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Procolophonids display unique tooth morphologies in relation to reptilian herbivory

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Abstract

Procolophonidae, a clade of stem reptiles, are hypothesized to be some of the first highly specialized herbivores to evolve following the end-Permian mass extinction event. That hypothesis is largely based on qualitative observations of tooth shape, which are highly subjective and not generalizable. Quantitative studies of reptilian tooth shape have employed relatively sophisticated methods to capture tooth complexity, but these approaches often require expensive equipment and software and are time intensive. In this study, we built a predictive model based on extant lizards to quantitatively predict the diets of procolophonids using simple measures of tooth morphology. We use linear discriminant analysis (LDA) to predict dietary ecology from tooth dimensions and phylogenetic MANOVA to test for significant differences in tooth dimensions for different diet categories. We report two key findings: (1) procolophonids are largely predicted as herbivorous but occupy a different area of the LDA space from extant lizards, and (2) simple metrics return similar results as complex methods, but with less confidence. We hypothesize that Triassic flora posed different mechanical and processing challenges from modern plants, which contributed to the unique tooth morphologies of procolophonids and likely other Triassic taxa.

Non-technical Summary

Procolophonids were a group of early lizard-like reptile ancestors that lived for over 60 million years. They were one of the few groups that survived one of the Big Five major mass extinction events in Earth's history (end-Permian mass extinction; 252 million years ago). Following the extinction, procolophonids are thought to have evolved adaptations for eating plants, including large, molar-like teeth. Unfortunately, historical evaluations of procolophonid teeth are limited to descriptive observations. While useful, these qualitative descriptions can vary from researcher to researcher and may not be objective or scalable. More recently, quantitative methods of evaluating tooth shape use sophisticated three-dimensional (3D) methods, but these methods are costly—financially and computationally—and as a result may not be available to all researchers. Here we build a predictive model based on living lizards to quantitatively predict the diets of procolophonids using relatively simple measures of tooth shape and size. In our study, we use a method called linear discriminant analysis to separate differences in our living lizard data (measurements of tooth shape and size) by finding a way to draw a boundary that best divides them by their diet. In addition, we tested to see whether our lizard tooth measures differed significantly by diet. Overall, we report two key findings: (1) procolophonids are largely predicted to eat plants but appear to practice a distinct "type" of plant eating from that of lizards, and (2) simple shape and size measures return relatively similar results to those of complex 3D methods. We hypothesize that the plants that procolophonids ate posed a different processing challenge from modern plants, likely contributing to the uniquely-shaped teeth of procolophonids.

Introduction

During periods of mass extinction ecosystem recovery, lineages diversify to occupy open niches after mass extinction events (Dineen et al., 2019; Grossnickle et al., 2019; Lowery and Fraass, 2019). As a result, organisms often "experiment" ecologically with newly available food sources and habitats. Changes in niche occupation are characteristic of mass extinction events, and such patterns are identifiable in mass extinction events throughout the fossil record. For example, net diversification rates are shown to increase for some clades following mass extinctions (Jablonski, 2005). In addition, some authors have found post-extinction radiations, evidenced by morphological divergences, in some clades (Antsey and Pachut, 1995; Foote, 1999; Jablonski, 2005). In general, as niches empty from an extinction event, a new diverse fauna will occupy them in the aftermath.

Survivors of mass extinction events can shed light on the mechanisms and selectivity of an extinction and the "strange world" that appears in the recovery period (Jablonski, 2001;

Hull, 2015). Further investigation of these taxa builds our understanding of what contributes to the survival of certain species, and even large clades, and to the extinction of others. For example, survivor taxa are hypothesized to possess advantageous traits favored during extinction environments, and post-extinction events are fertile ground for speciation (Ezcurra and Butler, 2018; MacDougall et al., 2019; Bertrand et al., 2022). This strange-world phenomenon is exemplified by the species that appeared following the end-Permian mass extinction, which often exhibited unusual morphologies (e.g., drepanosaurs [Renesto et al., 2010]; azendohsaurs [Flynn et al., 2010]; trilophosaurs [Mellett et al., 2023]). Furthermore, faunal turnover between the Permian and Triassic was profound, resulting in vastly different terrestrial ecosystems following the extinction, as well as the appearance of the first members of crown tetrapod clades in the fossil record (Viglietti et al., 2021). The end-Permian mass extinction's reputation as the "worst" mass extinction draws primarily from the marine realm, whereas terrestrial evidence is largely restricted to southern Africa (e.g., Wignall, 2007; Viglietti et al., 2021).

One of the few clades of stem reptiles to persist after the end-Permian mass extinction is Procolophonoidea Romer, 1956 (Watson, 1942; Bakker, 1977; Raup and Sepkoski, 1984; Modesto et al., 2001; Wignall, 2007). Procolophonoidea is a clade of small-bodied stem reptiles that lived during the Permian and Triassic (~265–201 Ma). Procolophonoidea refers to the larger clade encompassing Procolophonidae Lydekker, 1889, an exclusively Triassic clade, and their Permian relatives. Procolophonids and their Permian counterparts exploited several ecological niches, including insectivory (e.g., *Kitchingnathus untabeni* Cisneros, 2008b [Cisneros, 2008b]), durophagous omnivory (e.g., *Tichvinskia vjatkensis* Chudinov and Vjushkov, 1956 [Cisneros, 2008a]), and high-fiber herbivory (e.g., *Hypsognathus fenneri* Gilmore, 1928 [Colbert, 1946; Sues et al., 2000]). Because of gross tooth morphology, several studies concluded that post Permian–Triassic procolophonids evolved into herbivorous niches, contrasting with their insectivorous pre-extinction forebears (Gow, 1978; Cisneros 2008a; Pinheiro et al., 2021). However, inferences of procolophonid dietary ecology relied largely on qualitative descriptions of tooth shape and lack a quantitative basis, (e.g., Colbert, 1946; Gow, 1977a, 1978; Sues et al., 2000; Pinheiro et al., 2021). Previous work on procolophonid dentition was able to distinguish between dentitions "capable" of high-fiber versus non-high-fiber diets (Cisneros and Ruta, 2010). However, no comprehensive analysis of procolophonid dentition and its relationship to dietary ecology has been conducted, despite the wide variation in tooth morphology present in the clade (e.g., Fig. 1). Because we lack comprehensive analyses of procolophonid dietary ecology, the breadth of procolophonid ecology during the Permo–Triassic transition and the subsequent recovery is unknown.

Small-bodied tetrapods such as procolophonids represent important components of terrestrial ecosystems and can act as proxies of ecosystem health (Gusmão et al., 2024). Furthermore, an organism's diet is highly informative of its ecological role (Layman et al., 2015), and our ability to categorize ancient ecologies influences our subsequent interpretations of post-extinction recovery and niche occupation. To that effect, procolophonids are excellent proxies for ecosystem recovery in the Triassic, particularly as it applies to the evolution of herbivory. By analyzing the unusual dentition of procolophonids, we can explore the breadth of tetrapod diversification following one of the most devastating mass extinctions in Earth's history (Benton and Wu, 2022).

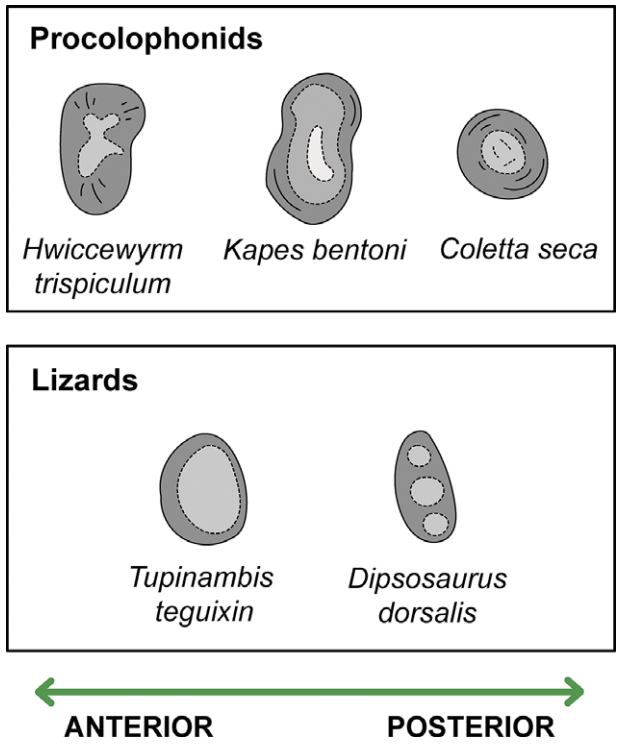


Figure 1. Line drawings of the last tooth in the tooth row of example procolophonids (top) and lizards (bottom) in occlusal view. Anterior (left). Posterior (right). Not drawn to scale.

Here we aim to quantitatively predict the dietary ecology of procolophonids using relatively simple measures of tooth shape and size. On the basis of our review of the literature, we hypothesize that procolophonids are a largely herbivorous clade with insectivorous origins. In this study, we focus on Procolophonidae, a Triassic clade, but include their close Permian relatives (owenettids and nyctiphruretids) to investigate ecological responses to disturbances on the scale of mass extinction events. To test our hypothesis, we developed a dataset of simple tooth measures for a representative sample of extant species of squamates to build a predictive model. We then use this model to infer diets in our fossil dataset. By doing this, we provide a framework for inferring the diets of extinct reptiles that can be used to interpret ecological breadth at different intervals in Earth's history and expanded on for future use.

Previous work

Many have inferred the diets of individual species of procolophonid, often as early representations of herbivory among Pan-Reptilia. The labiolingually expanded cheek teeth of *Hypsognathus fenneri* were associated with some kind of high-fiber herbivory (Colbert, 1946) or durophagy (Sues et al., 2000). These interpretations are supported by the presence of a prominent coronoid process and enlarged orbitotemporal opening, which accommodate larger jaw muscles consistent with herbivory (Sues et al., 2000). It was further suggested that *Procolophon trigoniceps* Owen, 1876 consumed a specialized diet of seeds, judging from the presence of heavily worn postcanine teeth that appeared capable of "crushing" (Gow, 1978). The early-diverging procolophonid *Oryporan insolitus* Pinheiro et al., 2021 has dentition associated with an herbivorous or

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durophagous omnivorous diet, judging from the presence of worn bulbous molar-like teeth with wide occlusal surfaces (Pinheiro et al., 2021).

