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Article

Why the long teeth? Morphometric analysis suggests different selective pressures on functional occlusal traits in Plio-Pleistocene African suids

Deming Yang, Asli Pisano, Joan Kolasa, Tea Jashashvili, Job Kibii, Ana R. Gomez Cano, Laurent Viriot, Frederick E. Grine, and Antoine Souron*

Abstract.—Neogene and Pleistocene African suids displayed convergent evolutionary trends in the third molar (M3) morphology, with increasingly elongated and higher crowns through time. While these features can prevent premature loss of masticatory functionality and potentially increase long-term reproductive success, changes in dental occlusal traits such as enamel complexity and thickness can also improve chewing efficiency and increase short-term energetic return. While both long-term and short-term benefits can contribute to the thriving of a lineage, the selective pressures associated with each category can be different. To examine how crown elongation correlates with these functional occlusal traits, we selected M3s of *Kolpochoerus*, *Notochoerus*, and *Metridiochoerus* from Kenya and South Africa, dated between 3.0 Ma and 0.4 Ma. To account for dental wear, we used micro-computed tomography imaging of unworn/slightly worn M3s to simulate wear progression within each tooth. We compared morphometric representatives of occlusal enamel complexity and thickness among the specimens following their respective wear trajectories. We found that M3 elongation correlates with higher occlusal complexity and thinner enamel in *Notochoerus* and *Metridiochoerus* lineages through time. In *Kolpochoerus*, enamel complexity and thickness were generally maintained through time, despite M3 elongation. The differences in M3 morphometric trends suggest that *Kolpochoerus* likely experienced a different set of selective pressures on functional occlusal traits compared with *Notochoerus* and *Metridiochoerus*. The shared evolutionary trends of M3 specialization among *Notochoerus* and *Metridiochoerus* suggest similar selective pressures on their chewing efficiency and the possibility of a dietary niche overlap in more xeric habitats.

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Introduction

Dental morphology has profound implications for the dietary ecology of mammals, because the primary function of mammalian teeth is to process food. One crucial aspect of dental morphology is its relationship with dental wear, which is tied to both chewing mechanics and food properties (e.g., Mills 1967; Rensberger 1973; Fortelius 1985; Lucas 2004). Dental wear can come from direct contact between tooth surfaces (attrition) or contact between teeth and extraneous material (abrasion), such as food and adhering dust/grit (e.g., Baker et al. 1959; Butler 1972; Rensberger 1973; Fortelius 1985). Because grasses carry an abundance of abrasive particles internally or externally, grass-eating mammals endure high dental wear rates (e.g., Rensberger et al. 1984; Lucas et al. 2000; Sanson et al. 2007; Karme et al. 2016). As a result, hypsodonty, which refers to teeth that are taller than they are wide, has evolved several times independently in different grass-eating herbivores (e.g., Simpson 1951; van Valen 1960; Janis and Fortelius 1988; Jernvall and Fortelius 2002; Ungar 2010; Madden 2014). On the other hand, hypsodonty induces a series of fundamental changes in the organization of dental tissues within a tooth and in the function of the occlusal surface as dental wear progresses (e.g., Fortelius 1985; Pérez-Barbería and Gordon 1998). Dentine wears more deeply on the occlusal surface than enamel, which creates enamel ridges and dentine basins as secondary features of a moderately worn tooth (e.g., Rensberger 1973; Janis and Fortelius 1988; Kaiser 2002). These features are functionally important, as they serve as shearing crests where food particles are mechanically broken down when upper and lower teeth come into occlusion (Lucas and Luke 1984; Hofmann 1989; Archer and Sanson 2002; Schmidt-Kittler 2002). Most herbivores have complex occlusal surfaces for cutting and grinding (e.g., Cope 1896; Butler 1956; Fortelius 1985; Ungar 2010). Hypsodont herbivores, in particular, have enamel and dentine layers that are almost perpendicular to the occlusal surface, to maintain the secondary shearing crests for the majority of the life spans of their cheek teeth (e.g., Janis and Fortelius 1988; Pérez-Barbería and Gordon 1998; Lucas 2004; Ungar 2015).

Extant pigs (family Suidae) are generally medium- to large-sized omnivores and are found in a variety of ecosystems around the world (Meijaard et al. 2011). Some African taxa (warthogs and giant forest hogs) are exceptional in that they diverged tremendously from omnivory and adopted highly herbivorous diets (e.g., Field 1972; d'Huart 1978; Viehl 2003; Kingdon 2015). This ecological divergence can be traced back to the late Miocene to mid-Pliocene (between 6 and 4 Ma) in Africa, during which a prominent dietary shift toward higher proportions of C_4 vegetation (typically tropical grasses) was a common response to the local climate and vegetation changes among herbivorous mammals (e.g., deMenocal and Bloemendal 1995; Vrba 1995; Bobe and Behrensmeyer 2004; Cerling et al. 2005, 2011, 2015; Ségalen et al. 2007; Uno et al. 2011, 2016; Herbert et al. 2016). Intriguingly, in the most common fossil suid lineages in Africa (*Notochoerus*, *Kolpochoerus*, and *Metridiochoerus*), the dental morphological innovations that supposedly corresponded to this dietary shift displayed convergent evolutionary trends of increased crown height (hypsodonty) and increased length of the third molars (M3s) by adding more cusp(id)s/pillars to the distal end (Cooke and Maglio 1972; White and Harris 1977; Cooke and Wilkinson 1978; Harris and White 1979; Kullmer 1999; Geraads and Bobe 2017). At the same time, an increase in the number of shearing crests and a decrease in enamel thickness have also been observed but not quantified in the M3s of Plio-Pleistocene fossil suids (Cooke and Wilkinson 1978; Harris and White 1979). Based on these dental features, common suid lineages have been divided into distinct species/chronospecies that have been used in biostratigraphic correlations across different Neogene and Pleistocene African sites (e.g., Cooke and Maglio 1972; White and Harris 1977; Cooke 2007).

Like other herbivores, suids supposedly evolved M3 hypsodonty as an adaptive trait to prevent premature loss of masticatory function when consuming large amounts of abrasive foods (Fortelius 1985; Janis and Fortelius

1988). Crown elongation has been associated with delayed sequential dental eruption, which permits the functionality of the cheek tooth row to be maintained, as early erupted permanent teeth become worn and nonfunctional (Janis and Fortelius 1988; Lanyon and Sanson 2006; Gomes Rodrigues et al. 2011). While both M3 hypsodonty and crown elongation are considered adaptive traits to abrasive diets, the number of shearing crests and enamel thickness are potentially associated with a different set of diet-related functionality. Intuitively, the more shearing crests a herbivore can pack onto an occlusal surface (being more complex), the more efficient it is at processing vegetation per chewing cycle (e.g., Schmidt-Kittler 2002; Ferretti 2003; Lucas 2004; Famoso et al. 2013; Gailer and Kaiser 2014; Schultz et al. 2020). On the other hand, thinner enamel can create higher occlusal stress at the shearing crests, which is more effective in breaking down tough and fibrous foods such as grasses, but at the cost of a higher dental wear rate (Fortelius 1985; Schmidt-Kittler 2002; Ferretti 2003). For suids that are known to have unspecialized gastrointestinal tracts (Kükenthal and Schmidt-Rhaesa 2017), increase in occlusal complexity and decrease in enamel thickness can theoretically improve short-term energetic return: fewer chews are required to process the same amount of food, and a higher net energy gain is achieved per unit of feeding time. By contrast, M3 crown elongation and particularly hypsodonty can improve long-term reproductive success: the life span of the tooth is extended, which may lead to more offspring in an individual's lifetime. While both categories of success can contribute to the thriving of a species or a lineage, the selective pressure can be different in either category. Neogene and Pleistocene African suids present an exceptional case study into these categories of natural selection with their long-surviving lineages and unique dental morphological evolution.

Unlike other herbivores, suids display complex cusp(id)/pillar configurations and diverse occlusal patterns in their M3s as dental wear progresses (Shaw 1939; Cooke and Maglio 1972; Harris and White 1979; Kullmer 1999). This feature makes it challenging to compare occlusal traits in specimens at different wear stages. Moreover, the morphometrical correlates and functional implications of M3 elongation are still not fully explored. For example, as fossil suids increased their M3 length, most of them also experienced a reduction in premolar/incisor size and function (Cooke and Wilkinson 1978; Harris and White 1979), which suggests a trend of a heavier reliance on M3s for mastication (Souron 2017). If this is the case, an increase in M3 length could also provide additional shearing functionality on the occlusal surface, potentially contributing to both short-term energetic return and long-term reproductive success. Such mechanisms could have offered some adaptive advantage for the grass-eating fossil suids, as they were as abundant as bovids during the Pliocene in eastern Africa (e.g., Bobe et al. 2002; Bobe and Behrensmeyer 2004; Lazagabaster et al. 2018).

