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Southernmost record of *Megadolodus* (Litopterna, Proterotheriidae, Megadolodinae) from the late Middle Miocene of Fitzcarrald, Peruvian Amazonia, and mesowear analysis of diet in megadolodine litopterns

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ARTICLE

SOUTHERNMOST RECORD OF *MEGADOLODUS* (LITOPTERNA, PROTEROTHERIIDAE, MEGADOLODINAE) FROM THE LATE MIDDLE MIOCENE OF FITZCARRALD, PERUVIAN AMAZONIA, AND MESOWEAR ANALYSIS OF DIET IN MEGADOLODINE LITOPTERNS

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ABSTRACT—Megadolodinae is a clade of tropical bunodont litopterns that includes three previously recognized species from Miocene fossil sites from northern South America. Here, we report an additional occurrence of *Megadolodus molariformis* from the Middle Miocene exposures at the Fitzcarrald arch (Peruvian Amazonia), based on dental material, which represents the southernmost record of the clade. This discovery further increases the faunal similarity between Fitzcarrald and the coeval La Venta fauna of Colombia. Given the convergent evolution of the bunodont dentition of megadolodines with suoids (Old World pigs and New World peccaries), we tested the hypothesis of frugivory in megadolodines with a mesowear angle approach using modern pigs and peccaries. These analyses differentiate the diet of modern suoids and suggest that megadolodines had a more abrasive diet than most of these taxa, except for the grazing warthogs. The dentition of megadolodines shows similar levels of abrasion to modern babirusas, thereby suggesting that the latter may represent an appropriate modern analog.

SUPPLEMENTARY FILES—Supplementary files are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

The South American Native Ungulates (SANUs) are a disparate group of herbivorous ungulates grouped into up to seven clades (Astrapotheria, Didolodontidae, Kollpaniinae, Litopterna, Notoungulata, Pyrotheria, and Xenungulata) that occur in the South American fossil record from the early Paleocene up to the Late Pleistocene (Croft et al., 2020). Because of their isolation from other continents (Simpson, 1980), the SANUs represent natural evolutionary experiments, characterized by convergent evolution of ecomorphologies similar to those of ungulates in other continents. Some examples include the large astrapotheres that, like proboscideans in other continents, had

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a trunk and tusks to strip vegetation (Johnson & Madden, 1997), and some toxodontids such as *Hoffstetterius* that had a keratinous horn on their heads like those of rhinoceroses on other continents (Saint-André, 1993).

The megadolodine litopterns are another example of convergent evolution, closely resembling suoids, today represented by Suidae (the 'Old World' pigs) and Tayassuidae (the 'New World' peccaries), in their large, bunodont molars, and their robust femora and short tibiae and metatarsal III relative to other modern ungulates (Cifelli & Villarroel, 1997; Orliac et al., 2010). The two most well-studied megadolodine genera, *Megadolodus* and *Neodolodus*, also possess sharp tusks, analogous to those of suoids (although formed from the incisors) (Carrillo, Suarez et al., 2023a). Three Megadolodinae species are currently recognized—*Megadolodus molariformis*, *Neodolodus colombianus*, and *Bounodus enigmaticus*, with *M. molariformis* and *N. colombianus* previously identified from the late Middle Miocene of Colombia (Carrillo et al., 2018; Carrillo, Suarez et al., 2023a; Cifelli & Diaz, 1989; Cifelli & Villarroel, 1997; Hoffstetter & Soria, 1986; McKenna, 1956), whilst *B. enigmaticus* is currently only known from the upper Urumaco Formation of Venezuela (Upper Miocene) (Carlini et al., 2006). The Megadolodinae therefore represent an extinct tropical ungulate clade, and one illustrating the faunal links between western Amazonian localities.

During the Middle Miocene, a number of factors drove the formation of a wetland system in Amazonia (Antoine et al., 2016; Hoorn, Wesselingh, Hovikoski et al., 2010; Hoorn, Wesselingh, Ter Steege et al., 2010; Hoorn et al., 2022; Jaramillo et al., 2017). Global sea level was intermittently high (Boonstra et al., 2015; Hoorn, 1993), and Andean uplift drove flexural (Hoorn, 1993; Sacek, 2014) and dynamic subsidence in the foreland basins (Bicudo et al., 2020; Eakin et al., 2014; Roddaz et al., 2010), as well as increased rainfall due to orogenic effects (Poulsen et al., 2010). The Pebas Mega-Wetland System (PMWS), resulting from these geological processes, covered ~1,000,000 km^2 and acted as an important biogeographic feature, driving the origination of a range of clades (Antoine et al., 2016; Hoorn et al., 2022; Marivaux, Adnet, Altamirano-Sierra, Pujos et al., 2016).

Few outcrops are available for the Middle Miocene interval in Western Amazonia (Antoine et al., 2013; Boivin et al., 2021; Marivaux et al., 2020; Negri et al., 2010; Stutz et al., 2022; Tejada-Lara et al., 2015) and much of our understanding of the faunal history of the region comes from three coeval locations from the late Middle Miocene Laventan Stage/Age (13.5–11.8 Ma; Madden et al., 1997)—La Venta in Colombia, and the Fitzcarrald Local Fauna and the TAR-31 fossil-bearing locality in Peru (Antoine et al., 2013; Negri et al., 2010; Tejada-Lara et al., 2015). The La Venta area in particular has been investigated for over a century (Carrillo, Jaramillo et al., 2023; Kay et al., 1997) and has yielded the most speciose vertebrate assemblage from northern South America, with at least 75 mammal species that have been described (Carrillo, Jaramillo et al., 2023; Wilson & Parker, 2023). In contrast, the Peruvian faunas of Fitzcarrald and TAR-31 have been discovered much more recently. Pioneering fieldwork performed in 2005 and 2007 along the Río Inuya, Río Mapuya, and Río Sepa led to the discovery of at least 24 mammalian taxa making up the Fitzcarrald local fauna (Antoine et al., 2007; Bianucci et al., 2013; Goillot et al., 2011; Pujos et al., 2013; Tejada-Lara et al., 2015). More recently, TAR-31 was discovered in 2015 and investigated until 2019. In sharing most of its mammalian components with La Venta (metatherians, xenarthrans, notoungulates, megadolodines, rodents, and a unique primate), the TAR-31 locality has been unambiguously assigned to the Laventan Stage/Age (Boivin et al., 2021; Marivaux et al., 2020; Stutz et al., 2022).

