and compare these data both within each pair, and between all the hard and soft-object feeders in our sample.

2 | MATERIALS AND METHODS

Our analysis includes 36 specimens representing six taxa (see Table 1). Each taxon in the analysis was assigned as either a high-wear or low-wear feeder based on the available observational data. All three of the high-wear taxa in our analysis have been previously described as hard-object feeders (see Table 1 and references therein). Previous observational and experimental work has shown that hard-object feeders are prone to higher levels of wear (Fleagle & McGraw, 1999; Galbany et al., 2014, 2020; Schmidt, 2010; Swan, 2016; Teaford et al., 2017; Teaford & Oyen, 1989a, 1989b). For example, taxa that eat hard diets such as mandrills (Fleagle & McGraw, 1999; Galbany et al., 2014) and mangabeys (Fleagle & McGraw, 1999; Swan, 2016) are known to experience higher levels of wear compared to closely related, soft-object feeding taxa. Moreover, Teaford and Oyen (1989b) fed vervets diets that differed in hardness and found that the hard-object diet produced more rapid tooth wear compared to the softer diet. Whereas we acknowledge that the abrasiveness of a given diet (i.e., the degree to which it causes wear) is the product of several factors such as the concentration of phytoliths, and the presence of grit or quartz in the soil, hard-object feeding seems to be a consistent vector for higher levels of wear in both observational and experimental work (Fleagle & McGraw, 1999; Galbany et al., 2014, 2020; Schmidt, 2010; Swan, 2016; Teaford et al., 2017; Teaford & Oyen, 1989a, 1989b).

The hominoid taxa in our analysis include *Pongo pygmaeus* and *Pan troglodytes/ paniscus*. Neither species of *Pan* are considered hard-object feeders (e.g., Scott et al., 2018). *Pongo* has been classified as eating a high-wear diet, as this taxon is known to consume both harder and tougher foods compared to *Pan* species (Vogel et al., 2008), and when compared to other great apes is characterized by a high instance of molar enamel chipping related to processing hard foods (Constantino et al., 2012) and higher levels of wear due to crushing (Fiorenza et al., 2015). Although *Pan* also occasionally consumes hard foods such as nuts, they do so less frequently and use tools of various types to open the hard exocarps first (Boesch & Boesch, 1983; van Casteren et al., 2016; Whiten et al., 1999). It should be noted that *Pan* may consume higher levels of phytoliths compared to *Pongo* (Rabenold & Pearson, 2011); therefore, signals of *Pongo* being prone to higher levels of wear based on hard-object feeding may be lower than expected when compared to *Pan*.

The cebid taxa in our analysis include *Sapajus apella* and *Cebus capucinus*. We classified *S. apella* as consuming the high-wear diet and *C. capucinus* as consuming a comparatively low-wear diet. Although

TABLE 1 Species included in the analysis and dietary information with associated references for each taxon

Superfamily/subfamily	Species (*n*)	Wear	References
Hominoidea	*Pongo pygmaeus* (8)	High	Rabenold and Pearson (2011), Taylor (2006), and Vogel et al. (2008)
	Pan sp. (4)	Low	Scott et al. (2018), Rabenold and Pearson (2011), and Vogel et al. (2008)
Cebidae	*Sapajus apella* (7)	High	Dumont (1995), Izawa (1979), Moynihan (2015), Port-Carvalho et al. (2004), and Rabenold and Pearson (2011)
	Cebus capucinus (7)	Low	Dumont (1995), Moynihan (2015), and Rabenold and Pearson (2011)
Pitheciidae	*Pithecia pithecia* (6)	High	Homburg (1998) and Norconk et al. (2013)
	Plecturocebus moloch (4)	Low	Crandlemire-Sacco (1988), Kay et al. (2013), and Norconk et al. (2013)

Note: N, number of specimens analyzed.