Evolutionary trends in the diet of procolophonoids are well studied, but there are gaps and uncertainties in the literature. Permian species possess small, peg-like teeth suited for insectivory (Cisneros, 2008a), and many Triassic species have labiolingually broadened, multicuspid teeth suited for herbivory (Gow, 1978). It was suggested that herbivory and durophagous omnivory were practiced by later-diverging members of Procolophonidae and that the advent of these dietary strategies was integral for the clade's Triassic radiation (Cisneros, 2008a). Dental morphologies required for herbivory likely appeared before procolophonids began eating fully herbivorous diets (Cisneros, 2008b). Features typically associated with insectivory and omnivory may have been later co-opted for herbivory by later diverging procolophonids (Pinheiro et al., 2021).

The abundant back and forth regarding the dietary ecology of procolophonids is not necessarily a firm consensus of what food items procolophonids ate or the mechanics needed to process certain foods (e.g., high-fiber plants). This is partially because we do not have a reliable proxy based on modern taxa from which to draw conclusions.

Predicting an organism's ecology from fragmentary fossils is a central challenge in paleontology. To ground such predictions, relationships between morphology and ecology must first be evaluated in extant taxa. Many aspects of dentition are critical for predicting dietary ecology, and methods have focused on the functionally relevant aspects of dental morphology. In mammals, relatively simple metrics, such as degree of hypsodonty and relative grinding area, have proven to be useful for predicting diet (Janis, 1988; Van Valkenburgh, 1989; Williams and Kay, 2001). More complex and computationally intensive ways to quantify tooth shape, such as Orientation Patch Count, Rotated (OPCr; Evans et al., 2007; Wilson et al., 2012; Evans and Pineda-Munoz, 2018), Dirichlet Normal Energy (DNE; Bunn et al., 2011), and Relief Index (RFI; Boyer, 2008), use three-dimensional (3D) models of teeth to generate metrics that describe the complexity, curvature, and relief of a tooth. Those methods are most effective when datasets incorporate the entirety of the dentition, instead of limiting to a specific tooth as is typical in mammal research (Crofts et al., 2020). Their utility is also limited when working with fragmentary fossil dentition. To their benefit, however, those methods focus solely on shape and mechanical function, so they are uninhibited by a need for homologous structures. As a result, they can be used across a variety of taxonomic groups. However, most work in this area focused on mammals due to their complex heterodont dentition, which complicates interpretations of unusual dentition in distantly related amniote clades (e.g., Demar and Bolt, 1981; Cisneros, 2008a; Reisz et al., 2022; Mann et al., 2023).

Compared with the extensive literature on mammals, research that evaluates the relationship between diet and dental morphology in reptiles is less abundant. Recent work in this area relied mainly on 3D topographic measures (e.g., OPCr) or geometric morphometric methods for describing tooth complexity (e.g., Zahradnicek et al., 2014; Melstrom, 2017; Lafuma et al., 2021; Fischer et al., 2022; Hoffman et al., 2023). Although these methods offered insights into adaptations for dietary ecology in reptiles, they are often less accessible to researchers with limited resources. However, linear measurements are one of the simplest and most accessible means of quantifying tooth shape and were used to provide dietary inferences of both extant and fossil species (e.g., Jones, 2009; Lafuma, et al., 2021; Singh, et al., 2021). However, studies such as these pertaining to reptiles are limited, hampering our ability to interpret ancient ecologies.

Methods

Sample and measurements. We selected extant squamate species for inclusion in our dataset to obtain a representative sample of dietary and phylogenetic diversity. Our extant sample includes 91 species of lizards with an average of two individuals per species (minimum 1, maximum 7) and was limited to adult individuals when possible. Because sex information is limited in herpetological collections, especially in historical collections, we did not control for sex in our study, although information on how sex differences impact tooth morphology is limited (Townsend et al., 1999). Our fossil sample encompasses 23 members of Procolophonoidea (including 20 species of procolophonids and two species of owenettids [Owenettidae Broom, 1939], the sister lineage to Procolophonidae), as well as one nyctiphruretid, a member of Procolophonomorpha Romer, 1964 (Modesto et al., 2003; Säilä, 2010).

We measured the labiolingual width (W) and mesiodistal length (L) of the last tooth in the tooth row of both sides of the maxillae and dentaries, when available, from extant specimens housed in the herpetology collections of the Field Museum of Natural History and the Yale Peabody Museum. We measured the last tooth in the tooth row because the last tooth in the tooth row is likely the most recently erupted tooth, and therefore we assume that the morphology of this tooth will not have damage or wear that would potentially bias our quantification of morphology and our inferences for ecology. Furthermore, previous work shows that the last tooth in the tooth row exhibits diet-specific morphology (Jones, 2009). Measurements were taken using Rexbeti digital calipers and Precision Measuring digital calipers. We collected data from fossil specimens using a combination of published images from the literature and direct measurements of specimens in the Vertebrate Paleontology collections at the Field Museum of Natural History and the Yale Peabody Museum. Digital measurements were taken from published images using FIJI (Schindelin et al., 2012).

From these measurements, we computed tooth area (A) and length/width ratio (R). A and R were calculated because they are meaningful indicators of tooth size and tooth shape, respectively. Measures of size (L, W, and A) were log-transformed before being incorporated into analyses.

Body size is also a well-known predictor of diet in both extant and extinct amniote groups (e.g., Pough, 1973; Carbone et al., 1999; Pineda-Munoz et al., 2016; Miller and Pittman, 2021). While snout–vent length (SVL) is the standard body-size proxy in reptiles, very little postcranial material is available for procolophonids, prohibiting its use here. Instead, we used head length (HL) as a proxy for body size in the extant and fossil datasets (e.g., Ortiz Rodriguez, 2012). Where HL data were not available in the literature, it was measured from museum collections, taken from a close relative of similar SVL, or estimated using group-specific regression equations from ElShafie (2024). Work on fossil taxa shows that close relatives (at least family level) have similar SVL/HL ratios (ElShafie, 2024). Source of HL data for each taxon is included in Supplementary Table 1. To ensure that HL is a good predictor of overall body size for our sample, we performed a regression analysis of log-transformed HL on log-transformed SVL (Supplementary Fig. 1). For fossil data, measurements of either HL or tooth-bearing bone length (TL) were collected.

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To infer the diets of fossil taxa, we compared their dentitions with those of extant lizards with well-attested diets (Cooper and Vitt, 2002; Melstrom, 2017; Meiri, 2024). Data of extant lizard diet were obtained from SquamBase, a comprehensive public database of key squamate trait data (Meiri, 2024). SquamBase uses a discrete dietary classification system in which taxa are recognized as carnivorous, herbivorous, or omnivorous. To distinguish insectivores (faunivores that specialize in eating insects and small arthropods) from carnivores that specialize in eating small vertebrates and their eggs, we referred to the supplementary dietary metadata information available in SquamBase. When diet information was not available from SquamBase, we gathered diet data directly from the literature. All carnivorous taxa were eventually excluded from our dataset because their body sizes routinely exceed the size range that is relevant for procolophonids.

Analyses. To determine whether the procolophonid diet can be predicted from fossil tooth dimensions, we first determined whether tooth dimensions in extant lizards are predictive of their dietary ecology. To do this, we performed a linear discriminant analysis (LDA). LDA is a commonly used supervised learning technique that predicts group membership from multivariate quantitative data. LDA works by first finding linear combinations of features in a training dataset that yield good prediction of the categorical group membership of observations, before then being applied to observations for which group membership is not known. LDA was conducted using the "lda" function in the "MASS" package (Venables and Ripley, 2002) for R (R Core Team, 2021). Prior probabilities on group membership were set to the observed proportions of the dataset: herbivorous = 0.30, insectivorous = 0.30, and omnivorous = 0.40. We used a leave-one-out cross-validation (CV) to find the posterior probability for each taxon to engage in each dietary ecology. To determine whether the inclusion of size with dental dimensions improves dietary predictions, we performed a total of two LDAs: (1) diet ~ ratio + area + head length and (2) diet ~ ratio + area.

Dietary ecology of each fossil species was predicted from both discriminant functions using the "predict.lda" function from the "MASS" package. Predicted diets and LD scores from both LDAs were then projected into the LDA space for extant species and mapped onto a time-calibrated phylogeny of Procolophonoidea modified from Mueller et al. (2024). Fossil occurrence data for time calibration were obtained from the Paleobiology Database (PBDB). We also acknowledge that Permian occurrences of procolophonids are dubious and that revisions to the Karoo Basin reptile dataset are ongoing. These updates may influence our results.

In addition to LDA, we used multivariate analysis of variance (MANOVA) to investigate which variables were guiding the differences between these groups. The influence of shared evolutionary history was investigated by conducting a phylogenetic MANOVA using the "aov.phylo" function from the "Geiger" package in R (Pennell et al., 2014). Phylogenetic MANOVA recomputes the MANOVA for a specified number of dependent variable datasets (here, n = 999) simulated under a Brownian motion model of evolution (i.e., without an effect of the independent variable) and then asks how frequently the observed effect size is larger than the randomized effect sizes. We used the extant squamate phylogeny from Pyron et al. (2013).

Results

Linear discriminant analysis. We performed two LDAs based on measures of tooth size and shape (R, A) (Fig. 2). The first LDA (LDA1) was performed with a proxy for body size (HL), and the second (LDA2) was performed without this proxy. In both LDAs, a gradient consistently presents between herbivorous, omnivorous, and insectivorous lizards (Fig. 2.1, 2.3). Notably, the correct classification rates for both LDAs are low (<60%) and thus severely limit our ability to interpret the results.

However, general patterns are still observable: herbivores tend to have more negative scores on LD1, insectivores tend to have more positive scores, and the LD1 scores of omnivores are intermediate between the two (Fig. 2.1, 2.3). Herbivores occupy a region of the LDA space associated with larger tooth areas, wider teeth, and larger body sizes (Fig. 2.1, 2.3). Conversely, insectivores occupy a region of the LDA space associated with smaller tooth areas, narrower tooth ratios, and smaller body sizes. Again, omnivores are intermediate to these. Overall group scores follow this pattern. However, when we project individual scores into LDA space, there is a great deal of overlap. For example, some herbivorous species fall into the positive space along LDA1 (occupied mainly by insectivorous taxa) (Fig. 2.1, 2.3). The removal of body size as a predictor (LDA2) does not appear to change where different dietary groups sit in LDA space.