In this study, we add to the mammalian faunal list of the Fitzcarrald Local Fauna through the recognition of a new record of a megadolodine litoptern from dental material (a single isolated tooth) unearthed in a new locality in 2017 (named URU-208—*Río Urubamba* fossil-bearing locality 208) by a team made up of several of us (POA, APP, FLC, LM, FP, and ASM; see author contributions). Alongside this megadolodine, a dozen vertebrate taxa are recognized at URU-208, including an unidentified stingray (dermal buckle), ray-finned fish (a large pimelodid catfish plus cynodontid, anostomid, and serrasalmine characiforms), a podocnemidid turtle (shell fragments), four crocodylomorphs (teeth of the sebecid cf. *Langstonia* sp., the caimanines *Caiman* sp. and *Purussaurus* sp., and an unidentified gavialoid), as well as two caviomorph rodents (a lower jaw and a molar assigned to '*Scleromys*' sp. and *Microsteiromys* sp., respectively). We also consider the implications of the megadolodine litoptern for understanding the paleoenvironmental conditions of Western Amazonia in the Middle Miocene.

Megadolodines have been suggested to be frugivores based on their bunodont dentition and thick enamel (Cifelli & Villarroel, 1997) and we use mesowear angles to quantify their diet relative to modern suoids with variable ecologies. Finally, we introduce a novel mesowear angle method for bunodont ungulates to test the hypothesis of similarity in the diets of megadolodines with those of modern suoids.

MATERIALS AND METHODS

Geological Context

The specimen was unearthed during an expedition in the Fitzcarrald Arch in 2017. The URU-208 outcrop (S10°42.579′, W73° 37.255′) is situated on the right bank of the *Río Urubamba*, upstream Atalaya city (Ucayali Department, Peruvian Amazonia), at the base of the cliffs located immediately downstream of the Santa Clara Native Community. The concerned deposits, assigned to the Middle to Upper Miocene Formation (Espurt et al., 2007; LAGESA & C.F.G.S., 1997), consist of pinkish channelized conglomerates intercalated with silts and clays, forming an island by the dry season. The tooth was found *in situ*, embedded within a loose conglomerate with a sandy matrix, which allowed for manual preparation.

Both the fossil-bearing facies and associated faunal elements (especially the crocodylomorph community and the rodents) allow us to consider URU-208 as a new locality of the Fitzcarrald Local Fauna, consistently Laventan in age (Antoine et al., 2007; Tejada-Lara et al., 2015).

Mesowear Analysis

We compare the mesowear signal of specimens of megadolodine litopterns to the signal from modern suoids to examine the diet of these fossil taxa. We largely focus on tropical rainforest suoids (e.g., *Babirusa*, *Dicotyles*, and *Tayassu*) as potential ecological analogs but also include some larger open-habitat taxa (*Phacochoerus*) and ecologically more generalist taxa (*Sus*) for comparison. As far as we are aware, all modern suoid specimens included here were from wild individuals.

When possible, the modern specimens were scanned using the Polycam 3D scanning application (Polycam Inc., 2023), using the photogrammetry mode on an iPhone XR, and these scans were then loaded into Blender v3.1.0 (Blender Online Community, 2022). For some modern specimens, measurements were taken manually using a handheld digital angle measuring device (Saarinen et al., 2015). For megadolodine specimens, we used published 3D models (Carrillo, Suarez et al., 2023b), Polycam scans of the dentition of museum specimens, and in some cases, angles were measured from photographs taken from a buccal and lingual direction using Fiji, an open-source software package for image processing (Schindelin et al., 2012).

The mesowear angle methodology uses principles that have been applied to other groups, including proboscideans (Saarinen et al., 2015), xenarthrans (Saarinen & Karme, 2017), and toxodontids (Wilson et al., 2024). In *Phacochoerus* and in two *Megadolodus* specimens (UNC-TATAC1 and UCMP 39270), angles were measured from the base of well-developed dentine valleys to the highest point of the ridges surrounding these valleys. In *Phacochoerus*, chosen dentine valleys were considered to represent a medium stage of wear, usually roughly halfway along the tooth (Saarinen et al., 2015). In the other specimens, we used intercusp facet angles as a mesowear angle (Saarinen & Lister, 2023; Saarinen et al., 2015; Xafis et al., 2020) (Fig. 1), with the angles measured between cusp tips and the valleys between them along intercusp wear facets. For all specimens (when possible), we took measurements on the buccal and lingual sides of the left and right dentition in both upper and lower jaws. We then separately averaged these angles for both the upper and lower dentitions, given that there were differences in the angles between the two. Where appropriate, we measured these intercusp facet angles on the second molar, but when this was either too heavily worn or unworn, either the first or third molar was used instead. Regardless of which tooth was used, the angles were measured between the metacone and the paracone and between the hypocone and the protocone in the upper molars (Table S1) as well as between the metaconid and the entoconid, and the protoconid and the hypoconid in the lower molars (Table S2). We tested for differences in mesowear angles between extant taxa using a non-parametric Kruskal–Wallis test. Visualizations of the resulting mesowear angles were made using *ggplot2* (Wickham, 2016) for R 4.1.1 (R Core Team, 2021).

