DIETARY CONSTRAINTS OF PHYTOSAURIAN REPTILES REVEALED BY DENTAL MICROWEAR TEXTURAL ANALYSIS

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Abstract: Phytosaurs are a group of large, semi-aquatic archosaurian reptiles from the Middle–Late Triassic. They have often been interpreted as carnivorous or piscivorous due to their large size, morphological similarity to extant crocodilians and preservation in fluvial, lacustrine and coastal deposits. However, these dietary hypotheses are difficult to test, meaning that phytosaur ecologies and their roles in Triassic food webs remain incompletely constrained. Here, we apply dental microwear textural analysis to the three-dimensional sub-micrometre scale tooth surface textures that form during food consumption to provide the first quantitative dietary constraints for five species of phytosaur. We furthermore explore the impacts of tooth position and cranial robustness on phytosaur microwear textures. We find subtle systematic texture differences between teeth from different positions along phytosaur tooth rows, which we interpret to be the result of different loading pressures experienced during food consumption, rather than functional partitioning of food processing along tooth rows. We find rougher microwear textures in morphologically robust taxa. This may be the result of seizing and processing larger prey items compared to those captured by gracile taxa, rather than dietary differences *per se*. We reveal relatively low dietary diversity between our study phytosaurs and that individual species show a lack of dietary specialization. Species are predominantly carnivorous and/or piscivorous, with two taxa exhibiting slight preferences for 'harder' invertebrates. Our results provide strong evidence for higher degrees of ecological convergence between phytosaurs and extant crocodilians than previously appreciated, furthering our understanding of the functioning and evolution of Triassic ecosystems.

Key words: phytosaur, diet, microwear, crocodile, piscivory, carnivory.

PHYTOSAURS are an important clade of extinct archosauriform reptiles from the Middle–Late Triassic (*c.* 240–201 Ma; Stocker *et al.* 2017; Jones & Butler 2018). Their fossils have a global distribution, and the clade currently contains around 40 species, with specimens collected primarily from fluvial, lacustrine and marine deposits (Parrish 1989; Hunt 1991; Kischlat & Lucas 2003; Stocker & Butler 2013; Kammerer *et al.* 2015; Butler *et al.* 2019). Numerous skeletal similarities have been described between phytosaurs and modern crocodilians, including their large body size, elongated rostra, conical teeth and overall body shape (Chatterjee 1978; Stocker 2012; Witzmann *et al.* 2014). This has resulted in numerous suggestions of ecological convergence between phytosaurs and crocodiles, with phytosaurs almost universally regarded as semi-aquatic carnivores and/or piscivores in Triassic food webs (Camp 1930; Colbert *et al.* 1947;

Eaton 1965; Chatterjee 1978; Hunt 1989; Hungerbühler 1998, 2000; Li *et al.* 2012; Stocker & Butler 2013). It has even been suggested that phytosaurs filled the ecological role of apex predator in some food webs (Hungerbühler 1998; Drumheller *et al.* 2014).

However, despite this high consensus on diet, the evidence supporting many phytosaur dietary hypotheses is, in fact, relatively weak. For example, hypotheses that are based on simple analogies between tooth shape and function in extant crocodilians and phytosaurs (Chatterjee 1978; Hunt 1989; Hungerbühler 1998, 2000) have rarely been subjected to explicit functional testing. Only a few crocodilians almost exclusively consume fish or tetrapods (e.g. the piscivorous gharial, *Gavialis gangeticus*; Hussain 1991). Most crocodilians are more generalistic and/or prefer other foods such as crustaceans (e.g. the American crocodile, *Crocodylus acutus*; Thorbjarnarson 1988). This

dietary diversity is known from observational studies and stomach content analyses (Grigg & Kirshner 2015; Bestwick *et al.* 2019) which, in some cases, contrasts with hypotheses of crocodilian diets that are based solely on tooth shape. Only rarely has this dietary diversity in extant crocodilians been considered in reconstructions of phytosaur palaeobiology. Fossilized stomach contents and bite marks on dinosaur bones have provided evidence of carnivory or piscivory in some phytosaurs (Chatterjee 1978; Hungerbühler 1998; Li *et al.* 2012; Drumheller *et al.* 2014) but these are limited to a handful of specimens. Furthermore, content fossils only provide 'snapshots' of entire diets and may be biased towards preservation of indigestible items (Bestwick *et al.* 2018). Robust reconstructions of phytosaur diets are therefore vital not only for understanding their ecological roles within Triassic food webs, but for providing broader insight into Triassic ecosystem functioning and ecological convergence with crocodilians (Jacobs & Murry 1980; Roopnarine *et al.* 2007; Drumheller *et al.* 2014).

A more robust approach to hypothesis testing involves dental microwear texture analysis (DMTA); quantitative analysis of the sub-micrometre scale three-dimensional textures that form on tooth surfaces during food consumption (Daegling *et al.* 2013; Bestwick *et al.* 2019). The relative difficulty experienced by consumers in piercing and/or processing food items determines the microwear patterns that form on teeth, which consequently provides direct evidence of diet (Daegling *et al.* 2013; Bestwick *et al.* 2019). The technique uses standardized texture parameters (Ungar *et al.* 2003; International Organization for Standardization 2012) to quantify microwear, and thus dietary, differences between species and/or populations, and therefore does not assume direct relationships between the morphology and inferred functions of teeth (Daegling *et al.* 2013; Purnell & Darras 2016). Non-occlusal (non-chewing) tooth texture differences between extant reptiles, including archosaurs, have been shown to exhibit dietary signals that reflect their diet over the last few weeks to months of life, even with low sample sizes (Bestwick *et al.* 2019; Winkler *et al.* 2019). The known relationships between microwear texture and diet in extant reptiles therefore provides us with a robust multivariate framework with which to quantitatively test and constrain phytosaur dietary hypotheses using DMTA (Bestwick *et al.* 2020*a*).

However, several endogenous non-dietary variables of phytosaur anatomy and functional morphology, and their potential roles in microwear texture formation, need to be considered. One variable is the position of sampled teeth within tooth rows. Across all major vertebrate groups, teeth that are positioned closer to the jaw adductor musculature are subjected to higher bite forces during jaw closure (Kammerer *et al.* 2006; Santana & Dumont

2009; Santana *et al.* 2010; Erickson *et al.* 2012; Porro *et al.* 2013). Although mechanisms of microwear formation are not fully understood (Calandra *et al.* 2012; Schulz *et al.* 2013*a*, *b*) changes in bite force along tooth rows during feeding may be expected to have some influence on intraspecific microwear textures. Many phytosaur teeth are preserved isolated from the jaws (Meyer 1861; Parrish 1989; Hungerbühler 1998; Datta *et al.* 2019), thus testing for microwear differences between tooth positions is important for understanding whether standardized sampling positions are needed in these extinct reptiles. Furthermore, unlike most modern reptiles, many phytosaurs exhibit heterodonty along their tooth rows, with distinctive morphotypes described from teeth positioned at the anterior tip of the rostrum, the premaxilla and the maxilla respectively (Hungerbühler 2000; Datta *et al.* 2019). Heterodonty supposedly enabled phytosaurs to feed on a greater range of food items, with some teeth better adapted for piercing and handling different items (Hungerbühler 2000). This idea, however, has yet to be explicitly tested and thus strengthens the need for investigation with DMTA.

Another variable to be considered is the morphological robustness of phytosaur skulls. In broad terms, morphologically 'gracile' phytosaurs are characterized by slender and tubular rostra and 'robust' phytosaurs are characterized by much deeper rostra, often with distinct crests along the dorsal margin (Hunt 1989; Hungerbühler 2002; Witzmann *et al.* 2014). There are some suggestions that the robust and gracile morphotypes from contemporaneous phytosaurs from the same geological sites represent sexual dimorphs of the same species (males and females, respectively; Zeigler *et al.* 2003; Hunt *et al.* 2006; Kimmig & Spielmann 2011). These morphotypes have been interpreted as evidence of dietary differences, with deeper rostrums facilitating predation on larger animals, usually tetrapods, and slender rostrums better adapted for capturing smaller animals, usually fish (Hunt 1989; Parrish 1989; Hungerbühler 2000; Heckert & Camp 2013). Hypotheses of dietary partitioning using cranial robustness and/or sexual dimorphism, however, have been subjected to little explicit testing (Wall *et al.* 1995; Irmis 2005). Determining whether phytosaur microwear texture differences can be explained by skull morphotype in addition to, or instead of, diet will provide more thorough understanding of how phytosaurs interacted with food items.

Here, we present the first application of DMTA to five species of phytosaur to test the hypotheses that microwear texture differs between phytosaur species and that microwear texture differences reflect dietary differences. We also use the results of microwear analysis to test hypotheses of niche partitioning between robust and gracile phytosaurs, and that morphological differences between teeth in different locations in the jaw reflect functional

differentiation. Hypotheses were tested using a multivariate framework comprising microwear texture data from extant crocodilians and varanid lizards with known diets (Bestwick *et al.* 2019). While no direct morphological or ecological comparisons have been made between phytosaurs and varanids, previous DMTA of reptiles has shown that microwear texture differences are more strongly linked to dietary differences than they are to tooth morphology or phylogeny (Bestwick *et al.* 2019, 2020*a*; Winkler *et al.* 2019). The varanid species included in the analysis exhibit diets that are both similar and different to the crocodilians and thus contribute a more robust multivariate framework.