Two significant discriminant functions were obtained for LDA1. Discriminant function 1 explained 95.73% of the variance between groups with the following coefficients: log(A) (–0.85), R (0.97), and HL (–0.77). Discriminant function 2 explained 4.27% of the variance between groups with the following coefficients: log(A) (–0.06), R (–2.03), and HL (–0.43). LDA1 correctly classified 57.8% of cases, where "correctly classified" is defined as the true diet having the highest posterior probability of the four categories. Two significant discriminant functions were obtained from LDA2. Discriminant function 1 explained 95.52% of the variance between groups with the following coefficients: log(A) (–1.09) and R (0.94). Discriminant function 2 explained 4.48% of the variance between groups with the following coefficients: log(A) (–0.23) and R (–2.05). LDA2 correctly classified 51.6% of cases.

Fossil data predictions. Procolophonids were overwhelmingly predicted to be herbivorous (16–17/23), and only one taxon (*Timanophon raridentatus* Novikov, 1991) was classified differently between LDA1 and LDA2 (as an omnivore and an herbivore, respectively) (Table 1). Surprisingly, no taxa were predicted to be insectivorous. In both LDAs, procolophonids and owenettids are generally restricted to the negative space along LDA1 (Fig. 2.2, 2.4). This region of the LDA space is associated with larger tooth areas and wider teeth. Notably, procolophonids and owenettids occupy a region of the LDA space largely unoccupied by extant squamates (Fig. 2.2, 2.4). Procolophonids that do overlap with extant squamates fall mainly within the "herbivore" convex hull (except *Kapes bentoni* Spencer and Storrs, 2002 in LDA1, which sits in a region occupied by both the "herbivore" and "omnivore" convex hulls) (Fig. 2.2, 2.4). However, the nyctiphruretid *Nyctiphruretus acudens* Efremov, 1938 sits in a region of LDA space in which all three convex hulls ("herbivore," "omnivore," and "insectivore") overlap and that is isolated from the procolophonoid taxa in the dataset (Fig. 2.2, 2.4). Posterior probabilities are generally low, but two general takeaways are possible. First, posterior probabilities are somewhat higher for LDA2 than for LDA1. Second, probabilities associated with predicted herbivorous procolophonids are generally higher than those for predicted omnivores and for any extant squamate, ranging as high as 0.87. In addition, in both LDAs, no procolophonids are predicted to be insectivorous, and the posterior probabilities for insectivory are always low, never rising above 0.04

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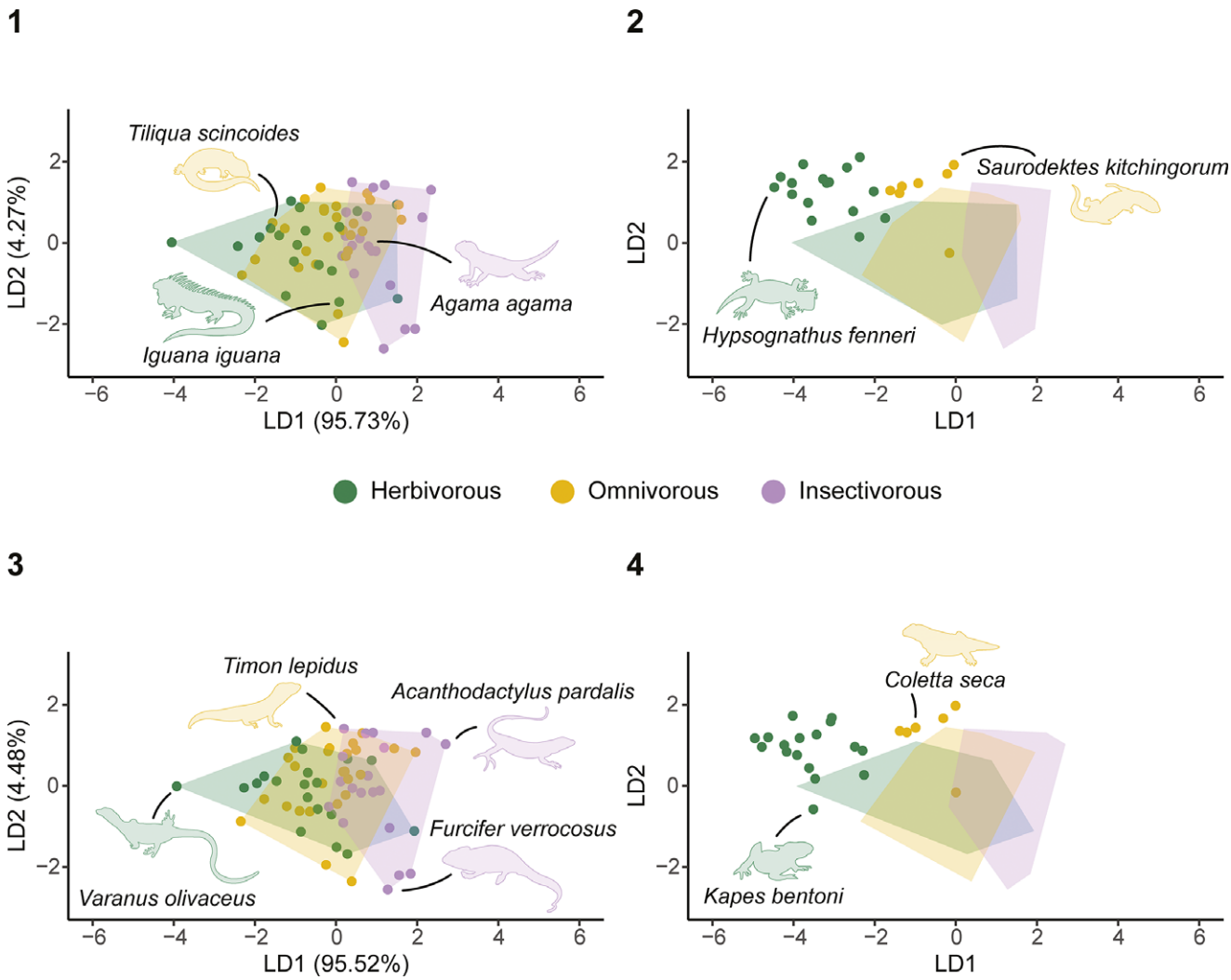


Figure 2. LDAs on tooth dimension data for extant and fossil data. (**1**) Extant squamate data (LDA1): bivariate plot of LD1 and LD2. Observed diet depicted as green (herbivory), yellow (omnivory), and purple (insectivory). (**2**) Procolophonoid and nyctiphruretid LDA1 diet predictions: bivariate plot of LD1 and LD2. Predicted diet depicted as green (herbivory), yellow (omnivory), and purple (insectivory). Convex hulls of Plot 1 (extant squamate data—LDA1) are superimposed for comparison. (**3**) Extant squamate data (LDA2): bivariate plot of LD1 and LD2. (**4**) Procolophonoid and nyctiphruretid data LDA2 diet predictions: bivariate plot of LD1 and LD2. Convex hulls of Plot 3 (extant squamate data—LDA2) are superimposed for comparison.

for procolophonids or 0.19 for owenettids. The LDA1 scores for extant specialized insectivorous taxa tend to be positive and >1, and the taxa in our dataset do not possess LDA1 scores in this range.

When we plotted the results of our LDA fossil predictions onto a phylogeny of procolophonoids and a close relative, we find the outgroup (*Nyctiphruretus*) and early diverging procolophonoids are recovered as omnivores, while later-diverging taxa are recovered as herbivores (Fig. 3). Contrary to our initial hypothesis, no taxa in our dataset are predicted to be insectivores. Our results suggest a stepwise evolution toward herbivory within Procolophonidae. Moving from the base of the tree to the more nested clades, LDA1 scores decrease substantially (e.g., *Saurodektes kitchingorum* Modesto et al., 2003 at –0.01/–0.03 versus *Hypsognathus fenneri* at –4.47/–4.52) (Fig. 3; Table 1). Furthermore, taxa within Leptopleuroninae Ivakhnenko, 1979 are entirely and consistently recovered as herbivores. In addition, when we plotted procolophonid tooth areas through time (Fig. 4), we found that procolophonid tooth size increased as the Triassic progressed. This is consistent with the hypothesis that dental complexity increased in procolophonids toward the end of the Triassic.

As mentioned, only one procolophonid, *Timanophon*, had different dietary classifications in each LDA. Because of this, we cannot distinguish whether it was an omnivore or strictly herbivorous. Curiously, *Timanophon* is found at a transition point in the clade where procolophonids become nearly exclusively herbivorous, except for *Procolophon trigoniceps* (Fig. 3).

Phylogenetic MANOVA. Tooth shape varies quantitatively among dietary guilds of extant lizards. Insectivores possess the narrowest (mean R = 1.61) and smallest (mean A = 0.246) teeth, whereas herbivores possess the widest (R = 1.49) teeth with omnivores intermediate (R = 1.40). Omnivorous and herbivorous teeth are, on average, similar in size to one another (A = 0.76 and 0.72) but much larger than those of insectivores (A = 0.246).