both cebid taxa are omnivorous with a wide dietary breadth, observational data suggest that *S. apella* consumes significantly more hard foodstuffs (Moynihan, 2015) such as the hard pod of the ice-cream-bean *Inga sapindoides* (Izawa, 1979). *Sapajus apella* has been observed cracking nuts with stones or by hitting them against harder tree branches, a behavior not observed in the more gracile *Cebus* (Barrett et al., 2018; Boinski et al., 2000; Izawa, 1979; Izawa & Mizuno, 1977); however, the former have nonetheless also been observed consuming several hard food items using their notably "powerful jaws" (Boinski et al., 2000, p. 741) that they do not process before ingesting (Izawa, 1979). Finally, the pitheciid taxa in our analysis include *Pithecia pithecia* (classified as consuming the high-wear diet) and *Plecturocebus moloch* (classified as consuming the low-wear diet). *Pithecia pithecia* has been described as a seed predator, with more than 53% of the diet coming from seeds annually and more than 86% coming from seeds in peak months (Homburg, 1998; Norconk et al., 2013). *Plecturocebus moloch* relies on a combination of fruits, insects, and leaves (Crandlemire-Sacco, 1988), and is described as the least specialized pitheciid for seed predation (Kay et al., 2013; Norconk et al., 2013). It should be noted that the classification of a taxon as consuming a more or less abrasive diet is specific to the particular comparison, implying that it may be inappropriate to form comparisons between members of our three pairs. For example, although we classify *P. moloch* as consuming the low-wear diet, this taxon is nonetheless a seed predator and may very likely consume a more abrasive diet compared to *Cebus* or *Pan*.

Unworn to lightly worn lower second molars (M_2) were chosen for analysis so that the volume of enamel is not underestimated due to the destructive processes of dental wear and because the volume of the pulp cavity decreases with age due to the deposition of secondary and tertiary dentine (Constant & Grine, 2001; D'Ortenzio et al., 2018; Drusini et al., 1997; Fabbri et al., 2015). To ensure our sample was only represented by molars with minimal wear, we measured the dentine exposure ratio (DER) for each specimen (see below). Micro-CT scans of each of the above taxa, except for *P. pygmaeus*, were downloaded from MorphoSource (Boyer et al., 2016; Copes et al., 2016) (Table S1). In addition, high resolution scans of *P. pygmaeus* mandibles were taken on a custom micro-CT system with 160 kV, 0.15 mA and a 1.00 mm Cu filter at the Bundesanstalt für Materialforschung und -prüfung (BAM), Berlin, Germany (see Table S1 for museum accession numbers). Scans range in isometric voxel size from 0.030 to 0.110 mm (see Table S1). It should be noted that comparisons made between scans that differ greatly in voxel size or between teeth that vary greatly in size may be problematic. We suggest, as we have done, limiting comparisons to scans that are of a similar voxel size and keeping comparisons to within families.

Micro-CT scans were segmented using 3D Slicer (Fedorov et al., 2012) to isolate the hard tissue (enamel + dentine) and the pulp using threshold-based and manual approaches. First, we used the thresholding tool to select a range of gray values to visually isolate the tooth within the scan based on selecting the relevant anatomy. Because the voxel sizes are very small relative to the area being segmented, there was little ambiguity in the anatomical limits, because the zone of uncertainty created by partial volume averaging was very thin. We then used the level tracing tool, which is a threshold-based tool that allows the user to define an outline where the pixels all have the same background value as the current selected pixel, functioning as a dynamic magic wand tool. The level tracing tool was used to ensure only the relevant anatomy was selected within a particular slice, as this tool can both add and remove regions from the lablemap. This tool was used to edit the lablemap slice by slice. We used a consistent brightness/contrast setting for each particular scan to keep baseline thresholds the same throughout the stack. We also used a consistent threshold range throughout each individual stack. Once segmented, the resulting meshes were automatically smoothed in 3D Slicer via the WindowedSincPolyDataFilter, and were imported into MeshLab (Cignoni et al., 2008) for the volumetric measurement. The PTP was calculated as:

$$\left(\frac{\text{Pulp Volume}}{\text{Enamel} + \text{Dentine} + \text{Pulp Volume}}\right) \text{x}\, 100\%.$$

Intraobserver error was assessed by one observer (KRS), who segmented and measured the volume of the pulp and the dental hard tissue for a single specimen of *Pan troglodytes* (MCZ 9493) a total of 10 times over a period of 3 weeks with at least 24 h between trials. We calculated the mean absolute percent difference (MAPD) of the error study trials following Grine et al. (2001) as:

$$\left(\frac{\text{Observed value} - \text{Sample mean}}{\text{Sample mean}}\right) \text{x}\, 100\%.$$

We measured the degree of wear for each of our specimens using the DER as described by Spradley et al. (2016) and Pampush et al. (2016). We used scaled two-dimensional images of the occlusal surface to measure the footprint of the tooth and the area of exposed dentine in ImageJ 1.53a (Abràmoff et al., 2004). The DER was calculated as:

$$\left(\frac{\text{Area of exposed dentine}}{\text{Area of the occlusal surface}}\right) \text{x}\, 100\%.$$

The statistical analysis was performed using PAST 3.26 (Hammer et al., 2001). We used the non-parametric Mann–Whitney *U* to test the null hypothesis for no difference of group medians between the high wear and low wear feeders of each pair.