In this study, we examined how functional occlusal traits vary as dental wear progresses within the life spans of the M3s, and how the increase in M3 crown length correlates with functional occlusal traits in sympatric suid lineages. We used micro-computed tomography (micro-CT) as a nondestructive method to virtually simulate the progression of dental wear using unworn or barely worn M3s of three different African fossil suid lineages (*Notochoerus*, *Kolpochoerus*, and *Metridiochoerus*). First, we built reference series of simulated "occlusal surfaces" along the trajectory of dental wear and adapted a measurement to quantify dental wear progression. Second, we developed/adapted morphometric measurements to quantify two functional occlusal traits, namely occlusal enamel complexity and enamel thickness, to investigate their variation patterns as dental wear progresses. Third, to examine the functional correlates of M3 elongation and its evolutionary significance, we compared the variation patterns of the occlusal traits among representative members of the three fossil suid lineages, as well as among extant African suids. Finally, we explored the evolutionary trends of the functional occlusal traits in different lineages in the context of their dietary ecology and potential selective pressures.

Materials and Methods

Suid Dental Materials.—The M3s of extant and extinct African suids have been chosen as the subject of investigation for the following reasons. First, M3s are the best represented in the suid fossil record due to their large sizes and good preservation (Harris and White 1979; Cooke 2007). Second, M3s are morphologically and morphometrically diagnostic, which is often crucial for species identification (Harris and White 1979; Kullmer 1999; Cooke 2007). Finally, in most fossil suid species, the M3s have become functionally more important than other teeth for food mastication (Cooke and Wilkinson 1978; Harris and White 1979; Kullmer 1999; Souron 2017), making their functional traits potential targets for natural selection.

To investigate how M3 elongation correlates with functional occlusal traits, we selected specimens from Kenya and South Africa that represent different levels of M3 elongation in three major fossil suid lineages (Fig. 1, Table 1). Due to a lack of an exhaustive phylogenetic analysis of fossil suid taxa, the taxonomy and phylogenetic relationships of some fossil suids are still debated (van der Made 1998; Fessaha 1999; Harris and Leakey 2003; Geraads 2004; Souron et al. 2015a; Cherin et al. 2018; Reda et al. 2019). The commonly accepted species that follow an ancestor–descendant relationship are: (1) the *Notochoerus euilus–Notochoerus scotti* lineage (subfamily: Tetraconodontinae; Cooke and Wilkinson 1978; Harris and White 1979; van der Made 1998; Bishop 1999); (2) the *Kolpochoerus limnetes–Kolpochoerus paiceae* lineage (subfamily: Suinae; Cooke and Wilkinson 1978; Souron et al. 2015a; Souron 2017); and (3) the *Metridiochoerus* sp.–*Metridiochoerus andrewsi–Metridiochoerus compactus* lineage (subfamily: Suinae; Harris and White 1979; White et al. 2006). Because of our limited access to micro-CT data, we chose specimens of *Metridiochoerus shawi* (Cooke 2005) instead of *Metridiochoerus* sp. to represent the early *Metridiochoerus* morphotype, because they share the same level of M3 elongation and similar occlusal morphologies (Cooke 2005; White et al. 2006). All representative species of the major lineages are considered sympatric in eastern Africa during the Plio-Pleistocene (Harris and White 1979; Cooke 2007; Bibi et al. 2018).

To provide a reference dataset for the Pliocene and early Pleistocene fossil specimens and to better understand the dietary implications of M3 crown elongation, we included extant warthog (*Phacochoerus africanus*) specimens and one late middle Pleistocene bushpig/red river hog (*Potamochoerus* sp.) specimen from Lake Eyasi, Tanzania (Supplementary Table 1). Warthogs are considered the only extant suids specialized on grass (Clough 1970; Field 1972; Cooke and Wilkinson 1978; Harris and Cerling 2002; Treydte et al. 2006; Souron 2017). They possess high-crowned and mesiodistally elongated M3s with numerous tightly packed pillars (Shaw 1939; Cooke and Wilkinson 1978; Kullmer 1999). *Potamochoerus* best resembles an ancestral dental morphotype with omnivorous diets (Meijaard et al. 2011; Souron 2017).

Micro-CT Scans to Simulate Dental Wear Progression.—Extinct African suids generally display flat occlusal topography in moderately worn teeth (Rannikko et al. 2020), most likely due to a high proportion of C_4 grass in their diets (Fortelius and Solounias 2000; Harris and Cerling 2002; Cerling et al. 2015). For this reason, dental wear progression can be simulated using micro-CT images perpendicular to the growth axis of unworn M3s (Adams 2005). Micro-CT images of Kenyan and South African materials were collected using a Nikon XTH 225 high-resolution X-ray CT scanner (2000 × 2000 pixels) at the Evolutionary Studies Institute, University of the Witwatersrand, South Africa, at 120–140 kV and 140–150 μA settings. The *Sus scrofa* (wild boar) specimens were scanned at PACEA/University of Bordeaux, using a General Electric (GE) Phoenix v|tome|x s240 X-ray microtomograph, at 100–120 kV and 200 μA settings. The *Phacochoerus africanus* specimens were scanned at the National Institute of Applied Sciences of Lyon, using a GE Phoenix Nanotom 180 at 150 kV and 90 μA. For fossil specimens, a 1 mm copper filter was used to limit the beam hardening effect. For extant specimens, a 0.1 mm copper filter was used. Voxel resolution ranged from 6 to 50 voxels/mm, depending

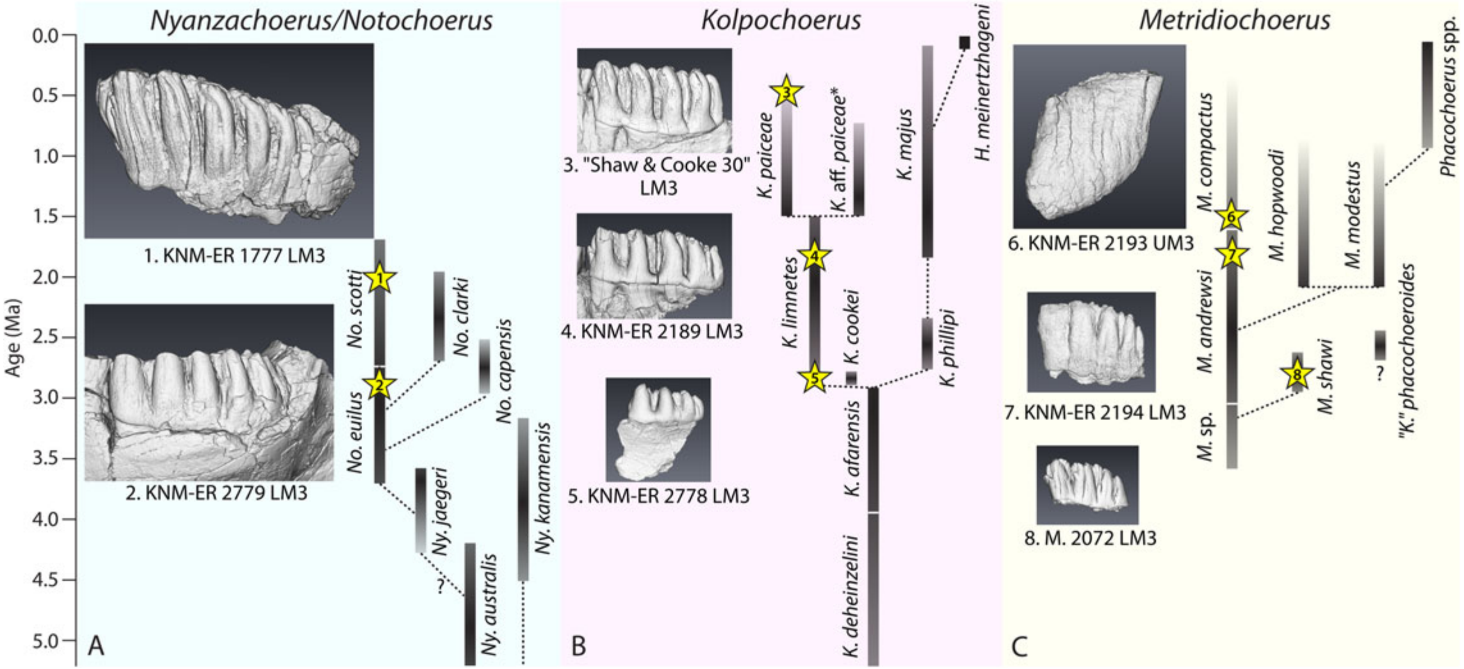

FIGURE 1. Selected Plio-Pleistocene suids, their previously proposed phylogenetic relationships between chronospecies, and images of representative specimens included in this study, showing trends of increase in hypsodonty and elongation in third molars. The systematics were adapted from White and Suwa (2004) for *Nyanzachoerus*/*Notochoerus* (A); Souron et al. (2015a) for *Kolpochoerus* (B); and Cooke (2005) and Cherin et al. (2018) for *Metridiochoerus* (C). Fossil suid chronospecies, their first and last appearance dates (FAD and LAD), and proposed systematic relationships are summarized and discussed in Appendix 1, section 1, Supplementary Material. *Ny.*, *Nyanzachoerus*; *No.*, *Notochoerus*; *K.*, *Kolpochoerus*; *M.*, *Metridiochoerus*; *H.*, *Hylochoerus*; asterisks (*) represent descendants of *Kolpochoerus limnetes* that became endemic to the Turkana Basin (usually called *K. olduvaiensis*; see Bibi et al. 2018); question marks (?) represent lineages of debated or unknown phylogenetic relationships. Images of fossil specimens are extracted from the 3D Visualization & Analysis Software, Avizo 7.1, displaying the upper buccal (specimen 6) or lower lingual view (all other specimens). The 3D surface renderings of specimens 1, 5, 6, and 7 were mirrored horizontally to make sure that all specimens display comparable views, with mesial cusp(id)s/pillars on the left of the image.