MATERIAL AND METHOD

Specimen material

Tooth microwear textures were sampled from five phytosaur species: *Machaeroprosopus pristinus*, *Mystriosuchus planirostris*, *Nicrosaurus kapffi*, *N. meyeri* and '*Smilosuchus lithodendrorum*'; see Bestwick *et al.* (2020*b*, table S1) for the complete specimen list. Phytosaur species were chosen to represent a range of taxonomic groups, spanning robust and gracile skull morphologies and included specimens that retained teeth from varied locations along the tooth row. Phytosaurs were designated as either robust or gracile based on previous descriptions of these morphotypes, e.g. Hunt (1989). Microwear texture data from 13 extant reptile species, comprising six crocodilians and seven monitor lizards from previously published work (Bestwick *et al.* 2019), was included as the extant multivariate framework. Extant and fossil specimens were sampled from the Field Museum of Natural History, Chicago, USA (FMNH); Grant Museum of Zoology, University College London, UK (LDUCZ); Natural History Museum, London, UK (NHMUK); University of Oxford Museum of Natural History, Oxford, UK (OUMNH); Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); Museum of Texas Tech University Paleontology collections, Lubbock, USA (TTU-P); Florida Museum of Natural History, Gainesville, USA (UF); and the National Museum of Natural History, Smithsonian Institute, Washington DC, USA (USNM). Schematic diagrams of extant reptile skulls are based on: *Crocodylus acutus*, UF 54201; *Gavialis gangeticus*, Wikimedia Commons; *Varanus olivaceus*, UF 57207; *V. prasinus*, UF 56949; *V. rudicollis*, UF 63622; those of phytosaur skulls are based on: *Machaeroprosopus pristinus*, UCMP 137319 (University of California Museum of Paleontology, Berkeley, USA); *Mystriosuchus planirostris*, SMNS 9134; *Nicrosaurus kapffi*, SMNS 4379; *N. meyeri*, SMNS 12593; '*Smilosuchus lithodendrorum*', UCMP 26688.

Dietary guild assignments of extant reptiles

Extant reptiles were selected to include taxa with well-constrained dietary differences determined from stomach content studies (Taylor 1979; Auffenberg 1981, 1988; Greene 1986; Losos & Greene 1988; Thorbjarnarson 1988; Sah & Stuebing 1996; Delany *et al.* 1999; Wallace & Leslie 2008; Laverty & Dobson 2013; Dalhuijsen *et al.* 2014; Rahman *et al.* 2017). Studies were chosen that provided dietary compositions as volumetric data (or frequency data at an absolute minimum; see Bestwick *et al.* 2020*b* for the full percentage breakdown for each species). Taxa that had not been subjected to ecological studies that provided volumetric or frequency breakdowns of diet were not sampled for study. Studies were also chosen that provided, where possible, representative sample sizes and close spatial proximity of the dietary study to the known location(s) from which the sampled specimens were collected. Extant reptiles were assigned to dietary guilds which account for the relative 'intractability' (roughly equivalent to hardness; Evans & Sanson 2005) of prey as food, based on Bestwick *et al.* (2019). Guilds include: carnivores (tetrapod consumers); piscivores (fish consumers); 'harder' invertebrate consumers (invertebrates with hard exoskeletons, e.g. beetles, crustaceans and shelled gastropods); 'softer' invertebrate consumers (invertebrates with less hard exoskeletons, e.g. crickets, grasshoppers, dragonflies, damselflies and ants); 'softest' invertebrate consumers (invertebrates with soft exoskeletons, e.g. invertebrate larvae, butterflies, moths, arachnids and millipedes); omnivores (combination of plant and animal matter).

Where possible, specimens of the same ontogenetic stage, usually adults, were sampled to minimize unconstrained variability introduced from potential ontogenetic dietary differences and more rapid tooth shedding rates in younger individuals (Berkovitz 2000). The availability of museum specimens allowed *Cr. porosus* to be split into adults and juveniles to reflect the known ontogenetic dietary shifts in this species (Taylor 1979; Sah & Stuebing 1996). Specimens with lower jaw lengths of < 50 cm were classified as juveniles; specimens with jaw lengths exceeding 50 cm were considered to be adults (Bestwick *et al.* 2019).

Extant reptiles were assigned to the same dietary guilds as in Bestwick *et al.* (2019): *Crocodylus porosus* adults (saltwater crocodile, n = 6), *Varanus komodoensis* (Komodo dragon, n = 4), *V. nebulosus* (clouded monitor, n = 11), *V. rudicollis* (roughneck monitor, n = 8) and *V. salvator* (Asian water monitor, n = 8) as carnivores (N = 37); *Cr. acutus* (American crocodile, n = 7) and *Cr. porosus* juveniles (n = 5) as 'harder' invertebrate consumers (N = 12); *V. niloticus* (Nile monitor, n = 8) and *V. prasinus* (emerald tree monitor, n = 7) as 'softer'

invertebrate consumers (N = 15); *V. olivaceus* (Gray's monitor, n = 6) as an omnivore (N = 6); and *Alligator mississippiensis* (American alligator, n = 8), *Caiman crocodilus* (spectacled caiman, n = 6), *Cr. niloticus* (Nile crocodile, n = 4) and *G. gangeticus* (gharial, n = 7) as piscivores (N = 25).

Caiman crocodilus exhibits seasonal dietary shifts, consuming more fish in the wet season (March–May) and more invertebrates in the dry season (August–September) (Laverty & Dobson 2013). To minimize potential season-based microwear variation, sampled *Ca. crocodilus* were specimens that had died early in the dry season and were classified as piscivores under the assumption that their tooth surface textures retained the piscivore signal accumulated during the wet season.

Sampling strategy

Phytosaur specimens were cleaned before sampling using an ethaline solvent gel, produced and applied according to Williams & Doyle (2010). Extant reptile teeth from dry skeletal specimens were cleaned using 70% ethanol-soaked cotton swabs to remove dirt and consolidant. Microwear data were acquired from non-occlusal (non-chewing) labial surfaces, as close to the tooth apex as possible. In extant reptiles, the mesial-most dentary tooth was sampled; in phytosaurs the premaxillary and maxillary teeth were sampled. Differences in sampling locations between extant and extinct reptiles are not an issue due to our experimental design. Phytosaur teeth are initially studied to test for microwear texture differences between teeth from difference positions of the tooth row and thus potential intra-jaw dietary partitioning. A lack of texture differences would indicate that tooth position is not a confounding variable in phytosaur microwear characteristics and that it is acceptable to project phytosaur teeth into multivariate texture–dietary spaces that comprise extant teeth from a single sampled position as part of phytosaur dietary reconstructions (see DMTA Statistical Analyses, below). To test for microwear differences along the tooth row, phytosaur jaws were divided into three regions: anterior teeth correspond to the mesial-most three/four teeth in the premaxilla and are morphologically characterized by greater robustness and apico-basal length relative to all other teeth in the tooth row (Bestwick *et al.* 2020*b*, fig. S1A); posterior teeth correspond to the seven to ten distal-most teeth in the maxilla (depending on species) that are morphologically characterized by an approximate phylloform ('leaf-shaped') morphology with slight to moderate apical recurvature, prominent serrated carinae and a labially convex D-shaped cross-section (Bestwick *et al.* 2020*b*, fig. S1C); middle teeth correspond to teeth located in between the anterior and posterior

regions and are morphologically characterized by their conical shape with a circular cross-section and may be carinated and/or possess serrations (Bestwick *et al.* 2020*b*, fig. S1B). It was not possible to sample all three tooth positions from every taxon due to the sporadic preservation of in situ teeth in phytosaur fossils. In some taxa ('*S. lithodendrorum*', *S. gregorii*, *Ma mccauleyi*) an additional set of large teeth occur at the transition between the premaxilla and maxilla. These teeth are slenderer than those of the terminal rosette, and none were included in this study due to preservation quality.

High fidelity moulds were taken of all teeth using President Jet Regular Body polyvinylsiloxane (Coltène/Whaledent Ltd., Burgess Hill, West Sussex UK). Initial moulds taken from each specimen were discarded to remove any remaining dirt and all analyses performed on respective second moulds. Casts were made from these moulds using EpoTek 320 LV Black epoxy resin mixed to manufacturer's instructions. Resin was cured for 24 h under 200 kPa (2 bar/30 psi) of pressure (Protima Pressure Tank 10 l) to improve casting quality. Small casts were mounted onto 12.7 mm SEM stubs using President Jet polyvinylsiloxane with the labial, non-occluding surfaces orientated dorsally to optimize data acquisition. All casts were sputter coated with gold for three minutes (SC650, Bio-Rad, Hercules, CA, USA) to optimize capture of surface texture data. Replicas produced using these methods are statistically indistinguishable from original tooth surfaces (Goodall *et al.* 2015).

Surface texture data acquisition

Surface texture data acquisition followed standard laboratory protocols (Goodall *et al.* 2015; Purnell & Darras 2016; Bestwick *et al.* 2019). Data were captured using an Alicona Infinite Focus microscope G4b (IFM; Alicona GmbH, Graz, Austria; software v. 2.1.2), using a 100× objective lens, producing a field of view of 146 × 100 μm. Lateral and vertical resolution were set at 440 nm and 20 nm respectively. Casts were orientated so that labial surfaces were perpendicular to the axis of the objective lens.