Institutional Abbreviations—**AMU-CURS**, Colección Paleontológica de la Alcaldía Bolivariana de Urumaco, Urumaco, Venezuela; **KNM**, National Museums of Kenya, Nairobi, Kenya; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MPV**, Museo Paleontológico de Villavieja, Villavieja, Colombia; **MUN-STRI**, Mapuka Museum, Universidad del Norte, Barranquilla, Colombia; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Perú; **MZH**, Finnish Museum of Natural History, Helsinki, Finland; **RMCA**, Royal Museum for Central Africa, Tervuren, Belgium; **VPPLT**, Vigías del Patrimonio Paleontológico, Museo de Historia Natural La Tatacoa, Villavieja, Colombia; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, U.S.A.; **UMZC**, University Museum of Zoology Cambridge, Cambridge, U.K.; **UNC**, Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá, Colombia.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Infraclass PLACENTALIA Owen, 1837
Order LITOPTERNA Ameghino, 1889
Family PROTEROTHERIIDAE Ameghino, 1887
Subfamily MEGADOLODINAE Cifelli & Villarroel, 1997
Genus *MEGADOLODUS* McKenna, 1956
MEGADOLODUS MOLARIFORMIS McKenna, 1956
Fig. 2A–D

Holotype— UCMP 39270, part of left mandible with complete m1, labial part of p4 and roots of p3 and m2, from UCMP Locality V4932 (Monkey Beds, Villavieja Formation, Middle Miocene, Laventan SALMA), Huila, Colombia.

Referred Material—MUSM 4963, isolated right upper molar (M1?).

Locality, Horizon, and Age—URU-208 (S10°42.579′, W73° 37.255′), Fitzcarrald Local Fauna, Ipururo Formation (Middle to Upper Miocene, Laventan SALMA), Ucayali Department, Peru.

Description—MUSM 4963 is a low-crowned bunodont upper molar with four roots. It is roughly quadrangular in occlusal view, with a length of 15.36 mm and a maximum width of 19.20 mm. It has been superficially eroded (smooth enamel surface) in a channel before deposition in the Ipururo conglomerate. It has thick enamel, characteristic of *M. molariformis* (Cifelli & Villarroel, 1997) and has a well-developed bulbous/inflated paracone, metacone, protocone, and hypocone, alongside a strong mesiolingual cingulum. Buccally, only the mesostyle is visible (very small but well-defined). The metastyle and parastyle are absent. The metaconule and paraconule are both conspicuous. The metaconule is equidistant between the metacone and the hypocone. The protocone is displaced distally compared with a buccolingual straight line connecting the paracone and paraconule. A preprotocrista connects the protocone to the paraconule and a preparaconular crista extends mesiobuccally to reach the base of the mesial flank of the paracone, where a parastyle would occur (although there is no parastyle). Such cristae are missing for the metaconule, which is isolated. There are four divergent roots (two buccal and two lingual, broken towards their tips), which are elongated buccolingually and compressed mesiodistally.

Remarks—MUSM 4963 is morphologically indistinguishable from specimens of *Megadolodus molariformis* known from the late Middle Miocene mammal assemblage in La Venta, Colombia (Carrillo, Suarez et al., 2023a; Cifelli & Villarroel, 1997). M1 and M2 in *M. molariformis* are very similar in overall morphology. In the two known Colombian specimens with upper teeth (UNC TATAC1 and VLPPT 1588), the M2 is the largest tooth, and the dimensions of MUSM 4963 are slightly smaller than those for previously described second upper molars in *M. molariformis*. On the basis of the size of the tooth, we consider it more likely that it represents a right M1. The currently uncataloged dental specimen from TAR-31 is a fragment of occlusal surface, the pattern of which is fully compatible with an upper molar of *M. molariformis* (Boivin et al., 2021; Carrillo, Suarez et al., 2023a; Cifelli & Villarroel 1997). Nevertheless, its fragmentary condition impedes further comparison with MUSM 4963.

Mesowear Angles

The mesowear angles in modern suoids show a large degree of interspecific variation, from <90° in *Dicotyles tajacu* and some specimens of *Sus scrofa scrofa* for example to >140° in the two species of *Phacochoerus* (Fig. 3). The mesowear angles in both lower (Kruskal–Wallis test: $\chi^2 = 48.771$, $df = 12$, $p < 0.0001$) and upper (Kruskal–Wallis test: $\chi^2 = 51.148$, $df = 11$, $p < 0.0001$) dentitions significantly differed between the species measured here. In many of the modern taxa, there is a large degree of intraspecific variation, which we propose reflects the variable, generalist diet of modern suoids. In general, there was more variation between different modern taxa in the upper molars and the angles measured in the upper toothrows were slightly higher than those in the lower toothrows. Of the 54 specimens for which both upper and lower teeth were available, 64.8% had higher mesowear angles in the upper dentition. The differences between modern taxa largely reflected known differences in their dietary preferences (e.g., *Phacochoerus* is known to consume more abrasive material as a result of a grazing lifestyle) (Souron, 2018), although the precise diet of each specimen was not known.