TABLE 1. Summary of fossil suid specimens included in this study; note that the number of main pillars in the third molars (M3s) corresponds to the degree of M3 elongation in each species; this number is determined by counting the large pillars on the lingual side of upper M3s or on the buccal side of lower M3s; the age estimates of Turkana basin specimens come from McDougall et al. (2012) with notes on stratigraphic provenance (Harris 1983; Bobe 2002); the age estimate of Makapansgat Member 3 comes from Herries et al. (2013); the age estimate of Vaal River Younger Gravel C comes from Helgren (1977); *No.*, *Notochoerus*; *K.*, *Kolpochoerus*; *M.*, *Metridiochoerus*; UM3, upper M3; LM3, lower M3.

Species	Site	Member	Age	No. of UM3s	No. of LM3s	No. of main pillars
M. compactus	East Turkana	KBS	~1.6 Ma	1	0	5
M. andrewsi	East Turkana	KBS	~1.8 Ma	0	1	4
M. shawi	Makapansgat	Member 3	~2.7 Ma	2	3	3
No. scotti	East Turkana	Upper Burgi	~2 Ma	1	1	7–8
No. euilus	East Turkana	Tulu Bor	~2.8 Ma	0	1	5
K. paiceae	Vaal River	Younger Gravel C	~0.4 Ma	0	1	4
K. limnetes	East Turkana	KBS	~1.8 Ma	0	1	4
K. limnetes	East Turkana	Tulu Bor	~2.8 Ma	0	1	3

on the size of the specimen (Supplementary Table 2).

Within each specimen, between 8 and 16 virtually simulated "occlusal surfaces" (slices) were created in Avizo 7.1 (Visualization Science Group) perpendicular to the growth axis of the tooth, using the mesial second pair of pillars as the reference (Fig. 2A). The number of simulated "occlusal surfaces" was determined based on the crown height of the specimen, and the spacing between "occlusal surfaces" is consistent within each specimen. After the slices were generated, they were manually processed in Adobe Photoshop CS6 to create segments of enamel, dentine, and coronal cementum if present (the step-by-step Adobe Photoshop protocol is presented in Appendix 2, Supplementary Material). The segmented images were then exported to the open-source image-analysis software Fiji (Schindelin et al. 2012) for measurements of occlusal features (the step-by-step Fiji protocol is presented in Appendix 2, Supplementary Material).

From the segmented images, progression of dental wear on the simulated "occlusal surfaces" was measured with the dentine exposure ratio (DER). DER was calculated as:

$$\mathrm{DER} = \mathrm{DA}/\mathrm{OccA} \qquad (1)$$

where DA is the "exposed" dentine area (Fig. 2C), and OccA is the occlusal area of the simulated "occlusal surface" (Fig. 2B). DER measures the area of dentine exposure as a fraction of the entire "occlusal" area. This simple measurement has been used to quantify dental wear in primate teeth (Elgart 2010; Galbany et al. 2011; Morse et al. 2013; Pampush et al. 2016) and generates continuous numerical data for each simulated "occlusal surface," instead of discrete numbers as in the previously established dental wear scoring system in fossil

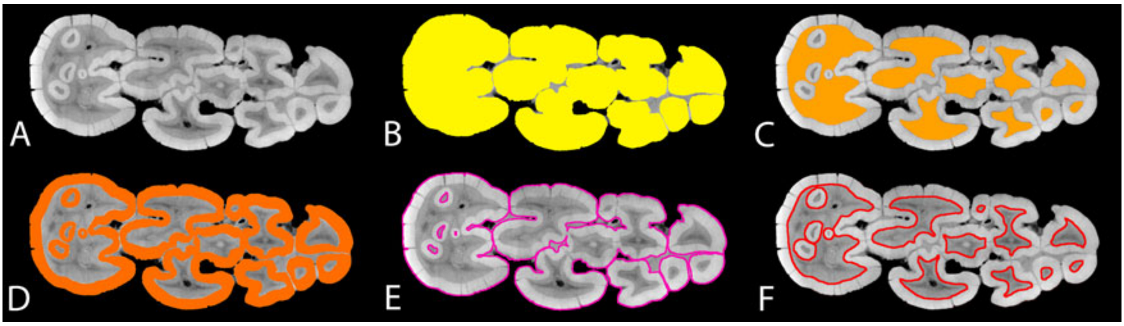

FIGURE 2. Demonstration of measurements for suid dental morphometrics; A, simulated "occlusal surface" (slice) derived from the micro-computed tomography (micro-CT) data of the right lower M3 of the M.2072 specimen from Makapansgat (Supplementary Table 7); B, OccA, occlusal area; C, DA, "exposed" dentine area; D, EA, enamel area; E, ECBL, enamel–cementum boundary length; F, EDBL, enamel–dentine boundary length.

suids (Kullmer 1999). Because the amount of spacing within each slice sequence is known, our method permits an investigation into how DER correlates with the "slice depth" of each simulated occlusal image, which represents the height of the crown that is virtually "worn out" in the wear simulation (Appendix 1, section 3, Supplementary Material).

From the same simulated "occlusal surface," the relative length of the enamel–dentine boundary (enamel–dentine boundary index [EDBI] or "enamel complexity") was calculated as:

$$\mathrm{EDBI} = \frac{\mathrm{EDBL}}{\sqrt{\mathrm{OccA}}} \qquad (2)$$

where EDBL is the length of the "occlusally exposed" enamel–dentine boundary measured in millimeters (Fig. 2F), and OccA is as defined for equation (1). EDBL or similar measurements have been used as a proxy for occlusal shearing capabilities in several studies (Lanyon and Sanson 1986; Schmidt-Kittler 2002; King et al. 2005; Morse et al. 2013), but it is often used within a single species. Here we adopted a scaling relationship in EDBI, dividing EDBL by the square root of OccA, which accounts for the dimensionality between the two measurements and makes this index independent of tooth size (Famoso et al. 2013; Pampush et al. 2016). EDBI has been used as a functional indicator for relative shearing capabilities in both extant and extinct herbivore teeth (Famoso et al. 2013, 2015). More importantly, it allows comparison of occlusal enamel complexity in species that display vastly different occlusal morphologies, such as between equids and ruminants (Famoso et al. 2015).

From the same simulated "occlusal surface," the average thickness of the "occlusal" enamel band (ET) on the simulated "occlusal" surface was calculated as:

$$\mathrm{ET} = 2 \times \mathrm{EA}/(\mathrm{EDBL} + \mathrm{ECBL}) \qquad (3)$$

where EA is the area of the "occlusally exposed" enamel band (Fig. 2D); EDBL is as defined in equation (2); and ECBL is the length of the "occlusally exposed" enamel–cementum boundary (Fig. 2E). Because coronal cementum is present in most suid species that have been included in this study, ECBL is an inclusive term that may comprise two elements. One element corresponds to the outer perimeter of the "occlusal" enamel band in species without coronal cementum, or in fossil specimens where coronal cementum is not preserved (Fig. 2E). The other element corresponds to the enamel–cementum boundary within the occlusal area, where it is present in late wear stages within enamel islets in hypsodont taxa (Fig. 2E). Essentially, ET is a proxy for occlusal enamel thickness that considers the occlusal enamel band as a stretched-out ribbon with a uniform width: the width (ET) equals the area of the band (EA) divided by the average length of the band, which is the average of the outer and inner enamel lengths ([EDBL + ECBL]/2).

The results of EDBI as an indicator of occlusal shearing capability (occlusal enamel complexity) and ET as an indicator of occlusal enamel thickness are visualized in a morphospace ("wear space," as in Pampush et al. 2016), consisting of the progression of dental wear corresponding to the series of simulated "occlusal surfaces" on the x-axis (measured by DER), and the respective functional trait on the y-axis (measured by EDBI or ET).

Error and Sensitivity Analyses.—We investigated potential sources of error that are introduced in different steps of image processing. Because our micro-CT images were manually processed, we investigated both inter- and intra-observer errors by repeating our measurements on the same specimens, including both fossil and extant ones (Appendix 1, section 5, Supplementary Material). Potential error associated with slice angle when 3D surfaces were rotated to virtually simulate dental wear was also investigated. The three sources of error associated with our methods are analyzed in detail in Appendix 1, Supplementary Material. The highest margin of the errors was used to provide upper and lower confidence limits to our measurements when results were illustrated.