All 3D data files were processed using Alicona IFM software (v. 2.1.2) to remove dirt particles from tooth surfaces and anomalous data points (spikes) by manual deletion. Data were levelled (subtraction of least squares plane) to remove variation caused by differences in tooth surface orientation at the time of data capture. Files were exported as .sur files and imported into Surfstand (v. 5.0.0; Centre for Precision Technologies, University of Huddersfield, UK). Scale-limited surfaces were generated by application of a fifth-order robust polynomial to remove gross tooth form and a robust Gaussian filter

(wavelength λ_c = 0.025 mm; Schulz *et al.* 2013*a*; Purnell & Darras 2016). ISO 25178-2 areal texture parameters (International Organization for Standardization 2012) were then generated from each scale-limited surface. ISO parameter details can be found in Table 1.

DMTA statistical analyses

Log-transformed texture data were used for analyses as some of the texture parameters were non-normally distributed (Shapiro–Wilk, p > 0.05). The parameter Ssk (skewness of the height distribution of the 3D surface texture; Table 1) was excluded from analysis as it contains negative values and thus cannot be log-transformed.

To test the hypotheses that microwear textures differ between teeth from different positions along phytosaur tooth rows, and between morphologically gracile and robust phytosaurs, analysis of variance (ANOVA) with pairwise testing (Tukey HSD) were used for each texture parameter between tooth row positions and robustness categories, irrespective of species. Where homogeneity of variance tests revealed evidence of unequal variances, Welch analysis of variance was used. Texture parameters that exhibited significant differences along tooth rows were subjected to principal components analysis (PCA) and canonical variates analysis (CVA; a form of linear discriminant analysis). The separation of tooth row positions along PC and CV axes was investigated using ANOVAs and Tukey HSD tests. Significant texture parameters which exhibit no pairwise differences under Tukey HSD comparisons were excluded from PCA and CVA. Phytosaur tooth specimens SMNS 12060 (*My. planirostris*; tooth specimen no. 4 in Bestwick *et al.* 2020*b*, all figs)

TABLE 1. Definition, description and categorization of the 21 ISO 3D texture parameters used in this study.

Parameter	Unit	Definition	Category
Sq	μm	Root mean square height of surface	Height
Sp	μm	Maximum peak height of surface; based on only one peak	Height
Sv	μm	Maximum valley depth of surface; based on only one valley	Height
Sz	μm	Maximum height of surface, calculated by subtracting the maximum valley depth from peak height	Height
Sa	μm	Average height of surface	Height
Ssk	–	Skewness of height distribution of surface	Height
Sku	–	Kurtosis of height distribution of surface	Height
S5z	μm	10 point height of surface, average value of the five highest peaks and the five deepest valleys	Feature
Sdq	–	Root mean square gradient of surface	Hybrid
Sdr	%	Developed interfacial area ratio	Hybrid
Sds	$1/mm^2$	Density of summits; number of summits per unit area making up surface	Hybrid
Ssc	1/μm	Mean summit curvature for peak structures	
Sk	μm	Core roughness depth; height of core material	Material ratio
Spk	μm	Mean height of the peaks above core material	Material ratio
Svk	μm	Mean depth of the valleys below core material	Material ratio
Smr1	%	Surface bearing area ratio (proportion of surface that consists of peaks above core material)	Material ratio
Smr2	%	Surface bearing area ratio (proportion of surface which would carry load)	Material ratio
Vmp	$μm^3/mm^2$	Material volume of peaks of surface	Volume
Vmc	$μm^3/mm^2$	Material volume of core of surface	Volume
Vvc	$μm^3/mm^2$	Void volume of core of surface	Volume
Vvv	$μm^3/mm^2$	Void volume of valleys of surface	Volume
Str	–	Texture aspect ratio	Spatial

Many parameters are derived from the areal material ratio curve: a cumulative probability density function derived from the scale-limited tooth surface by plotting the cumulative percentage of the tooth surface against height. The peaks (the highest 10% of the surface), valleys (the lowest 20% of the surface) and core material of tooth surfaces are defined on the basis of this curve; parts of the surface that are higher or lower than the core are defined as peaks and valleys respectively. Note that Sds and Ssc predate ISO 25178. Adapted from Bestwick *et al.* (2019).

and SMNS 4059 (*N. meyeri*; specimen no. 15) were excluded from the tooth row analysis as their location within the tooth row is unknown (Bestwick *et al.* 2020*b*, table S1).

To test the hypothesis that phytosaur microwear texture differences between species reflect dietary differences, PCA and CVA were first used to explore texture parameters exhibiting significant differences between reptile dietary guilds. ANOVA with pairwise testing was used on the values of each PC and CV axis to determine whether guilds occupy different areas of multivariate space along these axes. Spearman's rank was used to independently test for correlations between each PC and CV axis and dietary characteristics (e.g. proportion of diet that comprises vertebrates). Phytosaur microwear data were then independently projected onto the PCA and CVA axes of extant reptile dietary guild microwear differences. Phytosaurs were projected onto independent datasets that comprised both crocodilians and varanids (Bestwick *et al.* 2019) and a dataset that comprised only crocodilians to provide more robust constraints on phytosaur diets.

A Benjamini–Hochberg (B–H) procedure was used to account for the possibility of inflated Type I error rates associated with multiple comparisons (Benjamini & Hochberg 1995). The false discovery rate was set at 0.05. The B–H procedure was not needed for the Tukey HSD tests as it already accounts for inflated Type I error rates (Purnell *et al.* 2017).

All DMTA analyses were performed with JMP Pro 12 (SAS Institute, Cary, NC, USA) except for the B–H procedure, which used Microsoft Excel (McDonald 2014, p. 261).

# RESULTS

Phytosaur tooth position

Under ANOVA, none of the ISO parameters differ between tooth positions (Bestwick *et al.* 2020*b*, table S3). The CVA conducted on all texture parameters found significant differences between tooth position along CV axes 1 and 2 (CV 1: $F = 82.96$, df = 2, 14, p < 0.0001; CV 2: $F = 10.58$, df = 2, 14, p = 0.0016). The predictive model misclassified only 5.88% of specimens (Fig. 1). Tukey post hoc tests revealed significant differences along CV 1 between middle and posterior (p < 0.0001) and anterior and middle (p < 0.0001), and along CV 2 between anterior and posterior (p = 0.0013) and anterior and middle (p = 0.0159). The two parameters that exhibit the largest differences between tooth positions along both CVs 1 and 2 are Sdq (root mean square gradient of surface) and Sdr (developed interfacial area ratio; Fig. 1B; Table 1). In a general sense, the anterior and posterior tooth textures exhibit the

steepest gradients and the middle tooth textures exhibit the greatest complexity (Fig. 1; Table 1). Along CV 2, Sq (root mean square height of surface) exhibits large differences between tooth position; the posterior tooth textures exhibit the highest surface height (Fig. 1; Table 1).

Phytosaur robustness

Five ISO parameters significantly differ between robust and gracile phytosaurs (Sp, maximum peak height: $F = 8.36$, df = 1, 17, p = 0.0101; Sz, maximum height: $F = 9.91$, df = 1, 17, p = 0.0059; Sdq: $F = 3.10$, df = 1, 17, p = 0.0051; Sdr: $F = 10.27$, df = 1, 17, p = 0.0052; S5z, 10 point surface height: $F = 7.93$, df = 1, 17, p = 0.0119) (Bestwick *et al.* 2020*b*, table S4). PCA of these five parameters found that gracile and robust phytosaurs were significantly separated along PC 1 (76.1% of the total variation; $t = 3.83$, df = 17, p = 0.0013; Fig. 2A). CVA of these five parameters found that gracile and robust phytosaurs were significantly separated along CV 1 (100% of total variation; $t = 4.315$, p = 0.0005), with only 15.8% of cases misclassified (Fig. 2B). Sp, Sz and S5z capture aspects of the heights of surfaces and together they indicate that robust phytosaur microwear textures are higher (however, Sp and Sz are derived from the height of a single point in a surface and are therefore not reliable as indicators of the overall surface; Table 1). Robust phytosaurs also have the steeper gradients (Sdq) and greater complexity (Sdr) and therefore, in broad terms, have rougher tooth surface textures.