The measured angles in the megadolodine litopterns generally suggest that they were at the more abrasive end of the

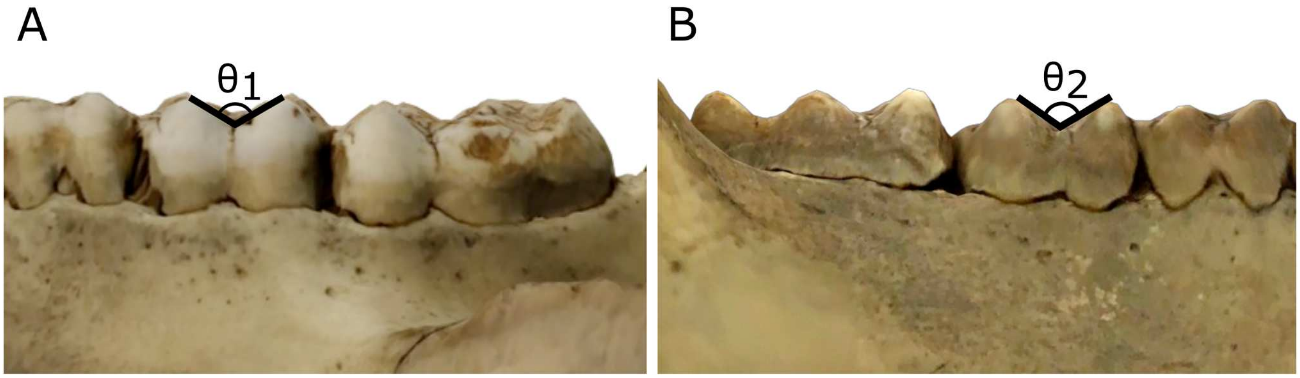

FIGURE 1. Intercusp facet angles measured in modern suoids and megadolodines from 3D scans. **A**, intercusp angle between paracone and metacone in right upper molar (M2), **B**, intercusp angle between paraconid and metaconid in right lower molar (m2) (*Babyrousa babyrussa*, UMZC H.12999, buccal view). **Abbreviation**: **θ**, measured intercusp angle.

dietary spectrum of our taxonomic sample, with larger (shallower) mesowear angles than most suoids measured here. There is a large degree of overlap between the mesowear angles in these fossil taxa and those of *Babyrousa babyrussa* specimens, as well as similarities with *Sus verrucosus* and *Sus scrofa andamanensis*, although the latter two taxa are represented with only a single specimen and should therefore be treated with caution. In the megadolodine taxa where more than a single specimen could be measured, we find some degree of intraspecific variation, suggesting a variable, generalist diet like that of modern suoids. In the case of the lower jaw of *Neodolodus colombianus*, three specimens were measured, which varied in mesowear angle by ~40°. MUN-STRI 16716 (132.5°) is a highly worn lower jaw from the Castilletes Formation of La Guajira, Colombia, whilst VLPPT 1696 is a lightly worn specimen from La Venta (91.5°). The variability in *N. colombianus* could result from habitat-related differences in diet or from wear stage. We have here included all megadolodines regardless of wear stage for completeness, but this example highlights the effect that this factor may cause in interpretation of diet by mesowear.

DISCUSSION

Southernmost Record of a Megadolodine

The recognition of *M. molariformis* in the Fitzcarrald fauna of Peruvian Amazonia represents the southernmost occurrence of