3 | RESULTS

In the intraobserver error study, the measurement of PTP varied by an average of 2.97%, with the MAPD ranging from 0.94% to 9.41% and the PTP ranging from 5.21% to 6.96% (see Table S2). Intraobserver error was therefore consistent with other analyses, such as previous measurements of enamel thickness (Selig et al., 2019; Skinner et al., 2015) and microwear (Grine et al., 2002) that range in

TABLE 2 Summary statistics for the measurement of the percent of tooth that is pulp (PTP), pulp volume, and volume of the enamel+dentine+pulp (tooth volume)

	P. pygmaeus	*Pan* sp.	*S. apella*	*C. capucinus*	*P. pithecia*	*P. moloch*
Tooth volume (mm^3)						
Mean	1683.923	667.349	69.303	57.903	33.123	23.219
Stand. dev	571.791	278.006	15.493	8.236	4.180	2.072
Coeff. var	33.956	41.658	22.355	14.224	12.619	8.924
Pulp volume (mm^3)						
Mean	137.982	29.395	4.744	1.884	3.136	1.456
Stand. dev	43.385	13.856	1.876	0.264	0.779	0.382
Coeff. var	31.443	47.139	39.544	14.005	24.829	26.210
PTP (%)						
Mean	7.705	4.211	6.373	3.199	8.600	5.832
Stand. dev	1.760	1.457	2.030	0.619	1.578	0.933
Coeff. var	22.844	34.599	31.852	19.353	18.350	16.004

Note: Stand. Dev, standard deviation; Coeff. Var, coefficient of variation.

mean error from 2.4% to 5.32% and 5.4% to 9.1% respectively. This suggests that our methodology has a high degree of reliability and repeatability, in line with other methods used for quantifying aspects of dental morphology.

Measurement of the DER shows that our sample is characterized by minimal levels of wear based on comparison with previous analyses (e.g., Spradley et al. 2010; Elgart, 2010; Morse et al., 2013; Pampush et al., 2016). Our sample ranges in dentine expose from 0% to 2.69% (see Table S1). This indicates that even in our most highly worn specimen (*Pongo pygmaeus* ZMB 6948), less than 3% of the total area of the occlusal surface is exposed dentine, suggesting that dental wear likely does not confound the measurement of pulp volume in our sample.

Results of the measurement of PTP are summarized in Table 2 and Figure 1 (see also Table S1). In all three pairs of taxa, the taxa that consume high-wear diets had a higher mean PTP compared to the closely related low-wear taxa. The Mann–Whitney *U* tests comparing each pair of taxa were all below the alpha value ($\alpha = 0.05$) (hominoids: $p = 0.030$, $U = 2.173$; cebids: $p = 0.002$, $U = 0$; pitheciids: $p = 0.043$, $U = 2$), suggesting that the high-wear taxa possess a significantly higher pulp volume in the M_2 than the respective low-wear feeders. Note that one specimen of *Pongo* (MCZ 50958) has a much higher dental tissue volume than all other included specimens of *Pongo*. This likely has to do with the presence of an accessory root in this specimen (see Figure S1).

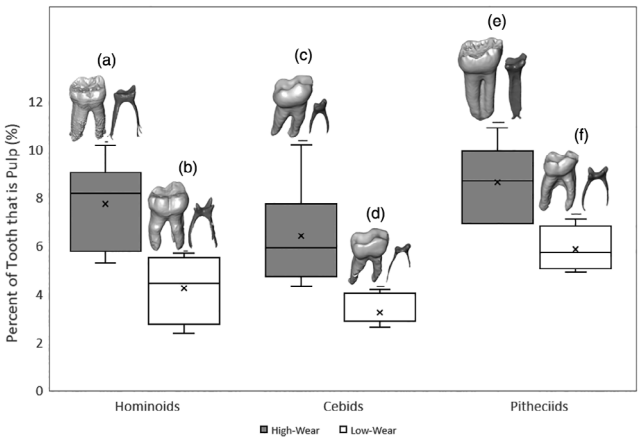

FIGURE 1 Box plots depicting the results of the measurement of PTP. The x denotes the mean, the horizontal lines denote the median, the boxes represent the upper and lower quartiles, and whiskers denote the highest and lowest values for each group. Micro-CT renderings of the hard tissue and pulp of (a) *Pongo pygmaeus* (EVA 6948); (b) *Pan troglodytes* (MCZ 9493); (c) *Sapajus apella* (MCZ31066); (d) *Cebus capucinus* (MCZ 5332); (e) *Pithecia pithecia* (USNM 374745); and (f) *Plecturocebus moloch*. Scale bar = 1 mm