MANOVAs were conducted to determine whether there is a significant difference between dietary categories in measures of tooth shape and size, with and without the inclusion of HL as a proxy for body size. When phylogenetic relatedness was accounted for, the effect was non-significant (p = 0.487). A second MANOVA was conducted to assess the effect of dietary ecology on measures of

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Table 1. Diet predictions for procolophonids and close relatives. Diet predictions, along with posterior probabilities, for both LDAs (LDA1 and LDA2) are reported along with diet predictions from the literature

Taxon	LDA1	Posterior probability	LDA2	Posterior probability	Literature
Acadiella psalidodon Sues and Baird, 1998	Herbivorous	0.66	Herbivorous	0.79	NA
Coletta seca	Omnivorous	0.58	Omnivorous	0.57	Nondurophagous omnivory (Hotton et al., 1997).
Cornualbus primus Silva-Neves et al., 2024	Herbivorous	0.61	Herbivorous	0.67	NA
Eomurruna yurrgensis Hamley et al., 2021	Herbivorous	0.55	Herbivorous	0.65	Durophagy; high-fiber herbivory (Hamley et al., 2021).
Haligonia bolodon Sues and Baird, 1998	Herbivorous	0.69	Herbivorous	0.84	Durophagous omnivory (Sues and Baird, 1998; Cisneros, 2008a).
Hwiccewyrm trispiculum	Herbivorous	0.78	Herbivorous	0.81	NA
Hypsognathus fenneri	Herbivorous	0.84	Herbivorous	0.85	High-fiber plant material; arthropods with resilient cuticles (Sues et al., 2000).
Kapes bentoni	Herbivorous	0.7	Herbivorous	0.75	High-fiber plant material; arthropods; hard-shelled invertebrates (Zaher et al., 2019).
Kitchingnathus untabeni	Omnivorous	0.54	Omnivorous	0.53	Insectivorous (Cisneros, 2008b).
Leptopleuron lacertinum Owen, 1851	Herbivorous	0.74	Herbivorous	0.76	Vegetation; hard-shelled invertebrates (Säilä, 2010).
Libognathus sheddi Small, 1997	Herbivorous	0.81	Herbivorous	0.82	Herbivory; durophagous omnivory (Pinheiro et al., 2021).
Oryporan insolitus	Herbivorous	0.71	Herbivorous	0.78	Herbivory; durophagous omnivory (Pinheiro et al., 2021).
Saurodektes kitchingorum	Omnivorous	0.63	Omnivorous	0.62	Insectivorous (Reisz and Laurin, 1991).
Phonodus dutoitorum Modesto et al., 2010	Herbivorous	0.7	Herbivorous	0.82	Durophagous (Modesto et al., 2010).
Procolophon trigoniceps	Omnivorous	0.52	Omnivorous	0.55	High-fiber plant material (Gow, 1977a).
Nyctiphruretus acudens	Omnivorous	0.48	Omnivorous	0.48	Insectivorous; “invertebrates” (Sennikov, 1996).
Ruhuhuaria reiszi Tsuji et al., 2013	Omnivorous	0.63	Omnivorous	0.62	Insectivorous or omnivorous; “hard-bodied insects” (Bradley and Nesbitt, 2017).
Sclerosaurus armatus Meyer in Fischer, 1857	Herbivorous	0.8	Herbivorous	0.8	Herbivorous (Sues and Reisz, 2008).
Scoloparia glyphanodon Sues and Baird, 1998	Herbivorous	0.82	Herbivorous	0.87	High-fiber herbivory (Jenkins and Bhullar, 2022).
Soturnia caliodon	Herbivorous	0.54	Herbivorous	0.65	High-fiber herbivory (Cisneros and Ruta, 2010).
Teratophon spinigenis Gow, 1977a (Gow, 1977b)	Herbivorous	0.8	Herbivorous	0.87	High-fiber herbivory (Cisneros and Ruta, 2010).
Tichvinskia vjatkensis	Herbivorous	0.55	Herbivorous	0.63	Herbivory; durophagous omnivory (Pinheiro et al., 2021).
Timanophon raridentatus	Omnivorous	0.49	Herbivorous	0.61	Herbivory; durophagous omnivory (Pinheiro et al., 2021).

tooth shape and size (R, A) without the inclusion of a body-size proxy. Again, there was a non-significant effect when phylogenetic relatedness was accounted for ($p = 0.446$).

Discussion

Procolophonids were highly specialized, unique herbivores, distinct from extant plant-eating lizards. By predicting dietary ecology in procolophonoids, we offer insight into post-extinction ecosystem dynamics and the macroevolutionary processes governing trends in ecological niche occupation. Contrary to our initial hypothesis, procolophonids do not have insectivorous origins. Rather, we predict that the earliest diverging procolophonids are omnivores. In times of climatic instability and consequent scarcity, dietary generalists such as omnivores are at an advantage because they can exploit a wider range of resources (e.g., McKinney, 1997; Sahney and Benton, 2008). However, some dietary specialists, such as extant herbivores, are found to possess the highest risks of extinction (Atwood et al., 2020). We suggest that exploiting generalist niches may have led to the initial success of procolophonids in the post-extinction landscape. However, there is mixed evidence of this pattern outside of Procolophonidae. Some specialist herbivore clades, such as dicynodonts, do survive the end-Permian extinction and persist into the Triassic (Smith and Botha, 2005; Botha-Brink and Angielczyk, 2010).

We found that procolophonids are overwhelmingly predicted to be herbivorous, with some omnivorous individuals, although there is very little overlap in the LDA space with any modern lizard taxa. No taxa in our sample were predicted to be insectivorous, contrasting with previous qualitative works (Gow, 1977a, 1978). Although

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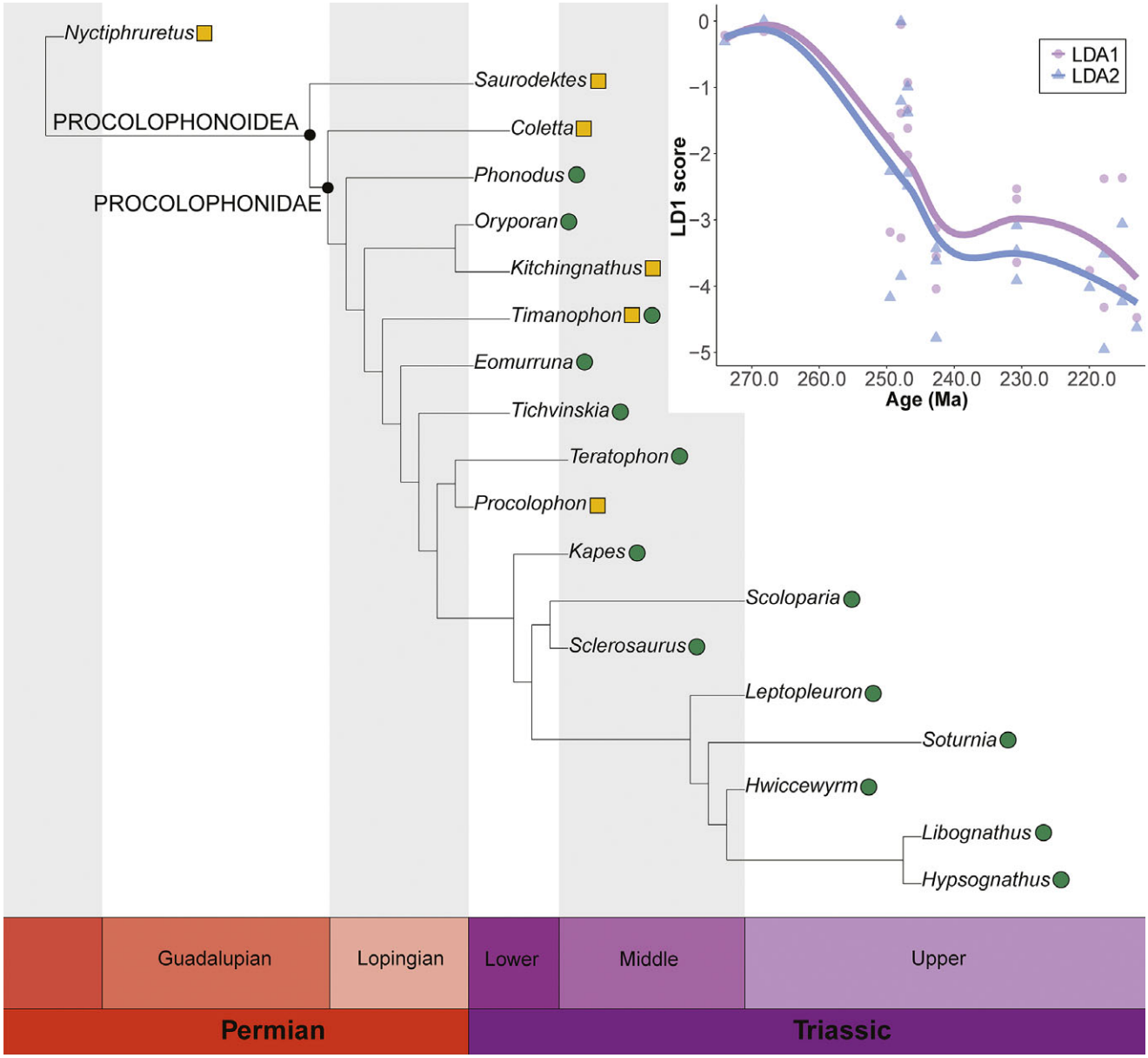


Figure 3. Phylogenetic distribution of predicted diets among Procolophonoidea and their close relatives. Time-calibrated phylogeny modified and inferred from Mueller et al. (2024). Diet predictions depicted as green circles (herbivory) and yellow squares (omnivory). The inset graph (top right corner) is a biplot of taxon age (in 10 Myr time bins) and LD1 scores. LD1 values from LDA1 and LDA2, respectively, are denoted by pink circles and blue triangles.

effect sizes are small and phylogenetic MANOVAs imply limited utility of the simple metrics for discriminating diet in the extant sample, diet estimates for procolophonids suggest that our models can be utilized for dietary prediction in fossil taxa, particularly those that have unique morphologies.

While low LDA correct classification scores hamper our ability to discriminate between diet categories in modern lizards, it is striking that procolophonids occupy a distinct area of the LDA space. Because of this distinct occupation, we hypothesize that procolophonids, while herbivorous, either ate plant matter or mechanically processed food distinctly differently from modern herbivorous lizards. We suggest that unique tooth morphologies permitted procolophonids to engage in a unique form of herbivory well suited for the consumption of the tough, fibrous plant material of the Triassic, which we detail further in the following. In addition, we highlight trends in procolophonid tooth shape throughout the Triassic and its relationship to the clade's progression toward specialized herbivory.