Due to the limited number of specimens available in our analysis, most of the chronospecies are only represented by a single specimen in our analysis (Table 1). To better interpret our results, we investigated intraspecific variation among nonassociated specimens from a single site, using five *M. shawi* M3s from Makapansgat (Table 1). We assumed that these specimens likely represent randomly selected individuals from the same population. For the same reason (limited available scans), not all species have both upper and lower M3s represented in our dataset (Table 1). For example, *M. compactus* is only represented by one upper M3 specimen in our dataset. To confidently interpret our results consisting of both upper and lower M3s in the same comparison, we compared upper and lower M3s within a single individual, using three associated pairs of upper and lower M3s of *S. scrofa* (Supplementary Table 1) and two associated pairs of upper and lower M3s of the common warthog (*Ph. africanus*; Supplementary Table 1). Results of the comparisons of extant specimens are reported in Appendix 1, section 6, Supplementary Material. We also examined whether upper and lower M3s of different individuals display a significant difference in the functional occlusal traits using *M. shawi* specimens from Makapansgat and *No. scotti* specimens from the Koobi Fora Formation (Appendix 1, section 7, Supplementary Material).

Results

Estimation of Measurement Errors.—Our error analyses showed that the measurements are associated with their respective errors in two different ways. The error for EDBI is linearly correlated with the EDBI value, while there is no significant trend for the errors associated with DER and ET (Supplementary Fig. 1, Supplementary Table 3). We decided to use a linear model to estimate the error associated with EDBI, while the error margins for DER and ET were set at constant values. Among the three sources of error that we investigated, intra-observer error produced the highest margins for DER at ±0.048, and ET at ±0.136 mm, while error associated with slice angle produced the highest margin of error for EDBI at ± (7.3% × EDBI + 0.12) (Table 2, Supplementary Table 4). The highest margins of error were used in constructing the confidence limits, which are presented as shaded areas around the raw data points in figures and Supplementary Material. Detailed analyses for the different sources of error, intraspecific variation, and sensitivity tests are also reported in Appendix 1, section 5, Supplementary Material.

TABLE 2. Sources of error associated with manual image processing in this study (see Appendix 1 for detailed analyses). The highest error margin in each measurement (bolded) is used to construct upper and lower confidence limits of the results; DER, dentine exposure ratio; EDBI, enamel–dentine boundary index; ET, enamel thickness.

Maximum error	DER	EDBI	ET (mm)
Interobserver	±0.031	±(5.5% × EDBI + 0.12)	±0.103
Intra-observer	**±0.048**	±(3.7% × EDBI + 0.12)	**±0.136**
Slice angle	±0.018	**±(7.3% × EDBI + 0.12)**	±0.048

Wear-induced Changes in Functional Occlusal Traits in Fossil Suids.—The two functional occlusal traits (EDBI and ET) experience substantial changes in almost all the wear simulations from early to late wear stages. The general pattern of change in EDBI as DER increases in all simulations resembles a quadratic relationship: EDBI increases quickly in all specimens as dental wear progresses in the early stages; it reaches a maximum value in most species when the M3s are moderately worn, corresponding to a DER ranging between 0.3 and 0.5; then it decreases as dental wear progresses in the late stages (Figs. 3, 4). Enamel thickness gradually decreases in all specimens as dental wear progresses, except for one specimen of *Kolpochoerus* (Fig. 5, KNM-ER 2189), the thickness of which increases slightly in the late stages as dental wear progresses.

Among the five *Metridiochoerus shawi* specimens from Makapansgat, the wear trajectories of occlusal enamel complexity (EDBI) show substantial overlap among lower M3s, among upper M3s, and between upper and lower M3s (Fig. 3). In comparison, the wear trajectories of enamel thickness are more variable among specimens but show some degree of overlap.

For EDBI, *Notochoerus* and *Metridiochoerus* occupy a similar wear space, showing a maximum EDBI between 10 and 18 (Fig. 4), while *Kolpochoerus* has consistently lower occlusal enamel complexity values (< ~9; Fig. 4),

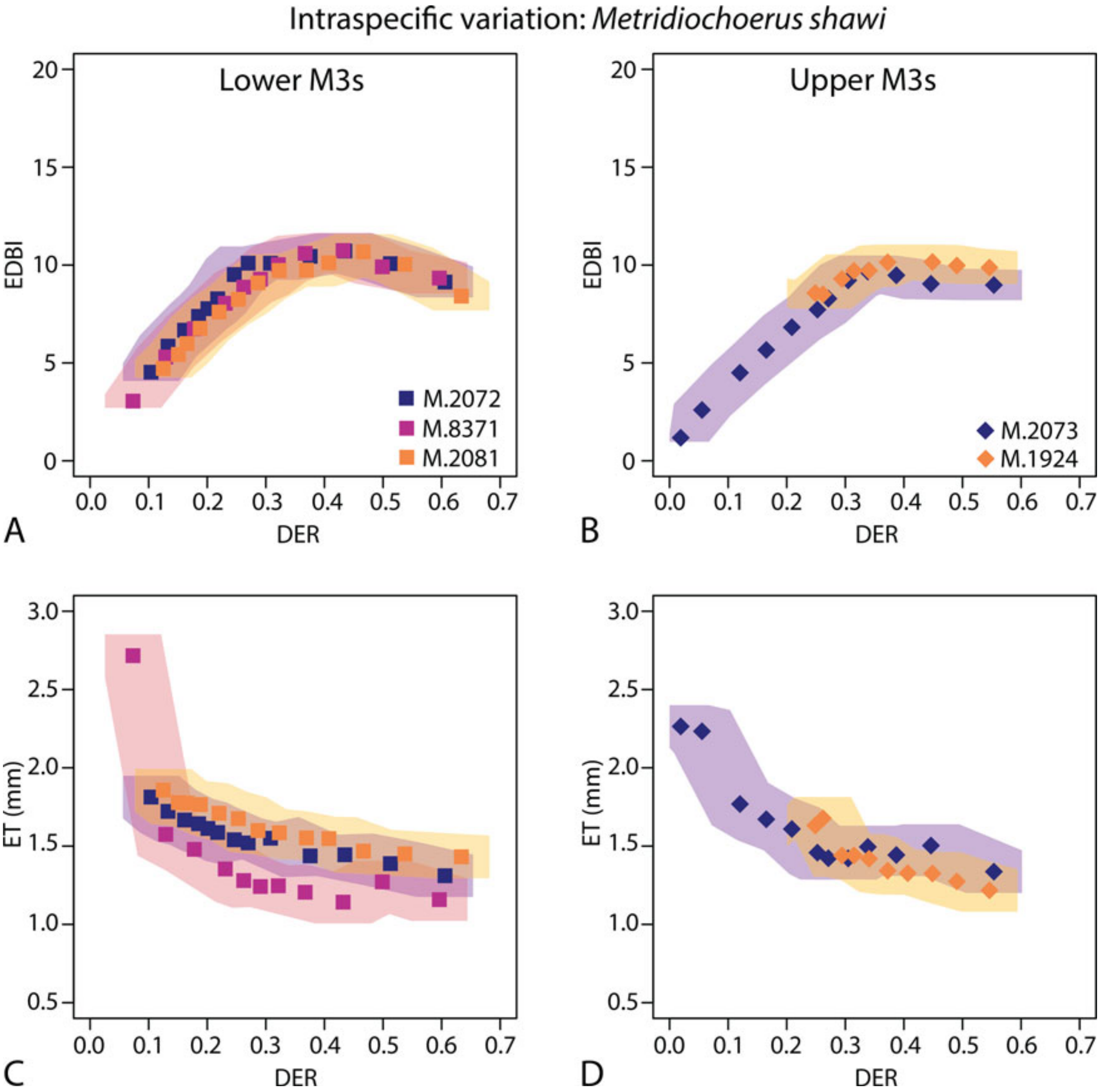

FIGURE 3. Investigating intraspecific variation of functional occlusal traits (EDBI in A and B, ET in C and D) using specimens of *Metridiochoerus shawi* from Makapansgat Member 3; results of lower third molars are in the left column (A, C); results of upper third molars are in the right column (B, D); shaded areas represent confidence limits of data points using the highest margins of error in Table 2; note that high values of enamel thickness are recorded in very early stages of dental wear, likely due to the fact that the enamel–dentine junction at the tip of the cusp(id)s is less perpendicular to the simulated occlusal surface, resulting in exaggerated enamel thickness values; DER, dentine exposure ratio; EDBI, enamel–dentine boundary index; ET, enamel thickness.