4 | DISCUSSION

Dental pulp plays an important role in the upkeep of dentine during life and our results suggest that an increased volume of pulp in the molars may provide an advantage to taxa that consume a highly abrasive diet or are prone to higher levels of dental wear. An enlarged pulp cavity houses a larger population of active odontoblasts, which may aid to prevent exposure of the vulnerable internal dental tissues as the pulp deposits additional dentine on the roof of the pulp cavity under high dental wear (e.g., Galbany et al., 2014; Swan, 2016). Further research should aim to test how differing levels of wear affect the PTP. However, even in cases of light wear and minimal dentine exposure on cusp tips, we observed in our sample evidence that dentine is deposited on the roof of the pulp cavity in the position of the wear facets, which would provide additional protection to the pulp (Figure 2). This observation is consistent with what has been described for tertiary dentine deposition obliterating the pulp horns in worn fossil hominin molars (Kupczik et al., 2019; Kupczik & Hublin, 2010).

Each of the three high-wear taxa in our analysis had a significantly higher PTP compared to a closely related low-wear taxon. This points to an adaptive mechanism for dealing with the effects of an abrasive diet that seems to be consistent across anthropoids and merits

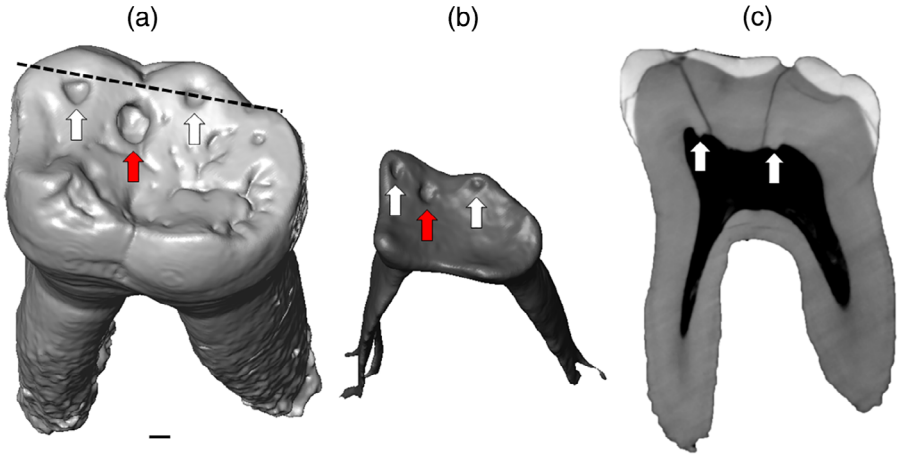

FIGURE 2 Reconstruction of the lower second molar of *Pongo pygmaeus* (ZMB 6948) demonstrating reparative dentine being deposited under light dental wear. (a) three-dimensional rendering of the enamel and dentine. White arrows indicate the presence of small wear facets on cusp tips, red arrow indicates the presence of a possible carious lesion. (b) three-dimensional rendering of the endocast of the pulp cavity. White arrows indicate depressions in the pulp from dentine being deposited on the roof of the pulp cavity in the position of wear facets, red arrow indicate depressions in the pulp cavity from dentine being deposited on the roof of the pulp cavity in the position of carious lesion. (c) two-dimensional slice (see hashed line in (a) for position of slice) through the molar with white arrows demarcating two additional deposits of dentine on the roof of the pulp cavity. These deposits caused the depressions observed in (b) and are the reparative processes underway to prevent pulp expose under dental wear. Scale bar = 1 mm

investigation in other mammalian taxa. Among the three pairs of taxa we included, the pitheciids had the smallest difference in mean PTP (*P. pithecia*: 8.60%, *P. moloch*: 5.83%). Moreover, *P. moloch* had the highest PTP among other low-wear taxa included in our analysis. This may be a product of phylogenetic relatedness or it may reflect the fact that *P. moloch* does consume some hard objects (albeit a lower quantity than *P. pithecia*) as a seed predator; however, it lacks many of the specializations seen in other seed predators such as crenulated enamel, which is consistent with our findings that it is less specialized for hard-object feeding.