Multiple Triassic small-bodied reptiles exhibit adaptations for herbivory (e.g., procolophonids [e.g., Cisneros and Ruta, 2010; Zaher et al., 2019; Pinheiro et al., 2021], opisthodontian and clevosaurid rhynchocephalians [e.g., Jones, 2009; Martínez et al., 2013], rhynchosaurs [e.g., Sethapanichsakul et al., 2023], and trilophosaurids [e.g., Mellet et al., 2023]). Further, some Triassic procolophonids and trilophosaurids share notable similarities in jaw and tooth morphology (e.g., bulbous, multicuspid molariform dentition [Chambi-Trowell et al., 2021; Foffa et al., 2022]). Our results may reflect a larger trend toward specialized herbivory among small-bodied reptile groups rather than an isolated instance within Procolophonidae. Herbivorous squamates today feed mainly on the

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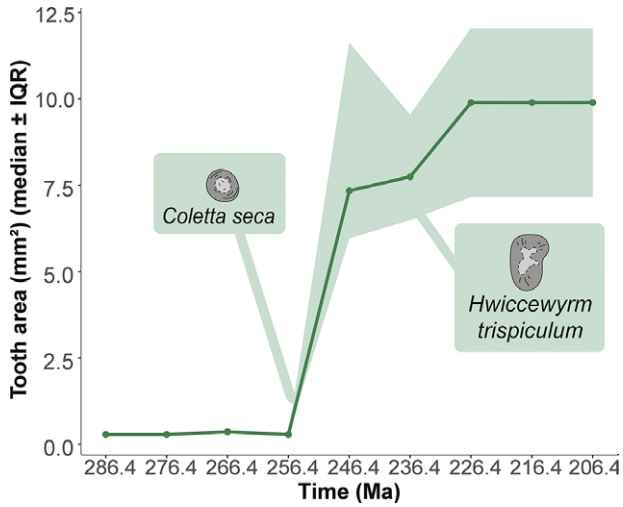


Figure 4. Ribbon plot comparing the distribution of procolophonoid tooth area (mm^2) by taxon age (in 10 Myr time bins). Median values (solid line) are shown for tooth area with shaded ribbon representing interquartile range (IQR). Line drawings of the last tooth in the tooth row of example procolophonids (*Coletta seca* Gow, 2000 and *Hwiccewyrm trispiculum* Butler et al., 2024) included to demonstrate general difference in average tooth area and morphology. Not drawn to scale.

flowers, fruits, and leaves of angiosperm plants (Cooper and Vitt, 2002; Soltis et al., 2018). The biochemical and mechanical properties of these food items fundamentally differ from those of the Triassic when gymnosperms were the dominant plant life—flowers and fruits, highly nutritious and easier-consumed food items, were not yet present (Kustatscher et al., 2018). At this time, herbivorous procolophonids had limited options ranging from eating tough, fibrous cycad leaves, seeds of Triassic plants, and the "bark" of these plants. Such plants were woody with high fiber content and would pose a considerable challenge to consume and digest both mechanically and biochemically (e.g., van Marken Lichtenbelt, 1992; Grauvogel-Stamm and Ash, 2005; Berthaume, 2016). In addition, as the Early Triassic progressed to the Middle and Late Triassic, plant life recovered from the end-Permian extinction, and a more mature flora evolved that was able to better support an herbivorous fauna (e.g., Hotton et al., 1997; Grauvogel-Stamm and Ash, 2005; Kustatscher et al., 2018). During this progression, the dentition of procolophonids continued to evolve to larger sizes (Fig. 4), and they were exposed to more dietary options, including gymnosperms such as cycads, ferns, lycopods, and sphenophytes (e.g., Grauvogel-Stamm and Ash, 2005; Kustatscher et al., 2018). Digesting plants such as these and extracting sufficient nutrients would require ample oral processing (i.e., chewing). The bulbous, molariform posterior marginal dentition present in many procolophonids would be effective for consuming these types of plants.

Procolophonids lack exact modern analogs because they consumed flora that was fundamentally different from what is around today. However, procolophonids show some general characteristics related to herbivory in modern taxa, but they appear to represent a more distinct ecomorphotype. For example, Procolophonidae possess multicuspid teeth, which are present in many extant herbivorous lizards (e.g., *Dipsosaurus dorsalis* Baird and Girard in Baird et al., 1852, *Iguana iguana* Linnaeus, 1758, and *Saara hardwickii* Gray in Hardwicke and Gray, 1827). However, the teeth of procolophonids are not laterally compressed like the teeth of extant iguanids (a prolific clade of herbivorous lizards) but rather wide and molariform, similar to durophagous lizards (e.g., *Tupinambis teguixin* Linnaeus, 1758 and *Dracaena guianensis* Daudin, 1802). In addition, many procolophonids possess an elaborate palatal dentition, with more teeth and distributed among the palatal bones, which many modern lizards lack (Mahler and Kearney, 2006; Zaher et al., 2019). While this may be a plesiomorphic trait retained in procolophonids, it is possible that, due to the greater elaboration of the palatal dentition, procolophonids used them actively to process plant matter. However, the function of palatal dentition in tetrapods has seldom been observed directly. Horned procolophonids also have a crown-to-crown occlusion system (e.g., *Soturnia caliodon* Cisneros and Schultz, 2003, *Hypsognathus fenneri*), a derived feature among the clade thought to be advantageous for high-fiber herbivory or durophagy (e.g., Colbert, 1946; Cabreira and Cisneros, 2009; Hamley et al., 2021). Occlusion systems are described in extant herbivorous lizards (e.g., *Pogona vitticeps* Ahl, 1926; Haridy, 2018), but they do not appear to occlude crown-to-crown as they do in the more derived procolophonids.

Alternatively, a major transition occurred in the evolution of insects during the Triassic (e.g., Zheng et al., 2018; Gui et al., 2023; Montagna et al., 2024). Entomofaunas are hypothesized to have modernized as far back as the Triassic, in the aftermath of the end-Permian extinction (e.g., Béthoux et al., 2005; Gui et al., 2024). By the Middle and Late Triassic, modern insect faunas had emerged and represented a significant portion of Triassic insect diversity (Gui et al., 2024). This modernization hypothesis is in line with a greater hypothesis surrounding the evolution of ecosystems following the Permian–Triassic boundary: that the beginning of the Mesozoic marks the beginning of modern terrestrial ecosystems (e.g., Benton and Wu, 2022). Such a change in the composition of the entomofauna may explain why our diet hypotheses for Early–Middle Triassic procolophonids contradict previous ones. We predict some Early and Middle Triassic-age procolophonids were omnivores, as opposed to insectivores (Table 1). Meaning that Early Triassic tetrapods were potentially consuming insects with different morphologies from those consumed by modern squamates and that modern squamate lineages (and their teeth) evolved alongside an entirely different entomofauna. Changes in insect morphology through time, and the associated mechanical challenges, may explain the difference in our findings. Extensive work by Singh et al. (2021) investigated the evolution of herbivory at the community level in early Mesozoic ecosystems using a combination of geometric and functional morphometric methods. Where our study focuses on Procolophonoidea and uses simple, linear measurements of dentition, Singh et al. (2021) analyzed Triassic and Jurassic tetrapods using the mandible. Singh et al. (2021) also included procolophonoid parareptiles in their dataset but did not include members before the Permian–Triassic boundary. In general, the conclusions of our study agree with those of Singh et al. (2021), notably, the transition of the clade from "tough generalist[s]" (owenettids, basal procolophonids, and procolophonines) to "crushing biter[s]" (leptopleurines) (Singh et al., 2021). On the basis of modern proxies, we also identify owenettids and basal procolophonoids as generalist omnivores and leptopleurines as durophagous specialists, likely specializing on plant materials. Among the procolophonines, however, we do predict a mix of generalist omnivory and herbivory. This difference is likely due to how our studies describe diet differently. In the present study, we restricted our descriptions of diet to the traditional categories—herbivore, omnivore, and faunivore (insectivore, in the case of procolophonoids)—whereas Singh et al. (2021) classified diet using a functional approach. Despite differences in methods, both studies support

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the conclusion that procolophonids were largely siloed into specialized herbivory by the end of the Triassic.

Traditional linear measurements remain an informative part of the ecomorphologist's toolkit. There is a current trend toward using increasingly complex metrics to quantify dental ecomorphology in the literature, but historically, simple measures based on ratios and linear measurements have proved useful for discriminating broad dietary categories (e.g., Janis, 1988; Van Valkenburgh, 1989; Williams and Kay, 2001; Jones, 2009). Here we used relatively simple measurements (area and ratio of the last tooth in the tooth row) as measures of tooth shape and size. We found that, in general, herbivorous taxa were more likely to have larger, wider teeth and that insectivorous taxa were more likely to have smaller, narrower teeth, supporting previous findings for lepidosaurs (e.g., Jones, 2009; Melstrom, 2017; Lafuma et al., 2021).

Conservatively, the discriminatory power of linear measurements in our study is limited. Low LDA correct classification scores (<60%) restrict our ability to discern between dietary groups in extant lizards, although patterns typically reported in previous studies of extant reptilian teeth are recovered. Because linear measurements offer a comparatively lower discriminatory power than more complex functional traits, such as OPCr or geometric morphometric descriptors of shape, they are not an effective predictive tool for highlighting more subtle differences in morphology. However, we show that linear measurements prove useful when studying taxa with extreme morphologies. Here these measures act as a quantitative basis for confirming the unique and derived dental morphology of procolophonids when compared with extant lizards with varying diets. Despite low correct classification scores, the distinct, separate location of fossil data in LDA space makes relative comparisons possible.

In support of previous findings, we demonstrated that there is an abundance of diversity in reptilian teeth that directly relates to dietary ecology (Jones, 2009; Melstrom, 2017; Lafuma et al., 2021). Furthermore, across different approaches of quantifying and describing diversity, we arrive at the same general patterns—our work using simple linear measurements of tooth shape recovered similar results to work that employed 3D methods to quantify tooth shape (Melstrom, 2017). Analyses that rely on 3D data are computationally and time-intensive to collect and are highly sensitive to data collection and cleaning methods (Spradley et al., 2017; Berthaume et al., 2019). Although our methods for evaluating the relationship between tooth morphology and diet lack the level of confidence that 3D methods may provide, we found the same ecomorphological relationships previously recovered. To that end, simple linear measurements offer a more accessible means of testing hypotheses related to diet and dentition in the fossil record, and they may provide an informative first approach in data exploration. Our findings also mirrored the relationships between tooth shape and diet in mammals: we found a similar pattern of labiolingually broadened, larger teeth belonging to herbivores and smaller, narrower teeth belonging to insectivores; with omnivorous tooth shapes as intermediate (Van Valkenburgh, 1989; Evans et al., 2007; Cuozzo et al., 2012; Wisniewski et al., 2023). Further work exploring whether modern mammals can be used as dietary proxies for disparate clades, such as Triassic reptiles, may elucidate the dietary breadth of extinct clades with unusual tooth morphologies.