which is similar to that of *Sus scrofa* (Appendix 1, Supplementary Material). In both *Notochoerus* and *Metridiochoerus* lineages, added pillars in geologically younger specimens correspond to higher maximum occlusal enamel complexity than in early members. *Metridiochoerus compactus*, the youngest member of the lineage, occupies a similar morphospace as *No. scotti*, the terminal member of the *Notochoerus* lineage (Fig. 4). Remarkably, the *Metridiochoerus* lineage achieved a similar range of maximum occlusal enamel complexity as the *Notochoerus* lineage with fewer pillars (Fig. 4). By contrast, *Kolpochoerus* displays almost no

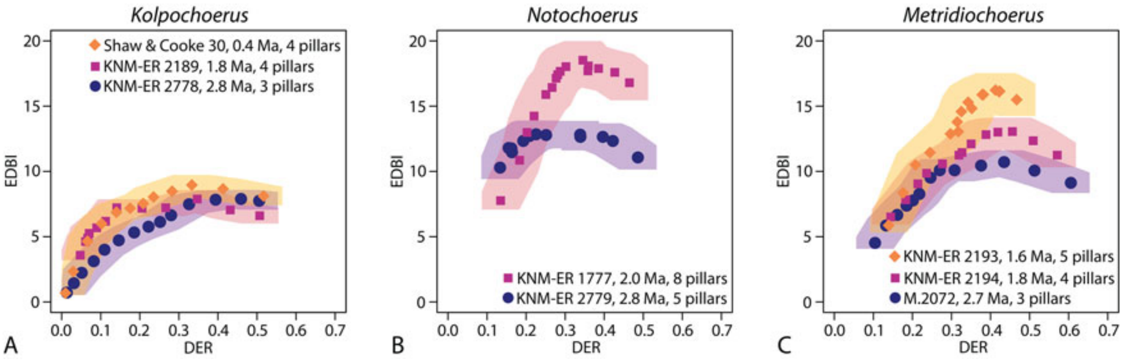

FIGURE 4. Comparing the correlations between third molar elongation (marked by the number of main pillars; Table 1) and occlusal enamel complexity (EDBI) in the three studied fossil suid lineages (A, *Kolpochoerus*; B, *Notochoerus*; C, *Metridiochoerus*); shaded areas represent confidence limits of data points ± the highest margins of error in Table 2; DER, dentine exposure ratio; EDBI, enamel–dentine boundary index.

trend of increased maximum enamel complexity. Instead, added pillars seem to correspond to a more abrupt increase in enamel complexity in early wear stages, which leads to an earlier achievement of maximum complexity as dental wear progresses (Fig. 4).

For enamel thickness, specimens of the *Kolpochoerus* lineage generally have thicker enamel in all wear stages compared with contemporaneous *Notochoerus* and *Metridiochoerus* spp., while the latter two occupy a similar morphospace. One specimen of the *Kolpochoerus* lineage (Shaw & Cooke 30, dated at ca. 0.4 Ma) exhibits lower enamel thickness values in the early wear stages, but all specimens converge on a similar thickness in mid- to late wear stages (Fig. 5). The two *Kolpochoerus* specimens younger than 1.8 Ma display a minimal decrease in enamel thickness as dental wear progresses. *Notochoerus scotti* has significantly thinner enamel compared with *Notochoerus euilus*, but *No. euilus* displays a minimal decrease in enamel thickness as dental wear progresses (Fig. 5). *Metridiochoerus shawi* and *Metridiochoerus andrewsi* display similar thickness patterns, while *M. compactus* has significantly thinner enamel than *M. shawi* and *M. andrewsi*. *Metridiochoerus compactus* also exhibits a minimal decrease in enamel thickness as dental wear progresses (Fig. 5). In general, an increase in M3 crown length is associated with similar patterns of change in enamel complexity and enamel thickness in *Notochoerus* and *Metridiochoerus* lineages over time, while

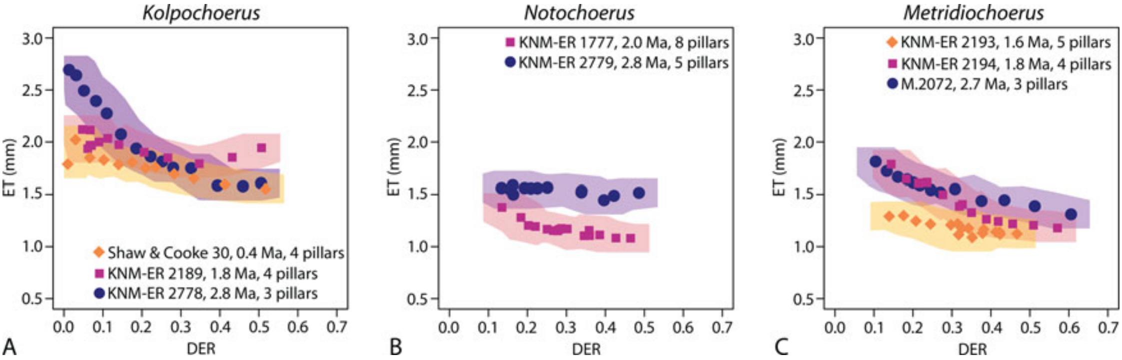

FIGURE 5. Comparing the correlations between third molar elongation (marked by the number of main pillars; Table 1) and occlusal enamel thickness (ET) in three studied fossil suid lineages (A, *Kolpochoerus*; B, *Notochoerus*; C, *Metridiochoerus*); shaded areas represent confidence limits of data points ± the highest margins of error in Table 2; DER, dentine exposure ratio.

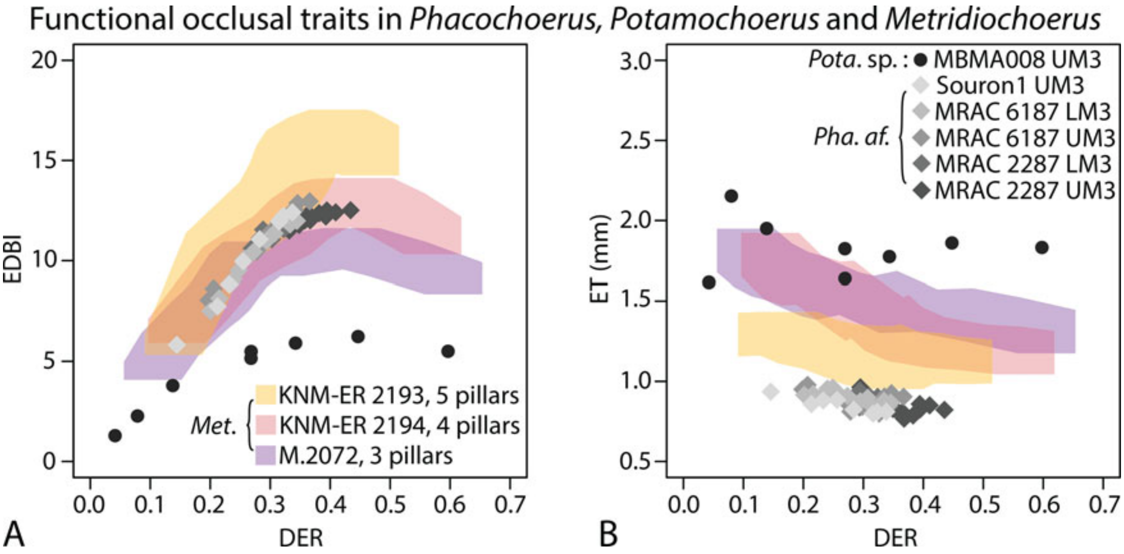

FIGURE 6. Comparing functional occlusal traits (EDBI in A, ET in B) of extant *Phacochoerus africanus*, Pleistocene *Potamochoerus* sp., and Plio-Pleistocene *Metridiochoerus* (Supplementary Table 7); *Potamochoerus* sp. is characterized by a generalized suid dentition (short and brachydont M3s), compared with dedicated grass eaters with specialized dentition such as *Phacochoerus* and *Metridiochoerus*; gray diamonds represent results of *Phacochoerus africanus* (*Pha. af.*); black filled circles represent results of *Potamochoerus* sp. (*Pota.* sp.); colored shades represent the confidence limits of the results of *Metridiochoerus* (*Met.*), as shown in Figs. 4 and 5.

the pattern is different in the *Kolpochoerus* lineage.

When comparing the EDBI values of extant *Phacochoerus africanus* and Plio-Pleistocene *Metridiochoerus*, those of *Ph. africanus* fall within the morphospace of *M. andrewsi* with four primary pillars. On the other hand, they display the thinnest enamel among all the suid specimens examined in this study (Fig. 6). *Potamochoerus* displays the lowest EDBI values (enamel complexity) and the thickest enamel among all the specimens examined (Fig. 6).