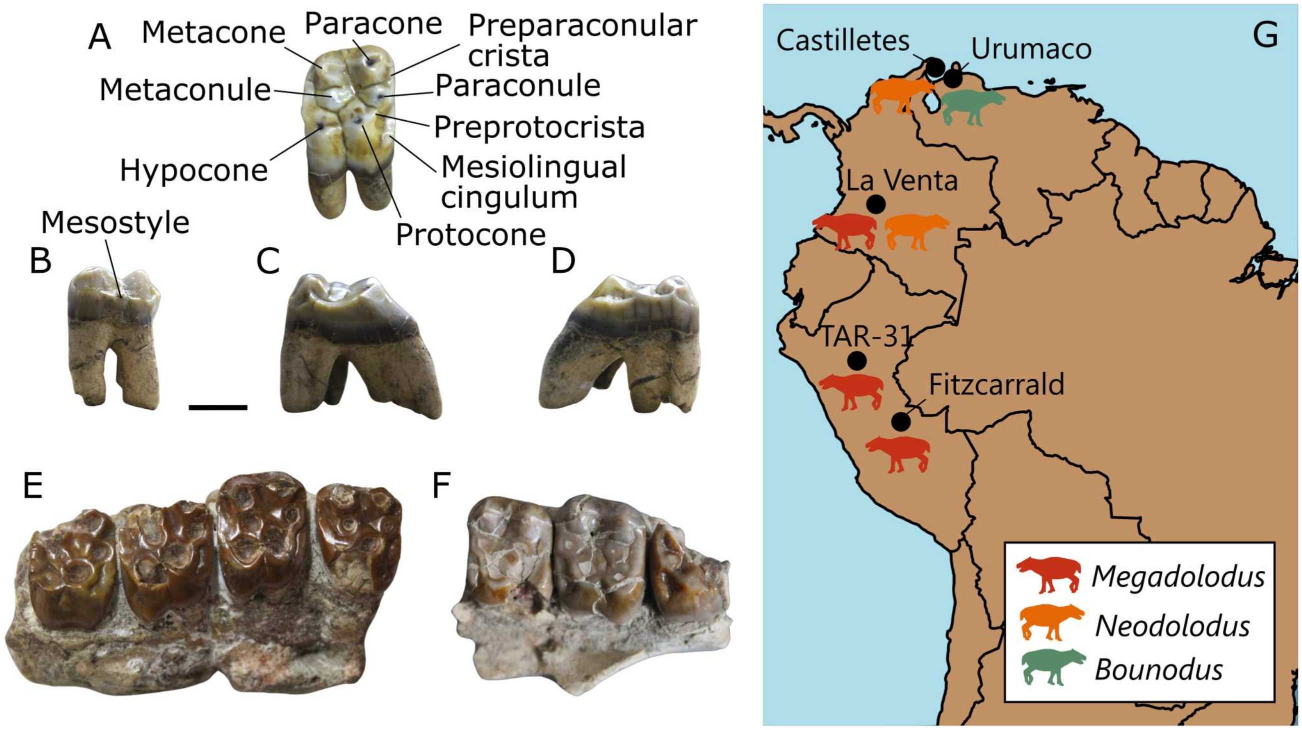

FIGURE 2. A–F. *Megadolodus molariformis* upper dentition. **A**–**D**. *Megadolodus molariformis* right M1 (MUSM 4963) from the URU-208 locality of the Fitzcarrald Local Fauna in **A**, occlusal, **B**, buccal, **C**, distal, and **D**, mesial views, respectively. **E**, UNC TATAC1, right maxilla with P4–M3. F, VPPLT 1588, left maxilla with M1–3. **G**, map of the occurrences of Megadolodinae in northern South America. *Megadolodus molariformis* silhouette from phylopic.org (Zimices/Julián Bayona, CC BY 3.0 DEED). Scale bar equals 10 mm.

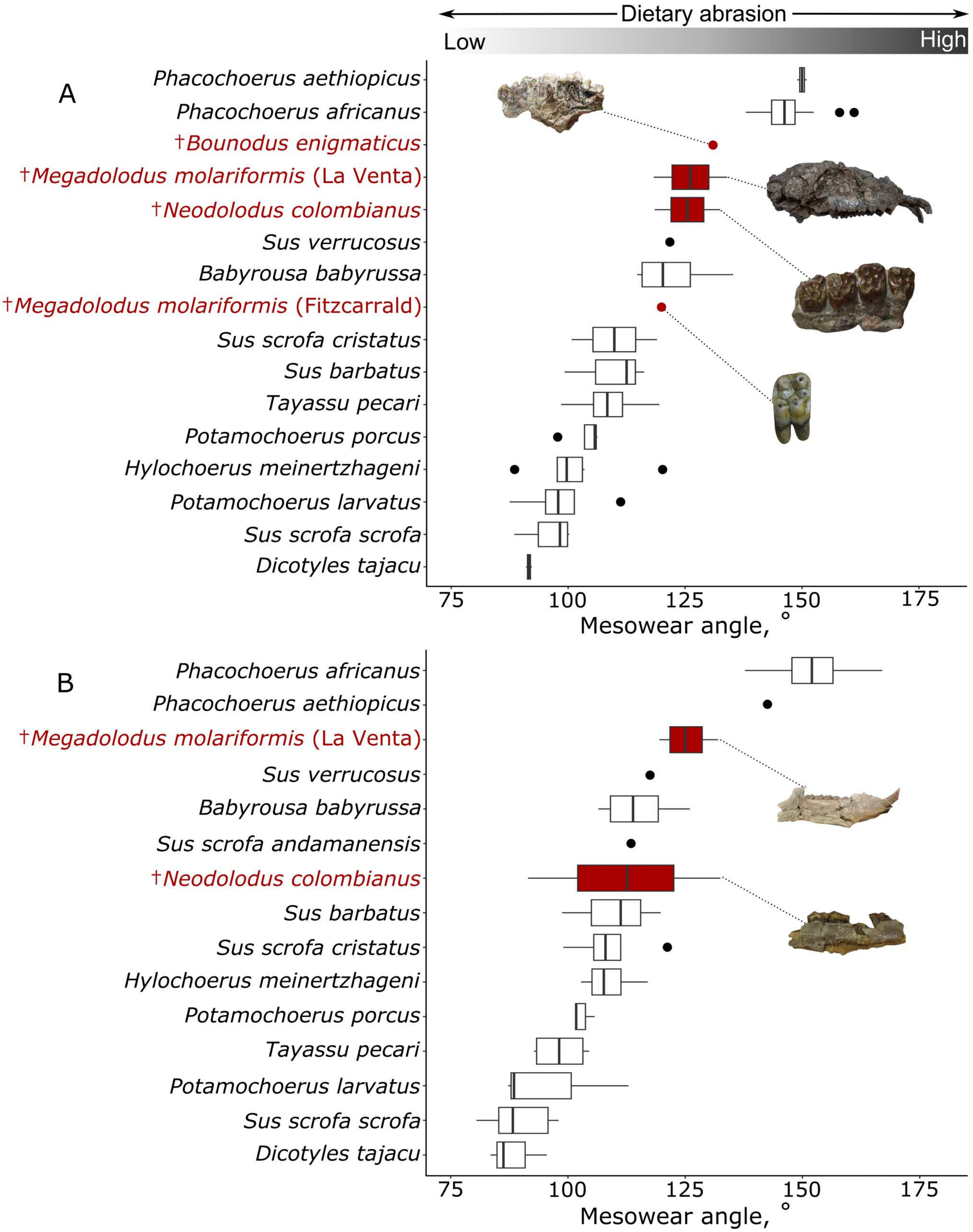

Figure 3. Mesowear angles for the extant suoids and megadolodine litopterns measured in this study. Megadolodines highlighted in red. **A**, upper dentition, **B**, lower dentition. Photographs are (top–bottom) VLPPT 1696, AMU-CURS 40, UNC TATAC1, MUSM 4963, VPPLT 974, and MUN-STRI 16716.