Increasing values in every tooth-related metric generally correlate with herbivory. More complex topography (OPCr), larger occlusal surface area, or higher cusp count were identified as indicative of plant-eaters, broadly across Tetrapoda (Evans et al., 2007; Jones et al., 2009; Melstrom, 2017; Lafuma et al., 2021; Wisniewski et al., 2023). Combining traits that predict herbivory may best emphasize the different facets of tooth morphology that contribute to plant-eating. Using both relatively simple measurements and more complex methods increases the amount of information with which we can make dietary predictions. This may be particularly useful for making future predictions about the types of plants being eaten (e.g., leaves versus roots) and the adaptations that facilitate eating different foodstuffs.

Given our results, we recommend that future analyses combine simple and complex methods when predicting dietary ecology, especially for extinct taxa. Different types of methods are especially helpful for accommodating the fragmentary fossil record and capturing different features of tooth shape. We can further investigate the relationship between morphology and diet by incorporating aspects of morphology other than teeth. Clearly, there is far more to food processing than the marginal (maxillary and mandibular) dentition, but analyses predicting diet tend to be limited to a few teeth or to specific tooth-bearing bones. In many amniotes, palatal rugosities, pharyngeal spines, and palatal dentitions are known or hypothesized to contribute to food ingestion and processing (Mahler and Kearney, 2006; Menegaz et al., 2008; Fraher et al., 2010). Incorporating such aspects of morphology into studies on diet in extant and extinct taxa will hopefully offer greater predictive accuracy and a more nuanced picture of the cohesive nature and function of food-processing systems.

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Data availability statement. Data and all supplemental materials are available from the Data Dryad Digital Repository: https://doi.org/10.5061/dryad.9kd51c5x8.

References

Ahl, E., 1926, Neue Eidechsen und Amphibien: *Zoologischer Anzeiger*, **v. 67**, p. 186–192.

Anstey, R.L., and Pachut, J.F., 1995, Phylogeny, diversity history, and speciation in Paleozoic bryozoans, *in* Erwin, D.H. and Anstey, R.L., eds., *New Approaches to Speciation in the Fossil Record*: New York, Columbia University Press, p. 239–284.

Atwood, T.B., Valentine, S.A., Hammill, E., McCauley, D.J., Madin, E.M.P., et al., 2020, Herbivores at the highest risk of extinction among mammals, birds, and reptiles: *Science Advances*, **v. 6**, n. eabb8458.

Baird, S.F., Girard, C., and Le Conte, J.L., 1852, Characteristics of some new reptiles in the Museum of the Smithsonian Institution; remarks upon the Coccinellidæ of the United States; description of a new species of Trombidium: *Proceedings of the Academy of Natural Sciences of Philadelphia*, **v. 6**, p. 125–146.

Bakker, R.T., 1977, Tetrapod mass extinctions—a model of the regulation of speciation rates and immigration by cycles of topographic diversity, *in* Hallam, A., ed., *Developments in Palaeontology and Stratigraphy*: Amsterdam, Elsevier, p. 439–468.

Benton, M.J., and Wu, F., 2022, Triassic Revolution: *Frontiers in Earth Science*, **v. 10**, n. 899541.

Berthaume, M.A., 2016, Food mechanical properties and dietary ecology: *American Journal of Physical Anthropology*, **v. 159**, p. S79–S104.

Berthaume, M.A., Winchester, J., and Kupczik, K., 2019, Effects of cropping, smoothing, triangle count, and mesh resolution on 6 dental topographic metrics: *PLoS One*, **v. 14**, n. e0216229.

Bertrand, O.C., Shelley, S.L., Williamson, T.E., Wible, J.R., Chester, S.G.B., et al., 2022, Brawn before brains in placental mammals after the end-Cretaceous extinction: *Science*, **v. 376**, p. 80–85.

Béthoux, O., Papier, F., and Nel, A., 2005, The Triassic radiation of the entomofauna: *Comptes Rendes Palevol*, **v. 4**, p. 609–621.

Botha-Brink, J., and Angielczyk, K.D., 2010, Do extraordinarily high growth rates in Permo-Triassic dicynodonts (Therapsida, Anomodontia) explain their success before and after the end-Permian extinction?: *Zoological Journal of the Linnean Society*, **v. 160**, p. 341–365.

Boyer, D.M., 2008, Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals: *Journal of Human Evolution*, **v. 55**, p. 1118–1137.

Bradley, A.B., and Nesbitt, S.J., 2017, A possible new specimen of *Ruhuhuaria reiszi* from the Manda Beds (?Middle Triassic) of southern Tanzania and its implications for small sauropsids in the Triassic: *Journal of Vertebrate Paleontology*, **v. 37**, p. 88–95.

Broom, R., 1939, A new type of cotylosaurian, *Owenetta rubidgei*: *Annals of the Transvaal Museum*, **v. 19**, p. 319–321.

Bunn, J.M., Boyer, D.M., Lipman, Y., St. Clair, E.M., Jernvall, J., and Daubechies, I., 2011, Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination: *American Journal of Physical Anthropology*, **v. 145**, n. 247261.

Butler, R.J., Meade, L.E., Cleary, T.J., McWhirter, T., Brown, E.E., Kemp, T. S., Benito, J., and Fraser, N.C., 2024, *Hwiccewyrm trispiculum* gen. et sp. nov., a new leptopleurine procolophonid from the Late Triassic of southwest England: *The Anatomical Record*, **v. 307**, p. 1390–1420.

Cabreira, S.F., and Cisneros, J.C., 2009, Tooth histology of the parareptile *Soturnia caliodon* from the Upper Triassic of Rio Grande do Sul, Brazil: *Acta Palaeontologica Polonica*, **v. 54**, p. 743–748.

Carbone, C., Mace, G.M., Roberts, S.C., and MacDonald, D.W., 1999, Energetic constraints on the diet of terrestrial carnivores: *Nature Letters*, **v. 402**, p. 286–288.

Chambi-Trowell, S.A., Whiteside, D.I., Skinner, M., Benton, M.J., and Rayfield, E.J., 2021, Phylogenetic relationships of the European trilophosaurids *Tricuspisaurus thomasi* and *Variodens inopinatus*: *Journal of Vertebrate Paleontology*, **v. 41**, n. e1999250.

Chudinov, P.K., and Vjushkov, B.P., 1956, New data on small cotylosaurs from the Permian and Triassic of the USSR: *Doklady Akademii Nauk SSSR*, **v. 108**, p. 547–550.

Cisneros, J.C., 2008a, Phylogenetic relationships of procolophonid parareptiles with remarks on their geologic record: *Journal of Systematic Palaeontology*, **v. 6**, p. 345–366.

Cisneros, J.C., 2008b, New basal procolophonid reptile from the Katberg formation (Lower Triassic) of the South African Karoo: *Palaeoworld*, **v. 17**, p. 126–134.

Cisneros, J.C., and Ruta, M., 2010, Morphological diversity and biogeography of procolophonids (Amniota: Parareptilia): *Journal of Systematic Palaeontology*, **v. 8**, p. 607–625.

Cisneros, J.C., and Schultz, C.L., 2003, *Soturnia caliodon* n. g. n. sp., a procolophonid reptile from the upper Triassic of Southern Brazil: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **v. 227**, p. 365–380.

Colbert, E.H., 1946, *Hypsognathus*, a Triassic reptile from New Jersey: *Bulletin of the American Museum of Natural History*, **v. 86**, p. 225–274.

Cooper, W.E., Jr., and Vitt, L.J., 2002, Distribution, extent, and evolution of plant consumption by lizards: *Journal of Zoology*, **v. 257**, p. 487–517.

Crofts, S.B., Smith, S.M., and Anderson, P.S.L., 2020, Beyond description: the many facets of dental biomechanics: *Integrative and Comparative Biology*, **v. 60**, p. 594–607.

Cuozzo, F.P., Ungar, P.S., and Sauther, M.L., 2012, Primate dental ecology: how teeth respond to environment: *Journal of Physical Anthropology*, **v. 148**, p. 159–162.

Daudin, F.M., 1802, *Histoire Naturelle des Rainettes, des Grenouilles et des Crapauds*: Paris, Levrault, 108 p.

Demar, R., and Bolt, J.R, 1981, Dentitional organization and function in a Triassic reptile: *Journal of Paleontology*, **v. 55**, p. 967–984.

Dineen, A.A., Roopnarine, P.D., and Fraiser, M.L., 2019, Ecological continuity and transformation after the Permo–Triassic mass extinction in northeastern Panthalassa: *Biology Letters*, **v. 15**, n. 20180902.

Efremov, I.A., 1938, Some new Permian reptiles of the USSR: *Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS*, **v. 19**, p. 771–776.

ElShafie, S.J., 2024, Body size estimation from isolated fossil bones reveals deep time evolutionary trends in North American lizards: *PLOS One*, **v. 19**, n. e0296318.

Evans, A.R., and Pineda-Munoz, S., 2018, Inferring mammal dietary ecology from dental morphology, *in* Croft, D., Su, D., and Simpson, S., eds., *Methods in Paleoecology. Vertebrate Paleobiology and Paleoanthropology*: Cham, Springer, p. 37–51.

Evans, A.R., Wilson, G.P., Fortelius, M., and Jernvall, J., 2007, High level similarity of dentitions in carnivorans and rodents: *Nature*, **v. 445**, p. 78–81.

Ezcurra, M.D., and Butler, R.J., 2018, The rise of the ruling reptiles and ecosystem recovery from the Permo–Triassic mass extinction: *Proceedings of the Royal Society B: Biological Sciences*, **v. 285**, n. 20180361.

Fischer, L.H., 1857, Über *Sclerosaurus armatus* Meyer, eine neue Saurier-Gattung aus dem Bunten Sandstein bei Warmbach gegenüber Rheinfelden: *Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefakten-Kunde*, **v. 1857**, p. 136–140.

Fischer, V., Bennion, R.F., Foffa, D., MacLaren, J.A., McCurry, M.R., Melstrom, K.M., and Bardet, N., 2022, Ecological signal in the size and shape of marine amniote teeth: *Proceedings of the Royal Society B: Biological Sciences*, **v. 289**, n. 20221214.