Discussion

Assumptions in Quantifying Functional Occlusal Traits.—Our method of simulating dental wear using micro-CT data is associated with several important assumptions. First, the occlusal surface is assumed to be completely flat, which corresponds to the assumption that dental abrasion is the primary cause of wear (Fortelius and Solounias 2000; Karme et al. 2016). For species with higher occlusal relief and non-flat occlusal topography, our measurement of occlusal enamel complexity (EDBI) likely underestimates the shearing capability of the true occlusal surface, especially at earlier wear stages. This bias applies to species that display non-flat occlusal topography in the M3s in early wear stages, such as in *Kolpochoerus* spp. and *Notochoerus euilus* (Rannikko et al. 2020). On the other hand, our results also suggest that enamel complexity reaches a maximum value or a plateau when the M3s are moderately worn (DER between 0.3 and 0.5). At this moderate wear stage, Rannikko et al. (2020) have observed that most species display relatively flat occlusal topography and low occlusal relief. Therefore, EDBI computed from simulated "occlusal" surfaces from micro-CT slices is likely less biased in representing the functionality of the occlusal surface in moderate and late stages of dental wear than in the early stage.

Second, our measurement of occlusal area excludes coronal cementum that is present in most fossil suid species. Coronal cementum was included by Rannikko et al. (2020) in their study of dental topographic features as dietary indicators, using extant suids (*Phacochoerus* and *Hylochoerus*) as reference species. We excluded coronal cementum from this analysis due to inconsistency in the preservation of coronal cementum among fossil specimens. We have also observed that coronal cementum is poorly preserved in isolated M3s, while it is often well preserved in specimens that are still in alveoli, due to the protection from the dentary or maxillary bones. Therefore, including coronal cementum in the analysis can introduce unnecessary noise due to the inconsistency derived from variable preservation states.

Third, all simulated "occlusal surfaces" are assumed to be perpendicular to the second pair of pillars in the M3s, to maximize the repeatability of the virtual simulation. However, it has been observed that as dental wear progresses, the eruption of the M3s is more rapid toward the distal end, resulting in a gradual rotation of the M3 cervix and a decrease in the angle between the cervical plane and the occlusal surface, especially in *Notochoerus* and *Metridiochoerus* (Shaw 1939; Harris and White 1979; Kullmer 1999). Our sensitivity test using arbitrarily tilted slices suggests that changing the slice angle does introduce deviations from the reference values, but the deviations fall within the confidence limit of our reported pattern (Appendix 1, Supplementary Material). While our reported patterns may deviate from the true patterns of functional change on the occlusal surface (more discussions in Appendix 1, section 5, Supplementary Material), we are still confident in our interpretation that the primary contributor to the striking difference in EDBI within the *Notochoerus* and *Metridiochoerus* lineages, respectively, is the degree of M3 elongation (number of main pillars) and the enamel folding pattern of the enamel–dentine junction. In addition, this study establishes the measurements for functional occlusal traits that can be expanded to widely available digital sources such as occlusal photographs.

Finally, our proxy for dental wear progression (DER) disregards the interplay between crown height and dental wear rate and assumes, in order to focus on selective forces related to short-term energetic return, that the life spans of the M3s are proportional among species. However, dental wear is known to be influenced by multiple factors, including ingesta properties (e.g., Baker et al. 1959; Fortelius and Solounias 2000; Lucas et al. 2000; Xia et al. 2015; Karme et al. 2016; Martin et al. 2019), enamel thickness (e.g., Molnar and Gantt 1977; Pérez-Barbería and Gordon 1998; Lucas 2004; Lucas et al. 2008), and enamel microstructure (Rensberger and von Koenigswald 1980; Fortelius 1985; Pfretzschner 1986; von Koenigswald and Clemens 1992; Maas and Dumont 1999; Bajaj and Arola 2009). These factors could influence the rate of dental wear progression, potentially contributing to long-term reproductive success. For instance, thicker enamel has been argued to be more resilient to dental wear (e.g., Janis and Fortelius 1988; Lucas et al. 2008), which can theoretically extend the life span of the tooth, contributing to an individual's long-term reproductive success. We interpret our results of enamel complexity and thickness primarily in the framework of chewing mechanism and occlusal functionality (more discussions in "M3 Elongation and Its Correlations with Functional Occlusal Traits"). Future studies that investigate the possible interactions between crown height, functional occlusal traits, and enamel microstructure will provide a more comprehensive picture of the selective forces in herbivore dietary ecology.

Proxies for Occlusal Complexity and Its Relationship with Diet.—Two-dimensional occlusal complexity as a functional trait has been investigated in two major ways among rodents, ruminants, equids, and suids (Schmidt-Kittler 1984, 2002; Kullmer 1999; Famoso et al. 2013; Gailer and Kaiser 2014). One way to quantify enamel complexity is known as structural density, *D*, which indicates the degree of folding in the enamel bands (Schmidt-Kittler 1984). The other way is to quantify the length of enamel band per unit area of the occlusal surface ("OEI" as in Famoso et al. 2013). Our measurement is a slight modification of the latter, using the length of the enamel–dentine boundary (EDB, or the occlusally exposed enamel–dentine junction) on the simulated occlusal surface instead of the length of the enamel band. We chose this measurement over the previously established ones for the following reasons. First, both structural density *D* and OEI describe a similar geometric relationship between the length of the enamel band and the area that is enclosed by the enamel band. The two measurements are essentially correlated but with slightly different assumptions (see further discussion in Appendix 1, section 8, Supplementary Material). For example, structural density *D* is efficient in detecting enamel folding in a single cusp(id)/pillar (Kullmer 1999; Schmidt-Kittler 2002), but not sensitive in accounting for repeated patterns, such as multiple pillars in suid M3s (Schmidt-Kittler 2002). Second, suid M3s experience substantial changes in occlusal enamel pattern at different wear stages (e.g., Kullmer 1999). As a result, the apparent enamel thickness of the occlusal surface also becomes variable at different wear stages. These features make it difficult to quantify the length of the enamel band consistently (as in Famoso et al. 2013), because a substantial difference exists between the outer perimeter and inner perimeter of the occlusal enamel band. For this reason, we chose to quantify the outer and inner perimeters separately (see "Materials and Methods" section). Third, the EDB has been associated with shearing mechanisms on the occlusal surface in many herbivores (Rensberger 1973; Schmidt-Kittler 1984, 2002; Archer and Sanson 2002; Kaiser 2002; Gailer and Kaiser 2014; Schultz et al. 2020). In particular, we have observed that the angle of the enamel edge at the EDB is sharper than that of the outer enamel edge in both extant and fossil suids, which theoretically creates higher puncture pressure or occlusal stress for breaking down fibrous plant tissue (Popowics and Fortelius 1997; Archer and Sanson 2002; Schmidt-Kittler 2002). Finally, measuring EDB length is consistent and repeatable using micro-CT data, because identifying the EDB is straightforward due to the difference in radiodensity between enamel and dentine. This pattern may not always persist due to taphonomic modifications during fossilization (Appendix 1, section 4, Supplementary Material), but in our case, all specimens presented here exhibit a clear difference in radiodensity between enamel and dentine (Fig. 2).

One substantial challenge in investigating suid M3s is the effect of dental wear progression on the morphology of the occlusal surface (Kullmer 1999), which makes quantitative assessments of occlusal traits difficult. Kullmer (1999) carried out the first comprehensive morphometric investigation of the geometric relationships between occlusal enamel complexity and dental wear in the mesial-most two pairs of pillars of fossil and extant suid M3s. In comparison, we investigated the functional implications of M3 crown elongation on the entire occlusal surface in the context of suid evolution. We also analyzed the evolutionary trend of enamel thickness in the context of occlusal complexity (discussed further in "Enamel Thickness").

Three-dimensional occlusal features, such as dental topographic parameters, have been widely used in primates, distinguishing dietary groups such as omnivores, folivores, frugivores, and insectivores (Ungar and M'Kirera 2003; Evans et al. 2007; Boyer 2008; Bunn and Ungar 2009; Bunn et al. 2011). Rannikko et al. (2020) carried out the first comprehensive study of 3D occlusal complexity in extant and fossil suids and successfully distinguished dietary groups such as omnivores, mixed feeders, and grazers. The estimated diets for fossil suids in Rannikko et al. (2020) are broadly consistent with previous interpretations from dental and postcranial morphology, stable isotopes, and microwear texture analyses (Cooke and Wilkinson 1978; Kullmer 1999; Harris and Cerling 2002; Bishop et al. 2006; Cerling et al. 2015; Souron et al. 2015b; Souron 2017; Lazagabaster 2019). In the context of diet and dental wear, dental topographic analyses correlate surface features created by dental macrowear and the species' actual diet, which are indicators of the realized diet of a species (e.g, Fortelius and Solounias 2000). In comparison, evolutionary trends in 2D complexity reflect how dental morphometrics changed as a result of diet-related selective forces. While our study does not address diet directly, we discuss the evolutionary trends of dental functional traits in the context of suid dietary ecology, informed by multiple lines of evidence that are generally independent of morphology (see discussion in "Evolution of Occlusal Traits in the Context of Fossil Suid Dietary Ecology"). It is also worth noting that evolutionary trends or functional interpretations of dental traits may not be consistent with the realized diet of a species, as behavioral adaptations can often mitigate some morphological constraints (e.g., Lister 2013, 2014; Gailer et al. 2016; Souron 2017).