Megadolodinae, with the Peruvian records expanding the range of this subfamily by ~1500 km southwards. It strengthens the close relationship between the Fitzcarrald Local Fauna, TAR-31, and La Venta mammalian assemblages, with at least 12 terrestrial mammal genera (and possibly as many as 19) shared between these three faunas (Boivin et al., 2021; Carrillo et al., 2015; Marivaux et al., 2020; Stutz et al., 2022; Tejada-Lara et al., 2015). The high faunal similarity between these localities presumably related to a partial continuity in the PMWS (Benites-Palomino et al., 2020, 2024; Salas-Gismondi et al. 2015, 2016). Combining data from these three assemblages with those from elsewhere, e.g., Contamana, Peru (CTA-57 and CTA-44 localities; Antoine et al., 2016), the Castilletes Formation, Colombia (Amson et al., 2016; Carrillo et al., 2018; Moreno et al., 2015; Suarez et al., 2016) and Miocene Ecuador (Cadena & Román-Carrión, 2018; Madden, 1990; Román-Carrión et al., 2021), there is increasing evidence for faunal and environmental consistency in the Middle Miocene of Western Amazonia. During this period, northwestern South America was dominated by the PMWS (Boonstra et al., 2015; Hoorn, Wesselingh, Hovikoski et al., 2010; Hoorn, Wesselingh, Ter Steege et al., 2010; Jaramillo et al., 2017; Mora et al., 2010), and the Colombian, Peruvian, and Ecuadorian faunas were all recorded on the western edge of the PMWS (Antoine et al., 2007, 2016; Benites-Palomino et al., 2020; Marivaux et al., 2020), which would have acted as an important biogeographic barrier for terrestrial mammals (Hoorn et al., 2022).

Although these Western Amazonian terrestrial environments are generally assumed to be similar, their exact nature is unclear (Carrillo, Jaramillo et al., 2023). Several studies, particularly of La Venta, suggest that the environment was likely to have been forested, though with closely associated freshwater habitats (Catena & Croft, 2020; Croft, 2001; Kay & Madden, 1997a, b; Spradley et al., 2019; Wilson & Parker, 2023), even if the extent to which there were open patches, possibly related to the action of megaherbivores (Kay & Madden, 1997a), is unknown (Carrillo, Jaramillo et al., 2023). Particularly given the limited paleobotanical data in La Venta (Carrillo, Jaramillo et al., 2023), one potential method of paleoenvironmental reconstruction during this period is through ecometrics, using the relationship between environmental variables and functional traits on a community level (e.g., the relationship between mean community hypsodonty and rainfall; Eronen et al., 2010; Fortelius et al., 2002; Liu et al., 2012; Oksanen et al., 2019; Short et al., 2021; Vermillion et al., 2018).

Bunodonty has been recognized as a significant trait in previous ecometric studies (e.g., Liu et al., 2023; Saarinen et al., 2021). Modern bunodonts are typically omnivorous or frugivorous and a high proportion of bunodonts in a community indicates a warm, wet, and forested environment in other continents (Saarinen et al., 2021). Bunodonty is prevalent in modern primates, but the preservation of primates in the Miocene is sparce (Žliobaitė & Fortelius, 2022), and with the exception of La Venta (Carrillo, Jaramillo et al., 2023b; Kay & Madden, 1997a, b) and TAR-31 (Marivaux et al., 2020), primates have largely not yet been recognized in the Middle Miocene sites of Western Amazonia (e.g., Fitzcarrald; Marivaux, Adnet, Altamirano-Sierra, Boivin et al., 2016). The recognition of a bunodont taxon in the Fitzcarrald fauna is significant as it represents the first evidence of this important trait here and suggests that bunodonty could be a valuable characteristic for paleoenvironmental reconstruction in South America. It also reinforces the importance of continued fieldwork and taxonomic collections work for trait-based environmental reconstructions, because the identification of *M. molariformis* changes community trait averages for the Fitzcarrald fauna.

Bunodont Mesowear and Modern Megadolodine Analogs

We find that mesowear angles differ between suoid species, reflecting dietary differences (Fig. 3) (Leus & Macdonald, 1997; Souron, 2018) and propose that these differences in mesowear angles can be used for dietary predictions in the fossil record of bunodont ungulates (both megadolodines and fossil suoids). Dietary differences between modern wild pigs have previously been identified using 3D dental topography (Rannikko et al., 2020), with *Phacochoerus* found as having a higher angularity and orientation patch count and lower mean surface slope, sharpness, and relief index for example. However, the mesowear angles that we measure here are faster and easier to measure than these methods, while nonetheless providing similar results. Furthermore, the mesowear angles specifically concentrate on worn features of the molar surface (dentine valleys and enamel facets) and can thus be argued to be more closely associated with wear effect specifically than for example mean surface slope. The angles are consistent with those from other taxa (Saarinen & Karme, 2017; Saarinen et al., 2015), with a larger (shallower) angle corresponding to a diet high in abrasive material.

However, the threshold between a browsing and grazing signal in modern suoids seems to be higher than in other taxa (Saarinen & Karme, 2017; Saarinen & Lister, 2023; Saarinen et al., 2015). We propose this could be a result of minute abraded brachydont (MABRA) syndrome (Fortelius & Solounias, 2000), given the relatively small size of most modern forest suoids. On the other hand, the comparatively high angles of the grazing *Phacochoerus* in relation to grazing proboscideans might also result from small size, as a combination of relatively thick enamel and small size of the dentine pits at the cusp tips. Additionally, with a very high percentage of grass in its diet, 90–100% according to Codron et al. (2007), *Phacochoerus* may have a more heavily grass-dominated diet than any extant or extinct proboscidean species (see Saarinen & Lister [2016, 2023] and Xafis et al. [2020] for comparative dietary information from proboscideans).