Flynn, J.J., Nesbitt, S.J., Parrish, J.M., Ranivoharimanana, L., and Wyss, A.R., 2010, A new species of Azendohsaurus (Diapsida: Archosauromorpha) from the Triassic Isalo Group of Madagascar: cranium and mandible: *Palaeontology*, **v. 53**, p. 669–688.

Foffa, D., Nesbitt, S.J., Kligman, B.T., Butler, R.J., and Stocker, M.R., 2022, New specimen and redescription of *Anisodontosaurus greeri* (Moenkopi Formation: Middle Triassic) and the spatiotemporal origins of Trilophosauridae: *Journal of Vertebrate Paleontology*, **v. 42**, n. e2220015.

Foote, M., 1999, Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids: *Paleobiology Memoirs*, **v. 25**, p. 1–116.

Fraher, J., Davenport, J., Fitzgerald, E., McLaughlin, P., Doyle, T., Harman, L., and Cuffe, T., 2010, Opening and closing mechanisms of the leatherback sea turtle larynx: a crucial role for the tongue: *Journal of Experimental Biology*, **v. 213**, p. 4137–4145.

Gilmore. C.W., 1928, New fossil reptile from the Triassic of New Jersey: *Proceedings of the United States National Museum*, **v. 73**, p. 1–8.

Gow, C.E., 1977a, Tooth function and succession in the Triassic reptile *Procolophon trigoniceps*: *Palaeontology*, **v. 20**, p. 695–704.

Gow, C.E., 1977b, New Procolophonids from the Triassic Cynognathus Zone of South Africa: *Annals of the South African Museum*, **v. 72**, p. 109–124.

Gow, C.E., 1978, The advent of herbivory in certain reptilian lineages during the Triassic: *Palaeontologica Africana*, **v. 21**, p. 133–141.

Gow, C.E., 2000, A new procolophonid (Parareptilia) from the Lystrosaurus Assemblage Zone, Beaufort Group, South Africa: *Palaeontologia Africana*, **v. 36**, p. 21–23.

Grauvogel-Stamm, L., and Ash, S.R., 2005, Recovery of the Triassic land flora from the end-Permian life crisis: *Comptes Rendus Palevol*, **v. 4**, p. 593–608.

Grossnickle, D.M., Smith, S., and Wilson, G.P., 2019, Untangling the multiple ecological radiations of early mammals: *Trends in Ecology and Evolution*, **v. 34**, p. 936–949.

Gui, S-M., Liu, Y-C., and Tian, L., 2023, Evolution of insect diversity in the Permian and Triassic: *Palaeoentomology*, **v. 6**, p. 472–481.

https://doi.org/10.1017/jpa.2025.10195 Published online by Cambridge University Press

Gui, S., **Gao, S.**, **Liu, Y.**, **Chu, D.**, **Dal Corso, J.**, **Tong, J., and Tian, L.**, 2024, The rise of modern-type entomofauna in the Triassic: *Journal of Insect Biodiversity*, **v. 60**, p. 64–74.

Gusmão, R.A.F., **Tessarolo, G.**, **Dobrovolski, R., and Gonçalves-Souza, T.**, 2024, Body size and trophic structure explain global asymmetric response of tetrapod diversity to climate effects: *Ecology and Evolution*, **v. 14**, n. e11047.

Hamley, T., **Cisneros, J.C., and Damiani, R.**, 2021, A procolophonid reptile from the Lower Triassic of Australia: *Zoological Journal of the Linnean Society*, **v. 192**, p. 554–609.

Hardwicke, T., and Gray, J.E., 1827., A synopsis of the species of saurian reptiles, collected in India by Major-General Hardwicke: *Zoological Journal London*, **v. 3**, p. 213–229.

Haridy, Y., 2018, Histological analysis of post-eruption tooth wear adaptations, and ontogenetic changes in tooth implantation in the acrodontan squamate *Pogona vitticeps*: *PeerJ*, **v. 6**, n. e5923.

Hoffman, D.K., **Hancox, J.P., and Nesbitt, S.J.**, 2023, A diverse diapsid tooth assemblage from the Early Triassic (Driefontein, South Africa) records the recovery of diapsids following the end-Permian mass extinction: *PLoS One*, **v. 18**, n. e0285111.

Hotton, N., III, **Olson, E.C., and Beerbower, R.**, 1997, Amniote origins and the discovery of herbivory, *in* Sumida, S., and Martin, K.L.M., eds., *Amniote Origins: Completing the Transition to Land*: San Diego, Academic Press, p. 207–265.

Hull, P., 2015, Life in the aftermath of mass extinctions: *Current Biology* **v. 25**, p. R941–R952.

Ivakhnenko, M.F., 1979, Permian and Triassic procolophonids of the Russian platform: *Trudiy Paleontologischeskogo Instituta Akademia Nauk SSSR*, **v. 164**, p. 1–80. [in Russian]

Jablonski, D., 2001, Lessons from the past: evolutionary impacts of mass extinctions: *Proceedings of the National Academy of Sciences of the United States of America*, **v. 98**, p. 5393–5398.

Jablonski, D., 2005, Mass extinctions and macroevolution: *Paleobiology*, **v. 31**, p. 192–210.

Janis, C.M., 1988, An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference, *in* Russell, D.E., Santoro, J.P., and Signogneau-Russell, D., eds., *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology*: Mémoires du Muséum National d'Histoire Naturelle (Série C) **v. 53**, p. 367–387.

Jenkins, K.M, and Bhullar, B.-A.S., 2022, Tooth implantation and attachment in *Scoloparia glyphanodon* (Parareptilia: Procolophonidae): *Bulletin of the Peabody Museum of Natural History*, **v. 63**, p. 27–30.

Jones, M.E.H., 2009, Dentary tooth shape in Sphenodon and its fossil relatives (Diapsida: Lepidosauria: Rhynchocephalia): *Frontiers in Oral Biology*, **v. 13**, p. 9–15.

Kustatscher, E., **Ash, S.R.**, **Karasev, E.**, **Pott, C.**, **Vajda, V.**, **Yu, J., and McLoughlin, S.**, 2018, Flora of the Late Triassic, *in* Tanner, L., ed., *The Late Triassic World*: Topics in Geobiolog, **v. 46**, p. 545–622.

Lafuma, F., **Corfe, I.J.**, **Clavel, J., and Di-Poï, N.**, 2021, Multiple evolutionary origins and losses of tooth complexity in squamates: *Nature Communications*, **v. 12**, n. 6001.

Layman, C.A., **Giery, S.T.**, **Buhler, S.**, **Rossi, R.**, **Penland, T.**, et al., 2015, A primer on the history of food web ecology: fundamental contributions of fourteen researchers: *Food Webs*, **v. 4**, p. 14–24.

Linnaeus, C., 1758, Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis (tenth edition): Vienna, Typis Ioannis Thomae, 824 p.

Lowery, C.M., and Frass, A.J., 2019, Morphospace expansion paces taxonomic diversification after end Cretaceous mass extinction: *Nature Ecology & Evolution*, **v. 3**, p. 900–904.

Lydekker, R., 1889, Part III—Palaeozoology. Vertebrata, *in* Nicholson, H.A., and Lydekker, R., eds., *Manual of Palaeontology for the Use of Students with a General Introduction on the Principles of Palaeontology* Volume **II**, Part 3: Edinburgh and London, William Blackwood and Sons, p. 889–1474.

MacDougall, M.J., **Brocklehurst, N., and Fröbisch, J.**, 2019, Species richness and disparity of parareptiles across the end-Permian mass extinction: *Proceedings of the Royal Society B*, **v. 286**, n. 20182572.

Mahler, D.L., and Kearney, M., 2006, The palatal dentition in squamate reptiles: morphology, development, attachment, and replacement: *Fieldiana Zoology*, **v. 2006**, p. 1–61.

Mann, A., **Henrici, A.C.**, **Sues, H.-D., and Pierce, S.E.**, 2023, A new Carboniferous edaphosaurid and the origin of herbivory in mammal forerunners: *Scientific Reports*, **v. 13**, n. 4459.

Martínez, R.N., **Apaldetti, C.**, **Colombi, C.E.**, **Praderio, A.**, **Fernandez, E.**, **Malnis, P.S.**, **Correa, G.A.**, **Abelin, D., and Alcober, O.**, 2013, A new sphenodontian (Lepidosauria: Rhynchocephalia) from the Late Triassic of Argentina and the early origin of the herbivore opisthodontians: *Proceedings of the Royal Society B*, **v. 280**, n. 20132057.

McKinney, M.L., 1997, Extinction vulnerability and selectivity: combining ecological and paleontological views: *Annual Review of Ecology, Evolution, and Systematics*, **v. 28**, p. 495–516.

Meiri, S., 2024, SquamBase—a database of squamate (Reptilia: Squamata) traits: *Global Ecology and Biogeography*, **v. 33**, n. e13812.

Mellett, M.P., **Kligman, B.T.**, **Nesbitt, S.J., and Stocker, M.T.**, 2023, Masticatory mechanisms, dental function, and diet in Triassic trilophosaurids (Reptilia, Allokotosauria): *Palaeodiversity*, **v. 16**, p. 99–124.

Melstrom, K.M., 2017, The relationship between diet and tooth complexity in living dentigerous saurians: *Journal of Morphology*, **v. 278**, p. 500–522.

Menegaz, R.A., **Sublett, S.V.**, **Figueroa, S.D.**, **Hoffman, T.J., and Ravosa, M.J.**, 2008, Phenotypic plasticity and function of the hard palate in growing rabbits: *The Anatomical Record*, **v. 292**, p. 277–284.

Miller, C.V., and Pittman, M., 2021, The diet of early birds based on modern and fossil evidence and a new framework for its reconstruction: *Biological Reviews*, **v. 96**, p. 2058–2112.

Modesto, S., **Sues, H.-D., and Damiani, R.**, 2001, A new Triassic procolophonoid reptile and its implications for procolophonoid survivorship during the Permo–Triassic extinction event: *Proceedings of the Royal Society B*, **v. 268**, p. 2047–2052.