Our study also underlines the importance of quantifying dental wear in studies of occlusal features such as dental topography (as in Rannikko et al. 2020). Without reference to dental wear progression, some dental topographic values could vary between specimens of different wear stages (e.g., Bunn and Ungar 2009; Pampush et al. 2016), potentially influencing the interpretability of topographic data. Future dental topographic studies that investigate the morphological or morphometrical diversity and dietary indications of worn teeth would benefit from quantifying dental wear progression for more consistent interpretations.

Enamel Thickness.—Unlike EDBI, our proxy for occlusal enamel thickness is not scaled by the square root of M3 occlusal area. We chose to present the "absolute" enamel thickness data instead of relative enamel thickness, primarily due to the observed evolutionary trend of M3 elongation, which would possibly lead to a biased interpretation of decreased enamel thickness over time. Alternatively, relative enamel thickness can be calculated as "absolute" enamel thickness divided by M3 width at the cervix, which is theoretically not affected by M3 elongation. When relative thickness is calculated as such, the general evolutionary pattern is similar to that of the "absolute" enamel thickness (Supplementary Fig. 2).

Both the *Notochoerus* and *Metridiochoerus* lineages exhibited an increase in enamel complexity but a decrease in enamel thickness over time. It is possible that the increase in enamel complexity is correlated with the thinning of enamel in these lineages. A similar correlation has been found in the evolution of Elephantidae, in which an increase in the plate number and the crown height of the M3s are associated with a decrease in enamel thickness (Maglio 1972, 1973; Ferretti 2003). This correlation has been explained as a solution to optimize occlusal stress in the shearing mechanism on the occlusal surface (Ferretti 2003). Our results support this explanation: as enamel complexity increases, the contact area between upper and lower teeth also increases, which would decrease the occlusal stress if enamel thickness remains the same. This would require an increase in masticatory muscle forces to achieve the same occlusal stress to break down tough and fibrous materials. However, an increase in masticatory muscle forces would require substantial restructuring of the masticatory apparatus to permit a larger muscle volume. Assuming that the body size of the animal remains the same, an increase in masticatory muscle forces indicates more energy expenditure in food processing, which would lead to a lower net energetic return for the same amount of food. Alternatively, if enamel thickness decreases, the same occlusal stress can be achieved without any increase in masticatory muscle forces, while the increase in enamel complexity alone can contribute to a higher chewing efficiency. Thinner enamel, however, is at the cost of a higher dental wear rate (Rensberger 1973; Janis and Fortelius 1988), which can explain why a decrease in enamel thickness is frequently associated with an increase in crown height in both suids and elephants (Maglio 1972, 1973; Harris and White 1979). The way that enamel thickness is associated with both occlusal shearing capability and crown height may have further implications for the evolutionary patterns of dental morphology/morphometrics in other mammalian herbivores.

M3 Elongation and Its Correlations with Functional Occlusal Traits.—We observed two distinct patterns in which higher shearing capability can be achieved by M3 elongation among fossil suids. M3 elongation in *Kolpochoerus* allowed a steeper increase in complexity during early wear stages and maintained maximum complexity for a longer life span of the tooth, whereas M3 elongation in *Notochoerus* and *Metridiochoerus* enabled higher maximum complexity. Both patterns increase the "area under the curve" in the wear space for enamel complexity, which can be interpreted as a higher "lifetime" shearing capability. However, the two distinct patterns suggest that M3 elongation influences the functionality of the occlusal surface in different ways. One fundamental distinction of the *Kolpochoerus* lineage is its much lower crown height compared with *Metridiochoerus* and *Notochoerus*, which is probably associated with almost no effect of M3 mesial drift compared with more hypsodont taxa. The combination of a lower crown and a minimal mesial drift allows most cusp(id)s/pillars to be worn in an early wear stage, which explains the pattern of a steeper increase in complexity during early wear stages. In comparison, the pillars in the M3s of the hypsodont taxa are constructed like an escalator: the mesial pillars come into occlusion first, followed by more distal pillars as dental wear progresses and the tooth slowly moves mesially. Although M3 elongation has been associated with the delayed dental eruption and dental mesial drift mechanisms in *Phacochoerus* and *Hylochoerus* (Janis and Fortelius 1988), it seems to have functioned differently in the *Kolpochoerus* lineage. Further investigations into the interplay between dental eruption, wear, hypsodonty, and M3 elongation will help to improve our understanding of their functional significance.

Our results support the hypothesis that adding more cusp(id)s/pillars to the distal end of the M3s increases the theoretical shearing capability of the M3 occlusal surface, potentially permitting more efficient comminution of fibrous vegetation (Souron 2017). However, they only apply to the M3s, whereas it is possible that as dental wear progresses, the functionality of the worn mesial cheek teeth is replaced by added cusp(id)s/pillars in the M3s with the mesial drift mechanism (Shaw 1939; Cooke and Wilkinson 1978; Janis and Fortelius 1988). It is worth noting that our methods could be easily adapted to occlusal photographs that capture different stages of dental wear on the entire tooth row in both extant and fossil herbivorous mammals. This approach also has great potential for collaborative research on a low budget, as numerous occlusal photographs have already been taken by many researchers.

Another way to evaluate the evolutionary trend in enamel complexity would be to scale the length of the occlusal shearing crests of the entire tooth row with body size instead of occlusal area. Body size is known to correlate with many diet-related physiological and morphological features such as basal metabolic rate (e.g., Kleiber 1947), tooth size (e.g., Creighton 1980; Fortelius 1985), and even chewing rate (e.g., Virot et al. 2017; Žliobaitė and Fortelius 2018). The incentive of investigating such a scaling relationship would be to examine M3 elongation and its relationship with the evolution of functional occlusal traits in the context of an animal's physiological limits instead of dental geometry, which is more aligned with our framework of discussions in the short-term versus long-term benefits. Unfortunately, to our knowledge, no reliable body-size estimation method based on dental or osteological metrics has been established for the suid body plan.

Evolution of Occlusal Traits in the Context of Fossil Suid Dietary Ecology.—We discussed M3 elongation and its correlations with functional occlusal traits with an explicit assumption that these traits are adaptive. In this case, our discussion of short-term energetic return and long-term reproductive success can distinguish selective pressures at different timescales. Theoretically, natural selection acting on an individual's immediate energetic return also has influences on its long-term reproductive success: when its short-term energetic needs are not met, there is no guarantee that long-term reproductive success will be achieved, as premature death can also be caused by diseases or predation (e.g., Brown et al. 1993; Sinclair and Arcese 1995; Chandra 1996; Demas 2004; Parsons 2005). On the flip side, reproduction is energetically costly: without being in a good energetic state, there is no guarantee that enough energy can be spared to invest in reproduction and in caring for offspring (e.g., Gittleman and Thompson 1988; Bronson 1989; Wade et al. 1996; Jönsson 1997; Schneider 2004). Therefore, it is reasonable to assume that morphological, physiological, and behavioral traits that can improve an individual's short-term energetic return would have more profound effects than traits that can only improve long-term reproductive success. This scenario applies to the context of dental morphology as well as dietary ecology. After all, the primary function of herbivore teeth is to process vegetation, not to tolerate dental wear (Janis and Fortelius 1988).

The shared evolutionary trends of increased hypsodonty and M3 elongation suggest that a high dental wear rate was a common and strong selective pressure among all fossil suid lineages included in this study. Indeed, contemporaneous and sympatric species of Plio-Pleistocene suids in eastern Africa showed high proportions of C_4 grasses in their diets, placing them close to the dietary range of dedicated grazers such as equids and alcelaphin bovids (e.g., Bibi et al. 2013; Cerling et al. 2015; Uno et al. 2018; Patterson et al. 2019). In this context, the developmental and genetic mechanisms of increase in M3 crown height, M3 elongation, and delayed dental eruption sequence in suids are less constrained than in other herbivores (e.g., Monson et al. 2019). Only a few other mammalian groups, such as proboscideans and rodents, display a combination of delayed dental eruption, molar hypsodonty, and crown elongation (Maglio 1972, 1973; Janis and Fortelius 1988; Gomes Rodrigues et al. 2011).

Despite the shared evolutionary trends, our results show that in the *Kolpochoerus limnetes*–*Kolpochoerus paiceae* lineage, M3 elongation did not correspond to a substantial increase in maximum occlusal enamel complexity or a substantial decrease in enamel thickness. The pattern suggests that in the investigated species of the *Kolpochoerus* lineage, the amount of selective pressure on occlusal traits for short-term energetic return was smaller than in investigated species of the *Notochoerus* and *Metridiochoerus* lineages. On the other hand, in both the *Notochoerus* and *Metridiochoerus* lineages, M3 elongation correlates with increased maximum occlusal enamel complexity and decreased enamel thickness. The striking similarity in the evolutionary trends suggests that the amount of selective pressure on occlusal traits was likely large and similar in both lineages. These interpretations further suggest that the *Kolpochoerus* lineage probably occupied a different ecological niche than those of *Notochoerus* and *Metridiochoerus*, whereas the latter two likely experienced some degree of niche overlap.