CVA of all 21 texture parameters produces significant separation between gracile and robust phytosaurs along CV 1 (100% of total variation; $t = -66.656$, p < 0.0001). Zero cases were misclassified from this model (Fig. 2C). Texture differences for the 16 parameters previously reported as non-significant (ANOVA) are very small in some instances. On average, robust phytosaurs have higher surface textures (higher Sq, higher Sa; average surface height), have a deeper core (higher Sk, core roughness depth), have larger core and core void volumes (higher Vmc, material volume of the surface core; higher Vvc, void volume of the surface core), and larger valleys and valley void volumes (higher Sv, maximum valley depth; higher Vvv, void volume of the surface valleys; higher Svk, mean valley depth below the core material) (Table 1). Robust phytosaur textures are also more uniform (lower Str, texture aspect ratio) with fewer, smaller peaks (lower Vmp, material volume of surface peaks; lower Smr1, proportion of surface that consists of peaks; lower Smr2, surface bearing area ratio) that comprise less of the surface texture (lower Sds, summit density) (Table 1). In broad terms, robust phytosaurs have rougher tooth surface textures when all ISO parameters are considered.
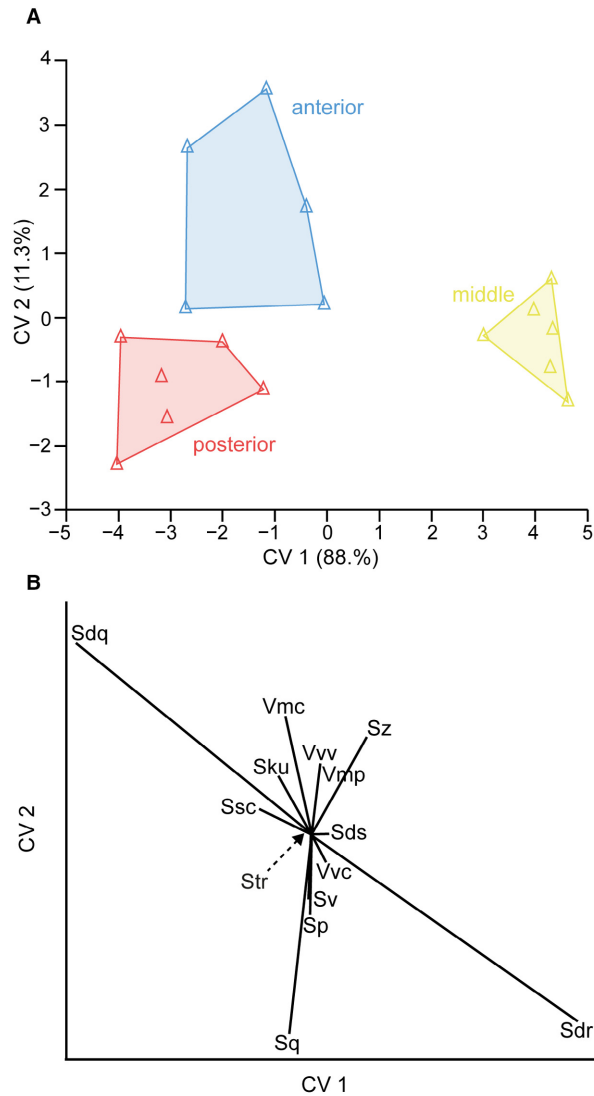
FIG. 1. A, CVA multivariate space of phytosaur dental microwear, constructed with 21 ISO textural parameters, grouped by tooth position. B, CVA biplot indicating the magnitude of each textural parameter on the CV axes defining maximum separation of tooth position, and the direction of maximum variation for each parameter along CVs 1 and 2. For parameter definitions, see Table 1.

Phytosaur dietary reconstructions

As previously documented, four texture parameters significantly differ between dietary guilds in the crocodile and varanid dataset (Spk, mean height of peaks above core material; Sds; Vmp; and Smr1; see Bestwick *et al.* 2019, table 2 for full ANOVA results). See Figure 3A–E and F–J for example digital elevation models of extant reptile and phytosaur tooth surfaces, respectively, from which texture data were acquired. PCA of these four parameters

separates extant reptiles into a texture–dietary space defined by PC axes 1 and 2 (Fig. 4; Bestwick *et al.* 2020*b*, fig. S2). PC 1 negatively correlates with proportions of total vertebrates in reptile diets and positively correlates with total invertebrates and PC 2 positively correlates with dietary proportions of 'softer' invertebrates (see Bestwick *et al.* 2019, table S3 for full dietary correlation results). ANOVA of the PCA results find that PCs 1 and 2 differ between guilds (PC 1, $F = 4.9316$, df = 4, 90, $p = 0.0012$; PC 2, $F = 4.6676$, df = 4, 90, $p = 0.0018$); piscivores differ from 'harder' invertebrate consumers and omnivores (PC 1, Tukey HSD); 'harder' invertebrate consumers differ from carnivores and 'softer' invertebrate consumers; 'softer' invertebrate consumers differ from piscivores (PC 2, Tukey HSD).

Projecting phytosaur data into this texture–dietary space plots them within the bounds of the extant reptiles and, as a whole, they tend to all cluster relatively close to zero along PCs 1 and 2 where most of the extant dietary guilds overlap (Fig. 4; Bestwick *et al.* 2020*b*, fig. S2). *Machaeroprosopus pristinus* specimens are broadly distributed along PC 1, the vertebrate–invertebrate dietary axis, and have similar PC 2 values of around zero. *Mystriosuchus planirostris* specimens generally exhibit positive PC 2 values and exhibit a greater degree of overlap with 'softer' invertebrate consumers along this axis than do other phytosaurs. *Nicrosaurus kapffi* specimens generally exhibit more negative PC 1 values than other phytosaurs and overlap more strongly with piscivores along this axis. *Nicrosaurus meyeri* specimens exhibit values close to zero along PCs 1 and 2 and the centroid of these points sits centrally within the space occupied by carnivores and piscivores. '*Smilosuchus lithodendrorum*' specimens exhibit the largest degree of clustering and plot very close to zero along PCs 1 and 2.

CVA of the four texture parameters separates extant reptiles in a texture–dietary space defined by CV axes 1 and 2 (together accounting for 97.2% of total variance; Fig. 5; Bestwick *et al.* 2020*b*, fig. S3). CV 1 positively correlates with proportions of tetrapods in reptile diets ($r_s = 0.3022$, $p = 0.0029$), CV 2 positively correlates with dietary proportions of total invertebrates ($r_s = 0.2753$, $p = 0.0069$) and with dietary proportions of 'softer' invertebrates ($r_s = 0.3226$, $p = 0.0014$) and negatively correlates with proportions of total vertebrates in reptile diets ($r_s = 0.3226$, $p = 0.0014$) and with dietary proportions of fish ($r_s = -0.2683$, $p = 0.0086$; Fig. 5; Bestwick *et al.* 2020*b*, fig. S3, table S5). ANOVA of the CVA results provides evidence of additional discriminatory power: CVs 1 and 2 differ between dietary guild (CV 1: $F = 7.277$, df = 4, 90, $p < 0.0001$; CV 2: $F = 3.918$, df = 4, 90, $p = 0.0056$); 'harder' invertebrate consumers differ from 'softer' invertebrate consumers, carnivores and piscivores; omnivores differ from carnivores and 'softer' invertebrate consumers
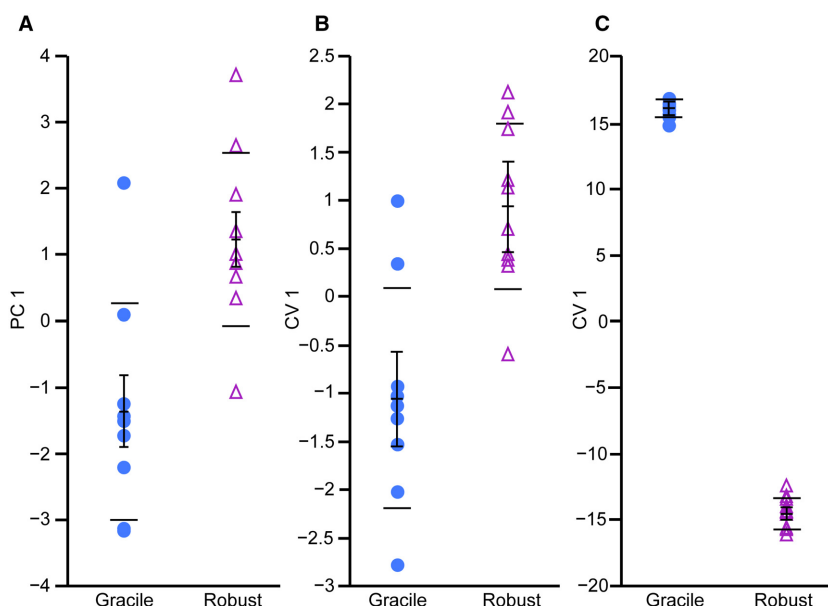
FIG. 2. Microwear texture discrimination between morphologically gracile and robust phytosaurs. A, principal component analysis (PCA) of the five ISO texture parameters (Sp, Sz, Sdq, Sdr and S5z) that distinguish phytosaur robusticities. B, canonical variates analysis (CVA) of the same five texture parameters. C, CVA of all 21 texture parameters used in this study. Each figure includes mean, standard error and 95% confidence intervals. For parameter definitions, see Table 1.

(CV 1, Tukey HSD); piscivores differ from carnivores and omnivores (CV 2, Tukey HSD).