Low-abrasion diets were recorded for several forest-dwelling omnivorous modern taxa, including *Dicotyles tajacu*, *Sus scrofa*, and *Potamochoerus larvatus*. In tropical forests, *D. tajacu* is primarily frugivorous, though also consumes a high proportion of leaves and fibers, particularly in the dry season (Desbiez et al., 2009; Keuroghlian & Eaton, 2008). *Sus scrofa* has an extremely varied diet, largely consisting of plant material, though it is an opportunistic feeder, and the diet likely varies between individuals (Keuling et al., 2018). In a record of *P. larvatus* diet from the southern and eastern Cape, South Africa, Seydack (1990) found that the majority of consumed food was from leaf litter and subterranean sources.

As in proboscideans, the relatively shallow dentine valleys found in the two warthog species studied here reflect a grazing lifestyle. Butynski & de Jong (2018) have described *Phacochoerus africanus* as a "hypergrazer," with a diet consisting of over 90% C4 grasses (Codron et al., 2007). *Phacochoerus aethiopicus* similarly mostly consumes C4 grasses (86%) (Nyafu, 2009). The fact that this strong grazing diet was reconstructed in the mesowear angles supports the application of these methods to suoids.

In other taxonomic groups, differences in mesowear angles are often considered to reflect changes in dietary abrasion associated with consumption of grasses (Saarinen & Karme, 2017; Saarinen et al., 2015; Wilson et al., 2024). At an elevated mesowear angle relative to the previous species mentioned are a heterogeneous group of suoids containing *Hylochoerus meinertzhageni*, *Tayassu pecari*, *Sus barbatus*, *Sus scrofa cristatus*, and *Potamochoerus porcus*. *Hylochoerus meinertzhageni* largely feeds on grasses in tropical rainforest environments (D'Huart, 1976), although these grasses are presumably relatively less abrasive than in other environments. *Potamochoerus porcus* consumes a large number of seeds as part of its diet (Melletti et al., 2018), and whilst our sample of this species is small, it is conceivable that hard seed predation would cause elevated abrasion compared with *P. larvatus*. This is also possible for *T. pecari*, as compared with *D. tajacu*, the seeds consumed by this species tend to be harder, presumably driving greater tooth wear (Kiltie, 1982). *Sus barbatus* seeks out the hard nuts of dipterocarps during masting (Caldecott, 1991; Leus & Macdonald, 1997; Luskin & Ke, 2018), and again the significant consumption of these nuts may be a part of the abrasive signal. An alternative factor that might influence abrasion is soil intake during rooting. However, we observe that some taxa that show high incidence of rooting behavior (e.g., *Sus scrofa scrofa*) (Keuling et al., 2018) have relatively sharp mesowear angles, and so we consider seed consumption a more likely hypothesis.

The megadolodines generally possess mesowear angles that are slightly higher than those in most modern suoids, thereby suggesting that they had a more abrasive diet than most of these living taxa. However, a variety of explanations could produce this result. One is increased grass intake, whilst another explanation could be the consumption of abrasive soil material. During the Middle Miocene, there was volcanic activity close to La Venta in Colombia (Mora-Rojas et al., 2023; Zapata et al., 2023). The prevalence of volcanic ash would increase dietary abrasion relative to regions without volcanic activity (Madden 2015; Smith et al., 1977). In contrast to La Venta, no evidence for volcanism has been observed in Peru around Tarapoto or Fitzcarrald. It is conceivable that this could explain why MUSM 4963 has a mesowear angle lower than in most La Venta *Megadolodus* specimens (Fig. 3A), although the value observed for MUSM 4963 is within the range of those at La Venta, and interindividual variability seems more likely. Mesowear analyses of other taxa at La Venta will help us to understand more about the paleoenvironment here, but other methodological approaches are needed for the non-bunodont ungulates, including the other proterotheriid litopterns *Mesolicaphrium sanalfonense* and *Villarroelia totoyoi* (Carrillo, Suarez et al., 2023a; Cifelli & Guerrero, 1997).

Given the variation within the diet of the suoids measured here, we believe that higher angles in megadolodines are most likely due to the increased consumption of hard fruits and seeds. In another group of fossil ungulates with no living relatives (e.g., Chalicotheriidae), microwear analyses have supported the idea that an abrasive mesowear signal is related to consumption of hard items such as fruit, seeds, and nuts (Schulz & Fahlke, 2009; Schulz et al., 2007; Semprebon et al., 2011). Future studies may similarly use other dietary proxies like microwear to corroborate the mesowear results here. However, one modern suoid taxon studied here, *Babyrousa babyrussa*, overlaps with the mesowear signal from the megadolodines.

Quantitative analyses of the diet of babirusas are limited, though it seems that they largely favor the consumption of fruit and seeds, particularly including the toxic *Pangium* (Leus, 1996; Leus & Macdonald, 1997; Macdonald, 2018; Sheherazade et al., 2018; Tulung et al., 2013). Contrary to other suids, babirusas do not have a well-developed rostral bone (*os rostrale*) in their nose, and this has been suggested to affect their dietary ecology, as they do not show the same level of rooting as other suoids (MacDonald, 1993). Megadolodine skulls are largely not available for comparison of this trait, with only one specimen from *Neodolodus colombianus* (VPPLT 1696). In this specimen, there are similarly no anterior rostral bones, though this could be because of damage, given that portions of the premaxilla and maxilla are missing (Carrillo, Suarez et al., 2023a). The ecological analogy of the megadolodines to modern babirusas, as indicated by the similar mesowear angles, is consistent with the interpretation of Cifelli and Villarroel (1997) that they were probably largely fruit eaters.