Overall, our results are consistent with studies analyzing variation in enamel thickness (e.g., Andrews & Martin, 1991; Daegling et al., 2011; Dumont, 1995; Kono, 2004; Lambert et al., 2004; Pampush et al., 2013; Rabenold & Pearson, 2011; Thiery, Gillet, et al., 2017; Thiery, Guy, & Lazzari, 2017) in that both thick enamel and a larger PTP seem to provide a selective advantage for dealing with a diet that is rich in hard, abrasive foodstuffs. Others have previously examined the dental morphology of hard-object feeders in aspects other that their thick enamel. For example, Galbany et al. (2014) studied the hard-object feeding mandrill (*Mandrillus sphinx*) and the soft-object feeding yellow baboon (*Papio cynocephalus*). They found that the mandrill is characterized by greater wear at a similar age compared to the yellow baboon. They also note that mandrills are characterized by flattened molars at an earlier age and argue that flatter molars may provide a biomechanical advantage for processing harder foods, as flat teeth provide a more uniform distribution of high occlusal forces (Kay, 1981). If this is the case, it follows that reinforcing the roof of the pulp cavity with extra dentine throughout life would provide additional support to the occlusal surface and would help prevent tooth fracture and pulp exposure, an idea consistent with our findings (see Kupczik & Hublin, 2010). Furthermore, Kupczik et al. (2009) examined molar surface area in a sample of primates and found that hard-object feeding catarrhine taxa (e.g., *P. pygmaeus*) have a relatively larger root surface area per crown surface area when compared to soft-object feeding taxa. However, they note that *S. apella* does not follow this trend. Therefore, an enlarged root surface area may be a covariate of dietary hardness (see Kupczik & Dean, 2008), but PTP seems to provide a clearer indication that abrasive foods are being consumed, at least among anthropoids, as both *P. pygmaeus* and *S. apella* are characterized by a high PTP.

It may be predicted that an enlarged pulp cavity could also provide an adaptive advantage to folivores, since their diet can be highly abrasive. We did not include any highly folivorous taxa in our analysis. However, some of the taxa we did include do eat some leaves. Rabenold and Pearson (2011) calculated the phytolith load (percentage of high phytolith containing plants in the diet) for a sample of extant primates and found that the *S. apella* had a higher phytolith load (61.07%) than *C. capucinus* (39.38%). However, they also note that *P. troglodytes* had a higher phytolith load (68.45%) than *P. pygmaeus* (40.32%). Our results show that *S. apella* and *P. pygmaeus* both have high PTP values, and in particular that *P. pygmaeus* is notably higher than *Pan* sp. Therefore, phytolith load is not enough to explain the differences we observed in PTP, although it may provide additional selective pressure for an enlarged pulp cavity in some taxa. It is worth noting that there is some debate with respect to the role of phytoliths versus dust in creating tooth wear (e.g., Ackermans et al., 2020; Merceron et al., 2016; Sanson et al., 2007; Schulz-Kornas et al., 2019, 2020). It is possible that differing dust or grit loads in the diet may also be influencing PTP. It should also be acknowledged that

evidence suggests that taurodont molars do not provide a biomechanical advantage to resisting high occlusal loading (Benazzi et al., 2015); however, it is possible that an enlarged pulp cavity may constitute an adaptation toward a specific (not necessarily high) occlusal loading regime involving high wear (Kupczik & Hublin, 2010).

Our research has implications for understanding the selective pressures that shape dental morphology in primate taxa and provide additional understanding of the functional relationship of dental pulp and diet. Moreover, our results provide added means for examining hypotheses about dental wear and diet in extinct taxa. For example, some have argued that *Paranthropus boisei* was a hard-object feeder based on patterns of microwear (Scott et al., 2005) and craniodental morphology (Teaford & Ungar, 2000). However, these claims have been refuted with subsequent microwear analyses (Ungar et al., 2008), analysis of phytoliths loads in the diet (Rabenold & Pearson, 2011), and using stable isotopes (Cerling et al., 2011). Analysis of the PTP in *P. boisei* could provide an additional line of inquiry in this debate. *Australopithecus sediba* has also been the subject of debate regarding its diet and hard-object feeding. For example, Henry et al. (2012) argued that *A. sediba* was a hard-object feeder based on their analysis of microwear. However, Ledogar et al. (2016) used finite element analysis to model the cranium of *A. sediba* and found that this taxon did not produce a sufficiently high bite force to consume a hard-object diet. Our method could provide additional insight into the dietary components of *A. sediba*. Finally, the adaptive causes of taurodontism (e.g., as observed in Neanderthals) continue to be a source of debate (e.g., Benazzi et al., 2015), which may be informed by study of PTP.

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AUTHOR CONTRIBUTIONS

Keegan Selig: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing-original draft. **Kornelius Kupczik:** Data curation; writing-original draft; writing-review and editing. **Mary Silcox:** Conceptualization; funding acquisition; resources; supervision; writing-original draft; writing-review and editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All micro-CT scans included in this analysis are available on MorphoSource.org, Duke University, or are available upon request. All raw data are available in the supplemental information.

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SUPPORTING INFORMATION

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

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