Projecting phytosaur data into this texture–dietary space also plots them within the bounds of the extant reptiles. The CVA predictive model is highly unreliable, misclassifying 65.6% of cases in the extant reptile dataset. In this model, 36.8% of phytosaurs are classified as carnivores, 26.3% of phytosaurs as 'softer invertebrate consumers, 21% as piscivores, 10.5% as 'harder' invertebrate consumers and 5.3% as omnivores. Phytosaurs are more closely clustered together to other specimens of the same taxon, and together as a clade within the texture–dietary space (Fig. 5; Bestwick *et al.* 2020*b*, fig. S3). *Machaeroprosopus pristinus* specimens, for example, are less broadly distributed along CV 1, the tetrapod dietary axis, and overlap with most dietary guilds along this axis. In contrast, *Ma. pristinus* specimens are more broadly distributed along CV 2, the vertebrate and fish–invertebrate and 'softer' invertebrate dietary axis. In this texture–dietary space *My. planirostris* specimens are relatively widely distributed along CV 1, occupying both positive and negative values along this axis, but also exhibit similar CV 2 values of around zero. *Nicrosaurus kapffi* specimens cluster close together around zero on CV 1 but are relatively distributed along CV 2. *Nicrosaurus meyeri* specimens are relatively widely distributed along CV 1 as two specimens overlap more strongly with carnivores while another overlaps with 'harder' invertebrate consumers. '*Smilosuchus lithodendrorum*' specimens all occupy positive CV 1 values, overlapping more strongly with carnivores and 'softer' invertebrate consumers, and occupy PC 2 values of around zero.

CVA of all 21 texture parameters separates extant reptiles along CV axes 1–3, which together account for 95%

of the total variance (CV 1, 57.8%; CV 2, 25.2%; CV 3, 12%; Fig. 6 and Bestwick *et al.* 2020*b*, fig. S4 showcase the texture–dietary space defined by CVs 1 and 2). CV 1 positively correlates with proportions of dietary tetrapods ($r = 0.3439$, $p = 0.0006$), 'softer' invertebrates ($r = 0.4111$, $p < 0.0001$) and dietary generalism ($r_s = 0.3433$, $p = 0.0007$) and negatively correlates with plant matter ($r_s = -0.3174$, $p = 0.0007$). CV 2 positively correlates with proportions of dietary 'softer' invertebrates ($r_s = 0.4595$, $p < 0.0001$) and dietary generalism ($r_s = 0.3179$, $p = 0.0017$), and negatively correlates with fish ($r_s = -0.2808$, $p = 0.0059$). CV 3 positively correlates with proportions of total invertebrates ($r_s = 0.3073$, $p = 0.0025$) and negatively correlates with total vertebrates ($r_s = -0.2637$, $p = 0.0098$; Fig. 6; Bestwick *et al.* 2020*b*, fig. S4, table S6). ANOVA of the CVA results provides evidence of additional discriminatory power: all three CV axes (CV 1 (Welch's ANOVA) $F = 9.7425$, df = 4, 22.636, $p < 0.0001$; CV 2, $F = 9.2908$, df = 4, 90, $p < 0.0001$; CV 3, $F = 4.4438$, df = 4, 90, $p = 0.0025$). Omnivores differ from all other guilds, 'harder' invertebrate consumers differ from carnivores and 'softer' invertebrate consumers, piscivores differ from 'softer' invertebrate consumers (Tukey HSD, CV 1). 'Harder' invertebrate consumers differ from carnivores, omnivores and 'softer' invertebrate consumers, piscivores differ from carnivores, omnivores and 'softer' invertebrate consumers (Tukey HSD, CV 2). Piscivores differ from carnivores and 'harder' invertebrate consumers (Tukey HSD, CV3).

Phytosaurs once again plot within the bounds of the texture–dietary space, although in this space they are perhaps more broadly distributed across the space and taxa do not cluster as strongly together (Fig. 6; Bestwick *et al.*
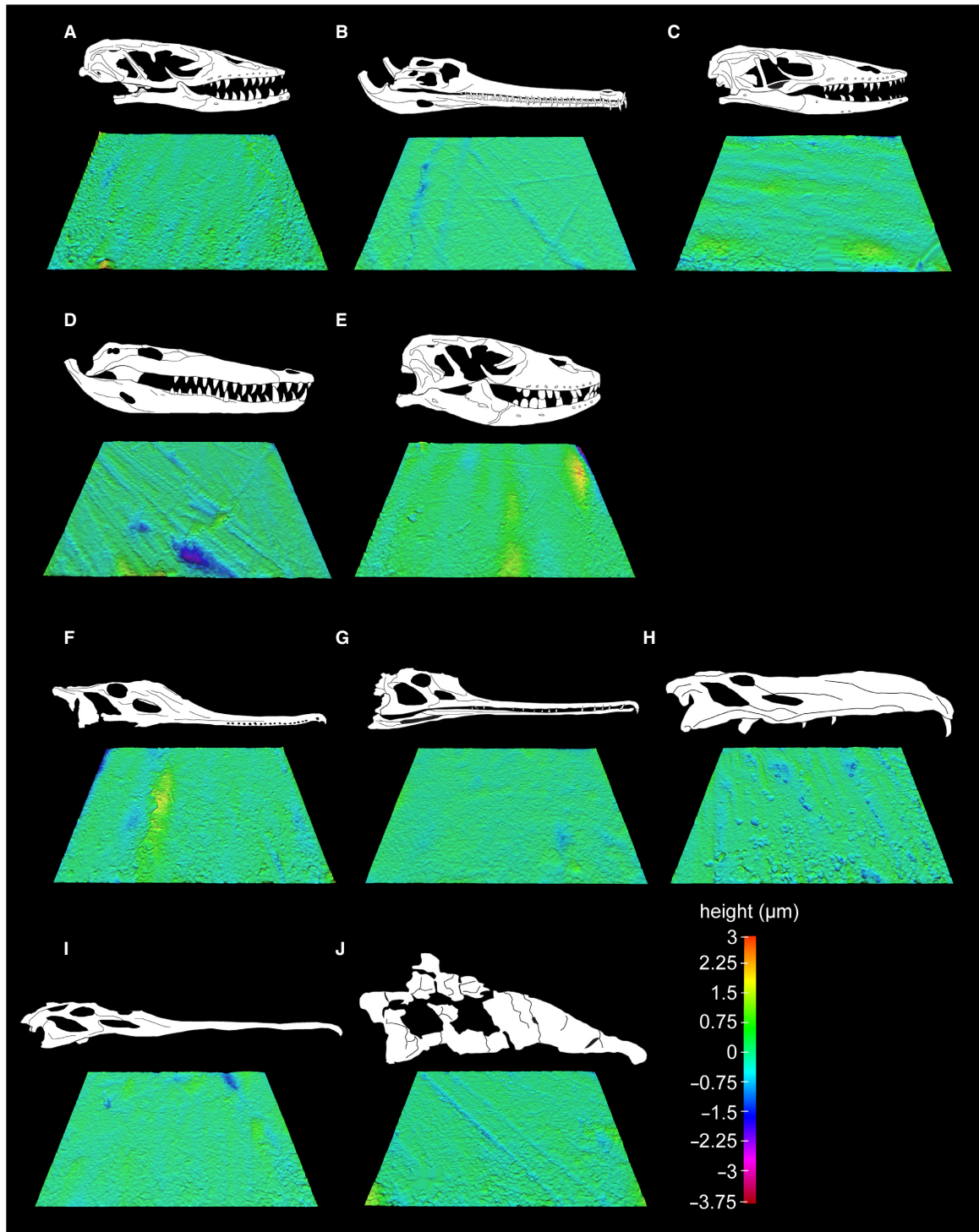
FIG. 3. Example scale-limited tooth surfaces of reptile dietary guilds and phytosaurs. A–E, reptile dietary guilds: A, 'softer' invertebrate consumer (*Varanus prasinus*; emerald tree monitor lizard); B, piscivore (*Gavialis gangeticus*; gharial); C, carnivore (*V. rudicollis*; roughneck monitor lizard); D, 'harder' invertebrate consumer (*Crocodylus acutus*; American crocodile); E, omnivore (*V. olivaceus*; Gray's monitor lizard). F–J, phytosaurs: F, *Machaeroprosopus pristinus* (PCA and CVA plot no. 3 in Bestwick *et al.* 2020*b*, figs S2–S5); G, *Mystriosuchus planirostris* (no. 6); H, *Nicrosaurus kapffi* (no. 7); I, *N. meyeri* (no. 14); J, '*Smilosuchus lithodendrorum*' (no. 19). Measured areas 146 × 110 μm in size. Topographic scale in micrometres. Skull diagrams of extant reptiles and phytosaurs not to scale (see Specimen Material for sources).
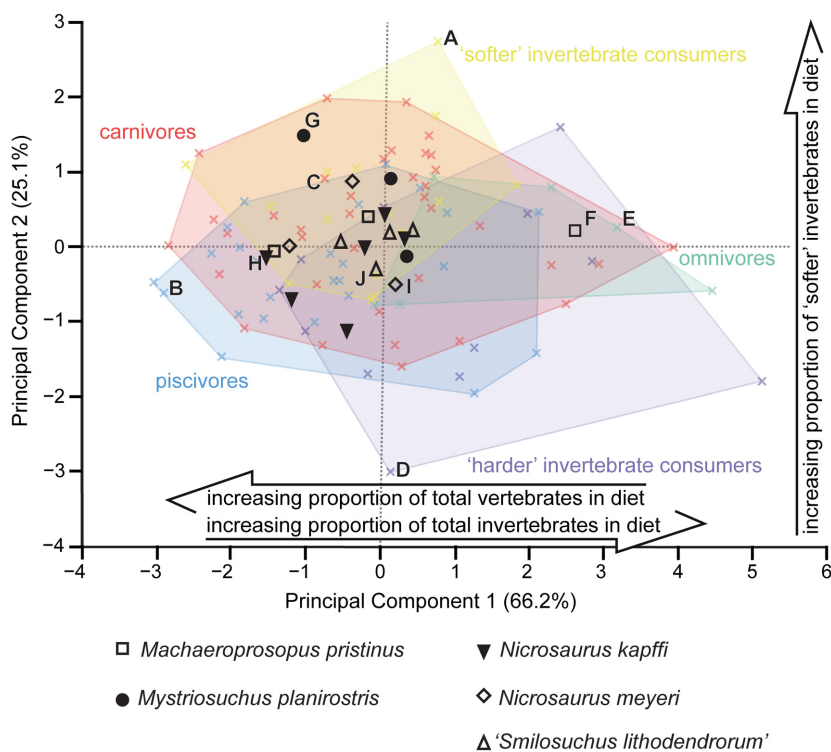
FIG. 4. Principal component texture–dietary space of four ISO texture parameters (Spk, Sds, Vmp and Smr1) for reptiles and phytosaurs. Texture–dietary space based on extant reptile data with phytosaurs projected onto the first two axes as unknown datum points. Specimens with associated letters represent surfaces A–J in Figure 3. Arrows show significant correlations of dietary characteristics along PC axes 1 and 2. Phytosaur specimen information corresponding to PCA plot number can found in Bestwick *et al.* (2020*b*).
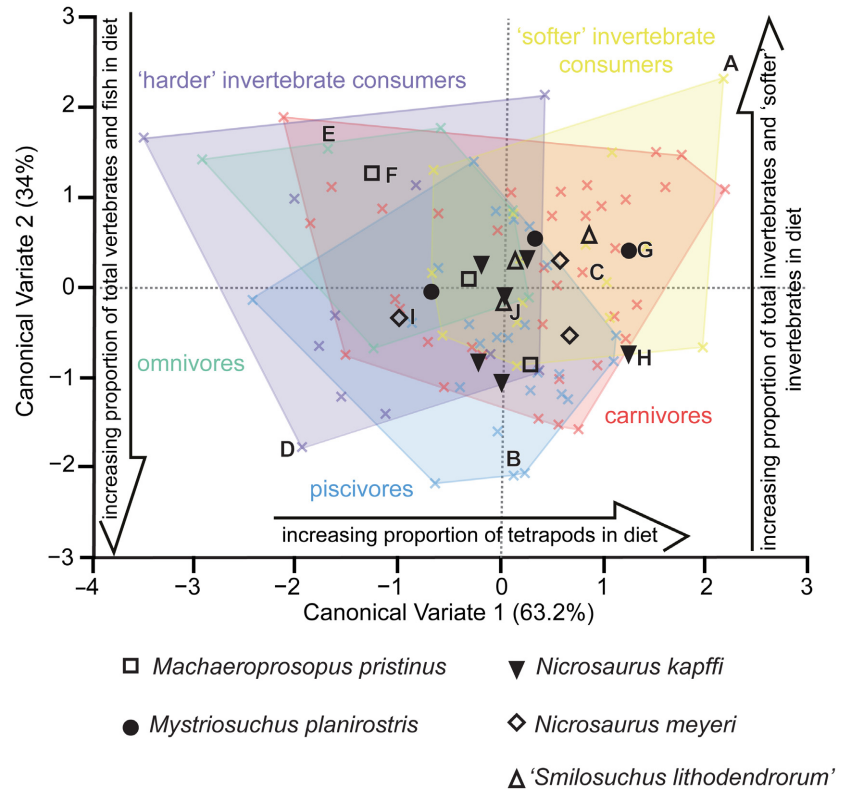
2020*b*, fig. S4). *Machaeroprosopus pristinus* specimens occupy negative CV 1 values and overlap most with 'harder invertebrate consumers along this axis. *Mystriosuchus planirostris* specimens occupy both positive and negative CV 1 values and overall overlap most strongly with extant carnivores along both dietary axes. *Nicrosaurus kapffi* specimens are relatively widely distributed across CVs 1 and 2, relative to other texture–dietary spaces, and in this space this phytosaur overlaps most strongly with carnivores and piscivores. *Nicrosaurus meyeri* specimens are broadly distributed across both CVs 1 and 2 and overlap most strongly with carnivores, piscivores and 'harder' invertebrate consumers along these axes. '*Smilosuchus lithodendrorum*' specimens are also broadly distributed across CVs 1 and 2 with one specimen even extending beyond the extant guilds along CV 2. Phytosaur misclassification in this model is reduced to 42.1% of cases; 52.6% of phytosaurs are classified as piscivores, 15.8% as carnivores, 15.8% as 'harder' invertebrate consumers, 10.5% as 'softer' invertebrate consumers and 5.3% as omnivores.