Interpreting the paleoecology of *Kolpochoerus* has been contentious primarily due to the somewhat inconsistent results from multiple lines of evidence. Stable carbon isotope analysis of *K. limnetes* teeth from the Shungura (ca. 2.7–1.9 Ma) suggests a high proportion of C_4 plants in the diet (Bibi et al. 2013; Negash et al. 2020), similar to that of *Notochoerus* and *Metridiochoerus* (Harris and Cerling 2002; Cerling et al. 2015). *Kolpochoerus* specimens from the same time interval display consistent dental microwear textures similar to that of extant *Phacochoerus*, also suggesting a grassy diet (Bishop et al. 2006; M. Louail and G. Merceron, personal communication). Dental topographic analysis, however, suggests that *K. limnetes* in the Turkana basin had less abrasive diets than typical grass-feeding suids such as *Metridiochoerus andrewsi* and *No. scotti* (Rannikko et al. 2020). One possibility of niche differentiation is that *Kolpochoerus* fed on different species of C_4 plants or different plant parts compared with *Notochoerus* and *Metridiochoerus* (Bishop et al. 2006; Rannikko et al. 2017). However, existing dietary proxies lack the differentiative power to support this possibility. Another possibility of niche differentiation is that *Kolpochoerus* preferred a different set of habitats compared with *Notochoerus* and *Metridiochoerus*. *Kolpochoerus* has been found to be more frequently associated with fluvial environments (Behrensmeyer 1978), displaying lower enamel oxygen isotope values with a likely water-dependent physiology (Harris and Cerling 2002; Patterson et al. 2019) and having postcranial ecomorphology indicative of less-open habitats (Bishop 1999; Bishop et al. 2006). Our interpretation of the dental evolutionary patterns is aligned with the second possibility, as a more mesic habitat could explain the relaxed selective pressure on occlusal traits associated with the *Kolpochoerus* lineage.

In comparison, the paleoecological interpretations of the *Notochoerus* and *Metridiochoerus* lineages have been more consistent. For earlier species such as *Notochoerus euilus*, dental microwear texture analyses suggest that they were predominantly grass eaters (Lazagabaster 2019), while dental topography and stable isotopes suggest that they were mixed feeders with an increase in dietary C_4 over time (Cerling et al. 2015; Rannikko et al. 2020). For later species such as *No. scotti* and *Metridiochoerus andrewsi/compactus*, multiple lines of evidence, including their specialized dentition (e.g., Cooke and Wilkinson 1978; Harris and White 1979; Kullmer 1999), stable isotopes (Harris and Cerling 2002; Cerling et al. 2015), and flat dental topography (Rannikko et al. 2020),

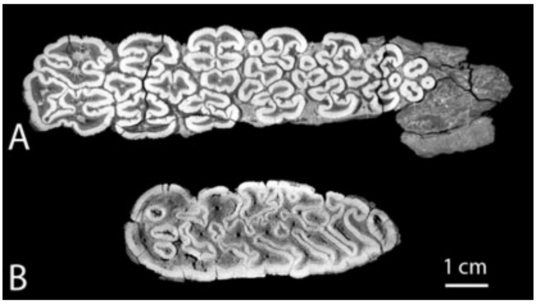

FIGURE 7. Comparing the enamel folding patterns of *Notochoerus scotti* (A, KNM-ER 1777, lower M3) and *Metridiochoerus compactus* (B, KNM-ER 2193, upper M3), when enamel complexity (EDBI) is at its highest value, respectively; *No. scotti* displays a high level of enamel folding within each pillar while the pillars are separated from each other; by contrast, *M. compactus* displays complex interconnecting patterns among the pillars.

support that both had predominantly grassy diets. Although there is no direct evidence to support their interspecific competition so far, our results suggest that *M. compactus* filled a similar ecological niche as *No. scotti*. Despite their similarities in the evolutionary trends of dental functional traits, we observed that higher enamel complexity is achieved in different ways in different lineages: *Notochoerus* increased the degree of folding within each single pillar, while the pillars stayed well separated into late wear stages, whereas *Metridiochoerus* increased the interconnectivity of the enamel bands among the pillars (Fig. 7). Such a difference is discernibly rooted in their distinct ancestries (see Appendix 1, section 1, Supplementary Material, for more information), whereby *Notochoerus* evolved from a tetraconodontine ancestor with well-defined individual pillars, while *Metridiochoerus* evolved from a suine ancestor with overall fewer constraints on the shape of the enamel–dentine junction, which manifests in a tendency of the pillars to fuse with each other as dental wear progresses. As a result, *Metridiochoerus* can reach a similar range of occlusal enamel complexity with fewer pillars (Fig. 4), which may indicate a reduced amount of dental tissue investment for a similar functionality. This theoretical advantage could explain the observation that as *Metridiochoerus* rose in relative abundance in the fossil record, *Notochoerus* experienced a rapid decline and eventually went extinct in the early Pleistocene (Patterson et al. 2017; Rannikko et al. 2017).

Finally, it is important to note that the number of fossil specimens included in this study is small due to the limited availability of micro-CT data, which undoubtedly limits the interpretation of our results. Future studies that investigate the variation of functional occlusal traits with a larger number of fossil specimens while using this dataset as a reference will help further our understanding of the potential biases in the methods. This could also facilitate investigations into the evolutionary patterns of functional occlusal traits in the context of regional climate and vegetation, as well as the associated changes in faunal composition and their diets (Bobe et al. 2002; deMenocal 2004; Cerling et al. 2011; Bibi and Kiessling 2015; Cerling et al. 2015; Uno et al. 2016; Faith et al. 2018). Nevertheless, our quantitative measurements can provide new dimensions in addition to conventional dental metrics such as M3 length and width, in which the morphological diversity of the occlusal surface can be documented and possibly distinguished among suid species or chronospecies.

Graminivory among Extant and Fossil Suids.— The unique dental characteristics of warthogs (*Phacochoerus* spp.) are exceptional examples of their dietary specialization in grass feeding. While *Phacochoerus* seems to exhibit the same relative length of shearing crests (EDBI) as *M. andrewsi* (Fig. 6), the absolute spacing between the shearing crests is much smaller in *Phacochoerus* spp. (Ewer 1958). In addition, the pillars in M3s of *Phacochoerus* spp. remain detached over the majority of a tooth's life span (Shaw 1939), which is different from the increasingly interconnected pillars found in the *M. andrewsi–M. compactus* lineage (Harris and White 1979). It has been proposed that the configuration of simple but high-density pillars in *Phacochoerus* spp. is a special adaptive trait for short grass feeding (Souron 2017), in which small mouthfuls of short grass can be efficiently comminuted with small and tightly packed pillars (Lucas 2004; Souron 2017). Notably, the body sizes of *Phacochoerus* spp. are much smaller compared with most Plio-Pleistocene *Metridiochoerus*. The differences in pillar configuration and body size between

Phacochoerus spp. and *Metridiochoerus* suggest that feeding strategy and body-size differentiation are potential mechanisms of niche partitioning among Plio-Pleistocene grass-feeding suids such as *Notochoerus* and *Metridiochoerus*. In addition, this comparison further suggests that the M3s of *No. scotti* and *M. compactus*, which display even higher EDBI values than those of *Phacochoerus africanus*, are highly specialized. Such levels of specialization likely occurred independently, as there was no substantial temporal overlap between the two species (Patterson et al. 2017; Rannikko et al. 2017). The factors that drove the dental specialization in these species are still unresolved. Future studies would benefit from examining suid dental specialization in the context of body-size evolution and changes in the graminivore guild.

Conclusion

We found that third molar elongation increases the theoretical chewing efficiency of the occlusal surface in all lineages but observed two distinct patterns. The *Notochoerus* and *Metridiochoerus* lineages increased their maximum occlusal enamel complexity, while the *Kolpochoerus* lineage achieved a higher “lifetime” complexity by reaching maximum complexity early in the wear progression. In *Notochoerus* and *Metridiochoerus*, an increase in maximum occlusal enamel complexity possibly correlates with a decrease in average occlusal enamel thickness. This shared evolutionary trend suggests that *Notochoerus* and *Metridiochoerus* likely experienced similar selective pressures on short-term energetic return, which further suggests niche overlap based on existing dietary interpretations. By contrast, the *Kolpochoerus* lineage maintained its maximum enamel complexity and average enamel thickness, which indicates relaxed selective pressures on short-term energetic return and a different ecological niche. The result that *Notochoerus scotti* and *Metridiochoerus compactus* display even higher enamel complexity than extant warthogs suggests that they were highly specialized grass feeders. Our methods can provide a complementary line of evidence to the existing analyses of diet-related dental traits. They can be expanded to other herbivore lineages that also underwent morphological changes in response to tough and abrasive diets.

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Data Availability Statement

The data underlying this article are available in the article and in its online Supplementary Material, which is available on DRYAD at: https://doi.org/10.5061/dryad.tmpg4f510.

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