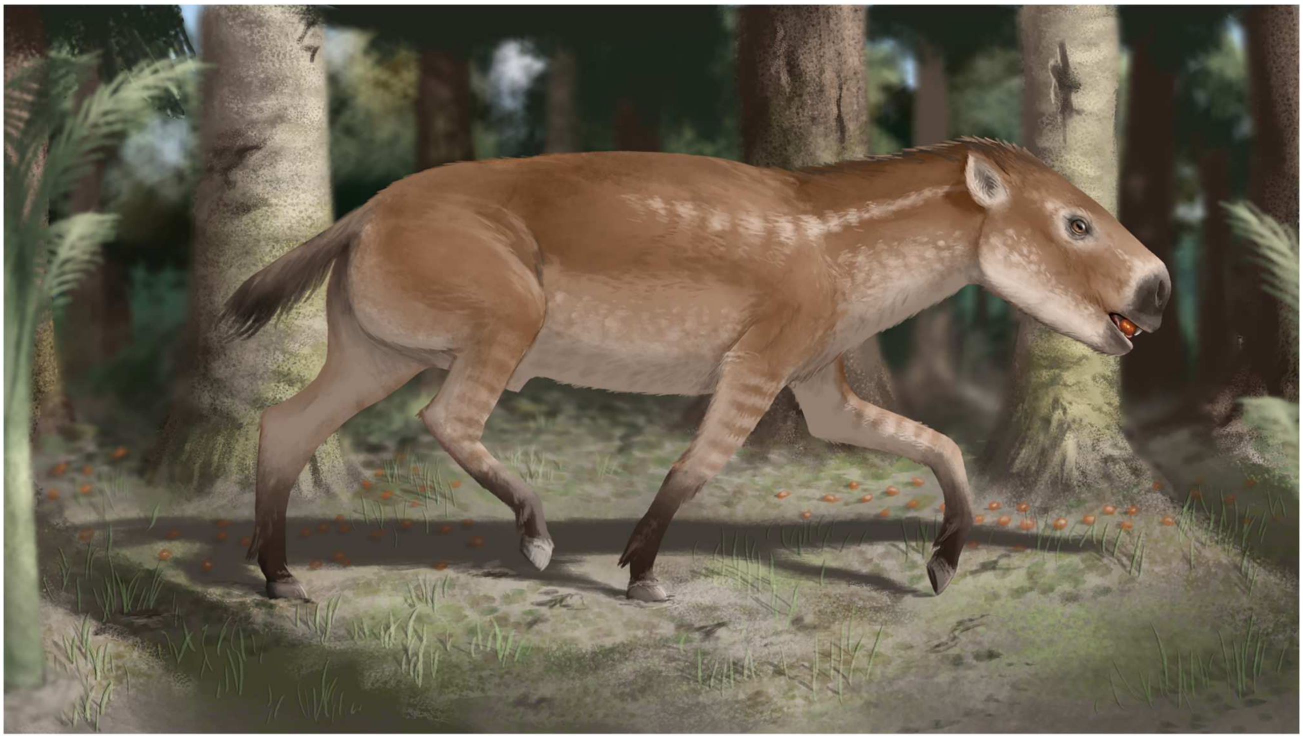

Figure 4. Artistic reconstruction of *Megadolodus molariformis* from the Middle Miocene URU-208 locality of the Fitzcarrald Local Fauna. Reconstruction by Miguel Hernandez.

CONCLUSION

We describe a bunodont upper molar from the late Middle Miocene Fitzcarrald Local Fauna of Peruvian Amazonia as belonging to the proterotheriid megadolodine *Megadolodus molariformis* (Fig. 4). This record further increases the faunal similarity between Fitzcarrald and other Middle Miocene faunas from Western Amazonia, including La Venta (Colombia) and TAR-31 (Tarapoto area, Peru). This similarity increases the confidence in assignment of the fauna of the Fitzcarrald arch to the Laventan stage.

We use a novel mesowear angle approach in suoids to test the hypothesis of frugivory in megadolodines, including *Megadolodus*. Modern suoids vary significantly in their mesowear angles, reflecting differences in their dietary ecology. The most similar modern suoid (in terms of mesowear angles) is the babirusa, which may represent a reasonable analog, given that no modern relatives remain. The variability in modern suoids suggests that the mesowear angles used here are potentially applicable more generally, and we suggest they could be applied to other types of bunodont ungulates, including fossil suoids in South America and in other continents.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material. Where permitted, 3D surface scans are available in Morphosource: https://morphosource.org/projects/000658581.

SUPPLEMENTARY FILES

Supplementary material—Tables S1–3. Tables S1 and S2 include the mesowear angles for the upper (Table S1) and lower (Table S2) molars measured here. Table S3 includes a list of the scanned specimens available on Morphosource.

AUTHOR CONTRIBUTIONS

Fieldwork was carried out by RSG, POA, ABP, FLC, LM, FP, and ASM. Museum collections visits were by OEW, JDC, and JS. OW and JS originally designed the project, in discussion with JDC, RSG, and POA. JS supervised the project. OEW conducted the analysis and created the visualizations. Original interpretations of the results were by OEW, JDC, POA, and JS. OEW, JDC, POA, and JS wrote the original manuscript. All authors provided critical feedback that improved the text, and contributed to editing and writing the final version of the manuscript.

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