CVA of all 21 ISO parameters for the extant crocodilian dataset separates guilds in a texture–dietary space defined by CV axes 1 and 2, which together form 100% of total variance (Fig. 7; Bestwick *et al.* 2020*b*, fig. S5). CV 1 positively correlates with proportions of total vertebrates in crocodilian diets (r_s = 0.4735, p = 0.0013) and negatively

correlates with total invertebrates (r_s = −0.4228, p = 0.0047). CV 2 positively correlates with total invertebrates in crocodilian diets (r_s = 0.4501, p = 0.0025) and with dietary proportions of 'harder' invertebrates (r_s = 0.5205, p = 0.0003), and positively correlates with proportions of total vertebrates in crocodilian diets (r_s = −0.3792, p = 0.0121) and with dietary proportions of fish (r_s = −0.5028, p = 0.0006; Bestwick *et al.* 2020*b*, table S7). ANOVA of the axes produces significant separation of dietary guilds (CV 1: F = 41.5073, df = 2, 40, p < 0.0001; CV 2: F = 5.5098, df = 2, 40, p = 0.0077). Tukey HSD tests reveal that all guilds are separate from each other along CV 1 (p < 0.0001), but no pairwise differences are exhibited along CV 2.

Projecting phytosaur data into this texture–dietary space plots all but one specimen (*N. kapffi*, TTU-P 13078, specimen no. 11) within the bounds of the extant crocodilians (Fig. 7; Bestwick *et al.* 2020*b*, fig. S5). Furthermore, all but two specimens (*N. kapffi*, SMNS 13078, specimen no. 11 and '*S. lithodendrum*', TTU-P 15661, specimen no. 6) overlap with piscivores along CV 1, and specimens of the same taxa do not cluster as closely together as in other texture–dietary spaces. This model misclassified 27.9% of specimens; 57.9% of phytosaurs were classified as piscivores, 26.3% carnivores and 15.8% as 'harder' invertebrate consumers.

FIG. 5. Canonical variate texture–dietary space of four ISO texture parameters (Spk, Sds, Vmp and Smr1) for reptiles and phytosaurs. Texture–dietary space based on extant reptile data with phytosaurs projected onto the first two axes as unknown datum points. Specimens with associated letters represent surfaces A–J in Figure 3. Arrows show significant correlations of dietary characteristics along PC axes 1 and 2. Phytosaur specimen information corresponding to PCA plot number can found in Bestwick *et al.* (2020*b*).

☐ *Machaeroprosopus pristinus*　　▼ *Nicrosaurus kapffi*

● *Mystriosuchus planirostris*　　◇ *Nicrosaurus meyeri*

△ *'Smilosuchus lithodendrorum'*

DISCUSSION

Microwear differences between tooth positions

Overall, our analyses show very subtle texture differences between teeth from different positions of the tooth row. In broad terms, the middle teeth have the most complex textures, the posterior teeth have the highest surface textures, and the posterior teeth and anterior teeth to a lesser extent, have the steepest slopes. Of the three ISO parameters that varied the most with tooth position (Sdq, Sdr and Sq), none differed between the extant reptile dietary guilds of Bestwick *et al.* (2019). These three parameters, however, did differ between similar dietary guilds of Winkler *et al.* (2019), although differences for Sdq and Sdr were small. This largely indicates that the subtle texture differences between tooth positions are not due to intra-jaw dietary partitioning.

The lack of texture differences largely contrasts with previous suggestions that the morphologically different teeth along the tooth rows of some phytosaurs, such as *N. kapffi*, were used to acquire and rudimentarily process different foods (Hungerbühler 2000). The fang-like, serrated anteriormost teeth were suggested to have seized and held soft and fleshy prey, the D-shaped, bicarinate posterior-most teeth were suggested to have seized large, harder prey, and the triangular middle teeth were

suggested to have dismembered food items of all sizes (Wall *et al.* 1995; Hungerbühler 2000). While our analyses cannot refute these suggestions of different behavioural uses along the tooth row, the large degree of textural similarity between teeth is indicative of food items with similar material properties being consumed along the entire tooth row.

It has been suggested that phytosaurs employed a head-shaking technique to process large items into smaller pieces before swallowing, passively cutting food material as it moved along their serrated teeth (Chatterjee 1978; Hungerbühler 2000). Such a technique has been demonstrably shown in carcharhinid sharks (Frazzetta 1988) and has been suggested in tyrannosaurid dinosaurs (Farlow & Brinkmann 1994). Alternatively, phytosaurs may have exhibited behaviours similar to the infamous 'death roll' performed by extant crocodilians, where individuals seize prey within their mouths and then spin around the long axis of their bodies in order to process large prey (Drumheller *et al.* 2019). Although the death roll has never been explicitly hypothesized for phytosaurs, the near universal occurrence of this behaviour among extant crocodilians (irrespective of skull ecomorphology, diet or phylogenetic relatedness; Drumheller *et al.* 2019) and the high degree of morphological convergence between crocodilians and phytosaurs (Chatterjee 1978; Stocker 2012; Witzmann *et al.* 2014) means that this
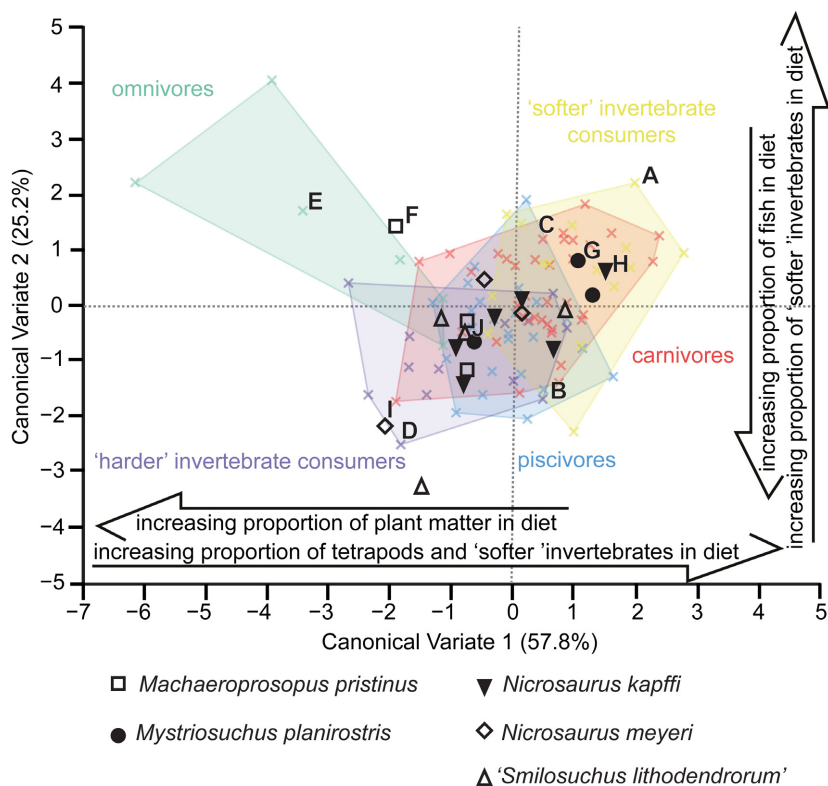
FIG. 6. Canonical variate texture–dietary space of 21 International Organization for Standardization (ISO) texture parameters for extant reptiles and phytosaurs. Texture–dietary space based on extant reptile data with phytosaurs projected onto the first two axes as unknown datum points. Specimens with associated letters represent surfaces A–J in Figure 3. Arrows show significant correlations of dietary characteristics along PC axes 1 and 2. Phytosaur specimen information corresponding to PCA plot number can be found in Bestwick *et al.* (2020*b*).

behaviour cannot be automatically ruled out for phytosaurs. The mechanisms behind microwear formation may be poorly understood (Calandra *et al.* 2012; Schulz *et al.* 2013*a*, *b*) but it is not unreasonable to suggest that these processing behaviours, if exhibited across the entire tooth row, could have resulted in similar intra-jaw tooth microwear textures (Blateyron 2013). Higher forces experienced by posterior teeth during this behaviour, as a result of being positioned closer to the jaw adductor musculature (Kammerer *et al.* 2006; Erickson *et al.* 2012; Porro *et al.* 2013), may have caused the subtle texture differences between posterior and the anterior and middle teeth, although this has yet to be unequivocally tested.

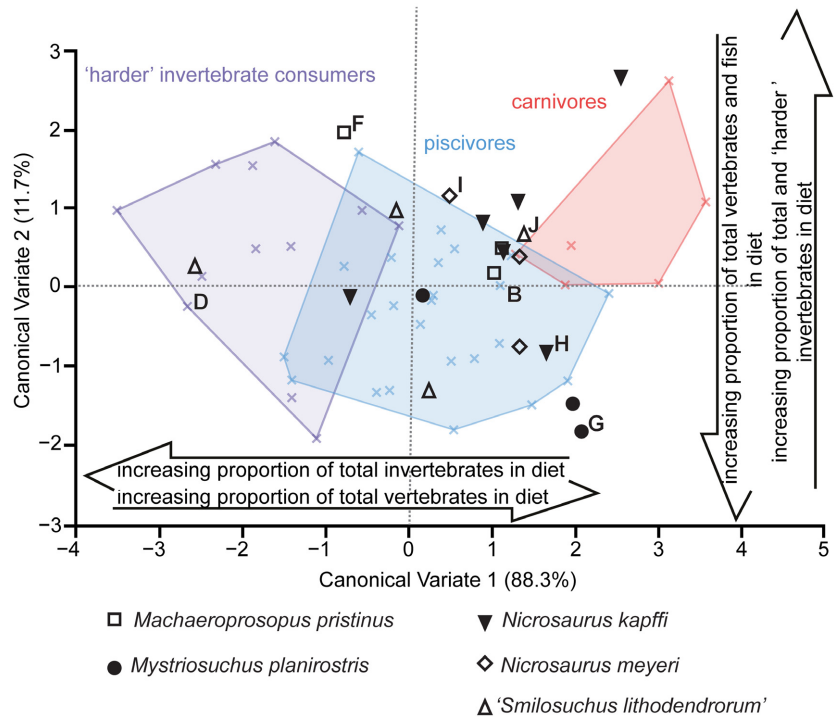*Microwear differences across a spectrum of robustness*

Overall, our analyses show that morphologically robust phytosaurs exhibit rougher tooth microwear textures than gracile phytosaurs. Of the five ISO parameters that differed the most (Sdq, Sdr, Sp, Sz, S5z), none differed between the extant dietary guilds from Bestwick *et al.* (2019), while Sdq and Sdr also exhibited small differences between the dietary guilds from Winkler *et al.* (2019). This indicates that texture differences between robust and gracile phytosaurs are minimally due to dietary differences.

At first glance, our analyses appear to corroborate previous suggestions of phytosaur dietary differences based on comparative anatomy with extant crocodilians; i.e. cranially robust taxa were more likely to have been carnivorous, and cranially gracile taxa were more likely to have been piscivorous (Hunt 1989; Parrish 1989; Hungerbühler 2000; Heckert & Camp 2013). Morphometric analyses of the skulls of extant crocodilians and odontocete whales found extreme morphological convergence between the highly piscivorous taxa; e.g. *G. gangeticus* and the La Plata river dolphin, *Pontoporia blainvillei*, respectively (Iijima 2017; McCurry *et al.* 2017*a*). These taxa independently exhibit elongate rostra and shallow mandibles, among other morphological similarities (Iijima 2017; McCurry *et al.* 2017*a*). Since these taxa are separated by nearly 300 million years of evolution (Lee 1999), it is reasonable to assume that similar morphologies in the skulls of gracile phytosaurs were also adaptations for piscivory. However, the microwear textures of robust and gracile phytosaurs do not occupy separate areas in any of the texture–dietary spaces of extant reptiles. This suggests that the material properties of consumed foods are similar for both morphological groups and that the relationship between robustness and diet is not as straightforward as previously assumed.

When phytosaurs are grouped by robustness, microwear texture differences may be showing a signal for

FIG. 7. Canonical variate texture–dietary space of 21 International Organization for Standardization (ISO) texture parameters for extant crocodilians and phytosaurs. Texture–dietary space based on extant crocodilian data with phytosaurs projected onto the first two axes as unknown datum points. Specimens with associated letters represent surfaces B, D, F–J in Figure 3. Arrows show significant correlations of dietary characteristics along PC axes 1 and 2. Phytosaur specimen information corresponding to PCA plot number can found in Bestwick *et al.* (2020*b*).

□ *Machaeroprosopus pristinus*
● *Mystriosuchus planirostris*
▼ *Nicrosaurus kapffi*
◇ *Nicrosaurus meyeri*
△ *'Smilosuchus lithodendrorum'*

prey size as opposed to diet *per se*. Larger items require more oral handling before consumption, most commonly tearing items into bite-sized pieces (Cleuren & De Vree 2000; D'Amore & Blumenschine 2009). This increases the frequency of tooth-food interactions which provides more opportunities for microwear textures to form, irrespective of the taxonomic identity of consumed foods (Bestwick *et al.* 2019). The skulls of consumers are also subjected to greater mechanical stresses and strains during these processing behaviours (Walmsley *et al.* 2013; McCurry *et al.* 2017*c*). Adductor muscle reconstructions of several phytosaurs found that the skulls of robust taxa were better suited for dealing with higher feeding-related mechanical loads and were therefore better adapted for predating larger items (Wall *et al.* 1995). More broadly, biomechanical modelling of several groups of extant taxa, including crocodilians and odontocetes, similarly found that taxa with elongate rostra are subjected to higher feeding-related stresses (Walmsley *et al.* 2013; McCurry *et al.* 2017*c*). In these taxa, cranial shape is a useful predictor of prey size, with consumption of larger items only exhibited by robust taxa (Metzger & Herrel 2005; McCurry *et al.* 2017*b*). That our analyses are consistent with anatomical comparisons and biomechanical models in both phytosaurs and extant taxa strongly indicates that morphologically robust and gracile phytosaurs may have partitioned resources by physical size, as opposed to the taxonomic identity or material properties, of consumed foods.

Reconstructions of phytosaur diets

Overall, the areas of occupied texture–dietary space in both the extant reptile and crocodilian-only datasets suggest that, as a clade, phytosaur dietary diversity was relatively low. The tendency for specimens to plot around the centre of the texture–dietary spaces, where most or even all of the extant guilds overlap, suggests that phytosaurs were likely to have been dietary generalists. The strong overlap of phytosaurs with piscivores and carnivores in the crocodilian-only texture–dietary space indicates that generalized phytosaur diets primarily consisted of vertebrates, with individual taxa exhibiting slight preferences for fish or tetrapods. This allows us to test previous dietary hypotheses and provide more refined characterization of the ecological roles that phytosaurs performed within Triassic food webs.

Our results broadly support previous inferences of diet based on comparative anatomy, content fossils and associations that phytosaurs were predominantly piscivorous and/or carnivorous (Chatterjee 1978; Hunt 1989; Hungerbühler 1998, 2000; Li *et al.* 2012; Heckert & Camp 2013; Drumheller *et al.* 2014; Stocker *et al.* 2017) albeit with higher degrees of dietary generalism than previously appreciated. Many inferences simply regard phytosaurs as obligate or near-obligate members of these dietary guilds. In reality, diet is often much more complex as lines of evidence do not always agree. For example, preserved stomach contents of the gracile phytosaur *Parasuchus hislopi* include temnospondyl, basal archosauromorph and rhynchosaur

remains (Chatterjee 1978), which starkly contrasts with ideas of obligate piscivory based on its anatomy (Hunt 1989). More broadly, several crocodilians which have traditionally been regarded as obligate piscivores based on their cranial anatomy, such as the false gharial (*Tomistoma schlegelii*) and the freshwater crocodile (*Crocodylus johnstoni*), in fact have much more variable diets that also include mammals, birds, reptiles and amphibians (Drumheller *et al.* 2014; Drumheller & Wilberg 2020; and references therein). Our extant multivariate frameworks do include dietary specialists such as *G. gangeticus* (Hussain 1991) and the carnivorous *V. komodoensis* (Auffenberg 1981), which both plot in the 'high vertebrate diet' areas of texture–dietary spaces (Bestwick *et al.* 2019). That phytosaurs generally do not plot in the same areas as the dietary specialists further indicates that these Triassic reptiles were, in ecological terms, more similar to extant reptiles with generalist and opportunistic diets.

Despite our data indicating that the study phytosaurs were dietary generalists, DMTA nevertheless provides quantitative constraints on phytosaur diets and ecological roles. *Mystriosuchus planirostris*, for example, has been interpreted a piscivore based on its slender rostrum and association with fluvial palaeoenvironments (Hunt 1989; Hungerbühler 1998). Though *My. planirostris* plots more strongly with piscivores in the crocodile-only texture–dietary space, this phytosaur shows slightly higher degrees of overlap with carnivores in the crocodilian and varanid texture–dietary spaces. This suggests that *My. planirostris* was predominantly a carnivore with fish probably comprising the remainder of its diet. Based on biomechanical modelling of other slender-snouted phytosaurs (Wall *et al.* 1995), it is not unreasonable to suggest that *My. planirostris* probably predated small tetrapods. *Nicrosaurus kapffi* has been interpreted as a carnivore based on its robust cranial morphology and its postcranial morphology that is indicative of a more terrestrial lifestyle, relative to other phytosaurs (Hunt 1989; Hungerbühler 2000; Kimmig & Arp 2010). However, since *N. kapffi* overlaps strongly with both carnivores and piscivores in the texture–dietary spaces, this phytosaur probably consumed both tetrapods and fish. *Nicrosaurus meyeri*, alternatively, has been interpreted as a piscivore based on its cranial anatomy (Hungerbühler & Hunt 2000). In our analysis, *N. meyeri* generally plots in similar areas of the texture–dietary spaces as *N. kapffi*, suggesting that both these phytosaurs had similar mixed diets. No explicit dietary hypotheses have been made for *Ma. pristinus*, but other slender-snouted phytosaurs from the same deposits as *Ma. pristinus* from the middle Norian Chinle Formation, western USA, have been interpreted as piscivorous (Parrish 1989). While this phytosaur does show some overlap with extant piscivores in the texture–dietary spaces, *Ma. pristinus* also shows the strongest degree of overlap

with 'harder' invertebrate consumers of all study phytosaurs. This suggests a broader dietary range than has previously been proposed for phytosaurs, and, given the likely combination of fish and 'harder' invertebrates in the *Ma. pristinus* diet, it is not unreasonable to suggest that this phytosaur could be an ecological analogue of *Ca. crocodilus* or *Cr. acutus* (Thorbjarnarson 1988; Laverty & Dobson 2013). Similarly, no explicit dietary hypotheses have been made for the robust taxon '*S. lithodendrorum*', although morphologically similar phytosaurs have been interpreted as carnivorous (Hunt 1989; Parrish 1989; Heckert & Camp 2013). However, the overlap with carnivores and piscivores in the crocodilian and varanid texture–dietary spaces and overlap with piscivores and 'harder' invertebrate consumers in the crocodile-only texture–dietary space suggests a much more diverse diet.

More broadly, our results provide novel insight into Late Triassic ecosystem functioning. Our study phytosaurs are known from the same geological formations from the middle–late Norian of western USA and central Europe (Stocker 2010; Kimmig & Arp 2010; Stocker & Butler 2013). These formations also include several other species of phytosaur that were not sampled (Stocker 2010; Kimmig & Arp 2010; Stocker & Butler 2013). Since DMTA indicates that phytosaurs exhibited large degrees of dietary overlap, it is reasonable to assume that there were potentially high levels of dietary competition between multiple phytosaur taxa, and with other archosaur clades, within Triassic food webs. This assumption is not unfounded as extant contemporaneous archosaurs also exhibit dietary competition, such as *Ca. crocodilus* and the black caiman, *Melanosuchus niger*, in the Amazon (Laverty & Dobson 2013). Several non-mutually exclusive factors could explain how Triassic ecosystems could support high levels of dietary competition. First, their semi-aquatic lifestyles would have enabled a degree of spatial partitioning from large, terrestrial archosaurs such as rauisuchids, which are largely regarded as carnivorous (Chatterjee 1978; Parrish 1989; Nesbitt *et al.* 2013; Drumheller *et al.* 2014). Second, dietary generalism and opportunism could have reduced intra-specific competition, as is exhibited by extant varanids (Losos & Greene 1988; Rahman *et al.* 2017) and some crocodilians (Rosenblatt *et al.* 2013, 2015). As mentioned above, size-based resource partitioning may have occurred between contemporaneous phytosaurs based on total body size, cranial robustness (e.g. between *N. kapffi* and *N. meyeri*) and/or sexual dimorphism. The final factor mentioned involves archosauromorph metabolisms. Histological studies, combined with phylogenetic bracketing, of archosauromorphs have suggested that phytosaurs possessed metabolisms intermediate between those of extant reptiles (ectothermic and poikilothermic) and of extant mammals and birds (endothermic and homoeothermic) (Cubo & Jalil 2019). Lower metabolisms in phytosaurs, relative to endotherms,

would have enabled individuals to consume fewer items to meet metabolic requirements, and thus lower competition levels (Grady *et al.* 2019; Jessop *et al.* 2020). This highlights the uniqueness of reptile-dominated ecosystems not only for the Late Triassic, but for the entire Mesozoic.

CONCLUSIONS

We used DMTA to provide the first quantitative evidence on the diets of phytosaurs and to explore possible impacts of tooth position and cranial robustness on tooth microwear textures. Our analyses find no evidence of dietary partitioning along phytosaur tooth rows. The very subtle textural differences found along tooth rows are interpreted as the result of different loading pressures that teeth experience during the acquisition and oral processing of food items. Despite the overall similarity of tooth texture along phytosaur tooth rows, we nevertheless recommend standardized sampling positions in future DMTA for robust dietary analyses and better understandings of phytosaur feeding behaviours. Our analyses find texture differences between cranially robust and gracile phytosaurs that are probably the result of prey size, and the higher biomechanical forces required to seize and process larger prey, rather than differences in the material properties of prey. These results, and subsequent implications for phytosaur diet, are somewhat consistent with biomechanical biting models of several clades of extant animal. However, further modelling of phytosaur biting behaviours would greatly increase our understanding on inter-specific resource partitioning. We provide the first quantitative constraints of phytosaur diets, revealing that phytosaurs were predominantly carnivorous and/or piscivorous with few preferences for 'harder' invertebrates. Overall phytosaur dietary diversity is relatively low with indications that taxa exhibited dietary generalism and opportunism, rather than strict niche partitioning. This not only contrasts with many hypotheses of phytosaur diets, but also shows higher degrees of ecological convergence with extant crocodilians than previously appreciated. Our analyses therefore support that phytosaurs were important components of Triassic food webs and reveal similarities between Triassic and modern ecosystems. Future application of DMTA to phytosaurs, particularly Middle and latest Triassic taxa, would further enhance our understanding of the ecological roles that phytosaurs performed within Triassic food webs and on the functioning and evolution of Triassic ecosystems.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.h70rxwdgs

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