Modesto, S., **Damiani, R.J.**, **Neveling, J., and Yates, A.M.**, 2003, A new Triassic owenettid parareptile and the Mother of Mass Extinctions: *Journal of Vertebrate Paleontology*, **v. 23**, p. 715–719.

Modesto, S., **Scott, D.M.**, **Botha-Brink, J., and Reisz, R.R.**, 2010, A new and unusual procolophonid parareptile from the Lower Triassic Katberg Formation of South Africa: *Journal of Vertebrate Paleontology*, **v. 30**, p. 715–723.

Montagna, M., **Magoga, G.**, **Stockar, R., and Magnani, F.**, 2024, The contribution of the Middle Triassic fossil assemblage of Monte San Giorgio to insect evolution: *Communications Biology*, **v. 7**, n. 1023.

Mueller, B.D., **Small, B.J.**, **Jenkins, X.**, **Huttenlocker, A.K., and Chatterjee, S.**, 2024, Cranial anatomy of *Libognathus sheddi* Small, 1997 (Parareptilia, Procolophonidae) from the Upper Triassic Dockum Group of West Texas, USA: *The Anatomical Record*, **v. 307**, p. 1421–1441.

Novikov, I.V., 1991, Novye Dannye po Prokolofoninam SSSR [New data on Procolophonines of the USSR]: *Paleontologicheskii Zhurnal*, **v. 1991**, p. 73–85.

Ortiz Rodriguez, D.O., 2012, *Body size evolution in procolophonoid parareptiles*: München, Ludwig-Maximilians-Universität.

Owen, R., 1851, Vertebrate air-breathing life in the Old Red Sandstone: *Literary Gazette, and Journal of Belles Lettres*, v. December 20, **1851**, p. 2.

Owen, R., 1876, *Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum*: London, British Museum, 242 p.

Pennell, M.W., **Eastman, J.M.**, **Slater, G.J.**, **Brown, J.W.**, **Uyeda, J.C.**, et al., 2014, geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees: *Bioinformatics*, **v. 30**, p. 2216–2218.

Pineda-Munoz, S, **Evans, A.R., and Alroy, J.**, 2016, The relationship between diet and body mass in terrestrial mammals: *Paleobiology*, **v. 42**, p. 659–669.

Pinheiro, F.L., **Silva-Neves, E., and Da-Rosa, A.A.A.**, 2021, An early-diverging procolophonid from the lowermost Triassic of South America and the origins of herbivory in Procolophonoidea: *Papers in Palaeontology*, **v. 2021**, p. 1–12.

Pough, F.H., 1973, Lizard energetics and diet: *Ecology*, **v. 54**, p. 837–844.

Pyron, R.A., **Burbrink, F.T., and Wiens, J.J.**, 2013, A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes: *BMC Evolutionary Biology*, **v. 13**, n. 93.

Raup, D.M., and Sepkoski, J.J., Jr., 1984, Periodicity of extinction in the geologic past: *Proceedings of the National Academy of Sciences of the United States of America*, **v. 81**, p. 801–805.

R Core Team, 2021, R: a language and environment for statistical computing: R Foundation for Statistical Computing, https://www.R-project.org/index.html.

https://doi.org/10.1017/jpa.2025.10195 Published online by Cambridge University Press

Reisz, R.R., and Laurin, M., 1991, *Owenetta* and the origin of turtles: *Nature*, **v. 349**, p. 324–326.

Reisz, R.R., Scott, D., and Modesto, S.P., 2022, Cranial anatomy of the caseid synapsid *Cotylorhynchus romeri*, a large terrestrial herbivore from the lower Permian of Oklahoma, USA: *Frontiers in Earth Science*, **v. 10**, n. 847560.

Renesto, S., Spielmann, J.A., Lucas, S.G., and Spagnoli, G.T., 2010. The taxonomy and paleobiology of the Late Triassic (Carnian-Norean: Adamanian-Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha): *Bulletin of the New Mexico Museum of Natural History and Science*, **v. 46**, p. 1–81.

Romer, A.S., 1956, *Osteology of the Reptiles: Chicago*, University of Chicago Press, 772 p.

Romer, A.S., 1964, *Diadectes* an amphibian?: *Copeia*, **v. 1964**, p. 718–719.

Sahney, S., and Benton, M.J., 2008, Recovery from the most profound mass extinction of all time: *Proceedings of the Royal Society B: Biological Sciences*, **v. 275**, p. 759–765.

Säilä, L.K., 2010, Osteology of *Leptopleuron lacertinum* Owen, a procolophonoid parareptile from the Upper Triassic of Scotland, with remarks on ontogeny, ecology, and affinities: *Earth and Environmental Sciences Transactions of the Royal Society of Edinburgh*, **v. 101**, p. 1–25.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., et al., 2012, Fiji: an open-source platform for biological-image analysis: *Nature Methods*, **v. 9**, p. 676–682.

Sennikov, A.G., 1996, Evolution of the Permian and Triassic tetrapod communities of Eastern Europe: *Palaeogeography, Palaeoclimatology, Palaeoecology*, **v. 120**, p. 331–351.

Sethapanichsakul, T., Coram, R.A., and Benton, M.J., 2023, Unique dentition of rhynchosaurs and their two-phase success as herbivores in the Triassic: *Palaeontology*, **v. 66**, n. e12654.

Silva-Neves, E., Da-Rosa, Á.A.S., Modesto, S.P., and Dias-da-Silva, S., 2024, *Cornualbus primus* gen. et sp. nov.: a new procolophonid (Reptilia: Parareptilia) from Upper Triassic of South America, first tetrapod from the Passo das Tropas Member of the Santa Maria Supersequence: *Journal of Systematic Palaeontology*, **v. 22**, n. 2373116.

Singh, S.A., Elsler, A., Stubbs, T.L., Bond, R., Rayfield, E.J., and Benton, M.J., 2021, Niche partitioning shaped herbivore macroevolution through the early Mesozoic: *Nature Communications*, vol. **12**, n. 2796.

Small, B.J., 1997, A new procolophonid from the upper Triassic of Texas, with a description of tooth replacement and implantation: *Journal of Vertebrate Paleontology*, **v. 17**, p. 674–678.

Smith, R., and Botha, J., 2005, The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction: *Comptes Rendus Palevol*, **v. 4**, p. 623–636.

Soltis, D., Soltis, P., Endress, P., Chase, M.W., Manchester, S., Judd, W., Majure, L., and Mavrodiev, E., 2018, *Phylogeny and Evolution of the Angiosperms*: Chicago, University of Chicago Press, 590 p.

Spencer, P.S., and Storrs, G.W., 2002, A re-evaluation of small tetrapods from the Middle Triassic Otter Sandstone Formation of Devon, England: *Palaeontology*, **v. 45**, p. 447–467.

Spradley, J.P., Pampush, J.D., Morse, P.E., and Kay, R.F., 2017, Smooth operator: the effects of different 3D mesh retriangulation protocols on the computation of Dirichlet normal energy: *American Journal of Biological Anthropology*, **v. 163**, p. 94–109.

Sues, H.-D., and Baird, D., 1998, Procolophonidae (Reptilia: Parareptilia) from the Upper Triassic Wolfville Formation of Nova Scotia, Canada: *Journal of Vertebrate Paleontology*, **v. 18**, p. 525–532.

Sues, H.-D., and Reisz, R.R., 2008, Anatomy and phylogenetic relationships of *Sclerosaurus armatus* (Amniota: Parareptilia) from the Buntsandstein (Triassic) of Europe: *Journal of Vertebrate Paleontology*, **v. 28**, p. 1031–1042.

Sues, H.-D., Olsen, P.E., Scott, D.M., and Spencer, P.S., 2000, Cranial osteology of *Hypsognathus fenneri*, a latest Triassic procolophonid reptile from the Newark Supergroup of Eastern North America: *Journal of Vertebrate Paleontology*, **v. 20**, p. 275–284.

Townsend, V.R., Jr., Akin, J.A., Felgenhauer, B.E., Dauphine, J., and Kidder, S.A., 1999, Dentition of the ground skink, *Scincella lateralis* (Sauria: Scincidae): *Copeia*, **v. 1999**, p. 783–788.

Tsuji, L.A., Sobral, G., and Müller, J., 2013, *Ruhuhuaria reiszi*, a new procolophonoid reptile from the Triassic Ruhuhu Basin of Tanzania: *Comptes Rendus Palevol*, **v. 12**, p. 487–494.

van Marken Lichtenbelt, W.D., 1992, Digestion in an ectothermic herbivore, the green iguana (Iguana iguana): effect of food composition and body temperature: *Physiological Zoology*, **v. 65**, p. 649–673.

Van Valkenburgh, B., 1989, Carnivore dental adaptations and diet: a study of trophic diversity within guilds, *in* Gittleman, J.L., ed., *Carnivore Ecology, Behavior, & Evolution*: Dordrecht, Springer, p. 410–436.

Venables, W.N., and Ripley, B.D., 2002, *Modern Applied Statistics with S* (fourth edition): New York, Springer, 510 p.

Viglietti, P.A., Benson, R.B.J., Smith, R.M.H., Botha, J., Kammerer, C.F., et al., 2021, Evidence from South Africa for a protracted end-Permian extinction on land: *Proceedings of the National Academy of Sciences of the United States of America*, **v. 118**, n. e2017045118.

Watson, D.M.S, 1942, On Permian and Triassic tetrapods: *Geological Magazine*, **v. 79**, p. 81–116.

Wignall, P., 2007, The End-Permian mass extinction—how bad did it get?: *Geobiology*, **v. 5**, p. 303–309.

Williams, S.H., and Kay, R.F., 2001, A comparative test of adaptive explanations for hypsodonty in ungulates and rodents: *Journal of Mammalian Evolution*, **v. 8**, p. 207–229.

Wilson, G.P., Evans, A.R., Corfe, I.J., Smits, P.D., Fortelius, M., and Jernvall, J., 2012, Adaptive radiation of multituberculate mammals before the extinction of dinosaurs: *Nature*, **v. 483**, p. 457–460.

Wisniewski, A.L., Nations, J.A., and Slater, G.J., 2023, Bayesian prediction of multivariate ecology from phenotypic data yields new insights into the diets of extant and extinct taxa: *American Naturalist*, **v. 202**, p. 192–215.

Zaher, M., Coram, R.A., and Benton, M.J., 2019, The Middle Triassic procolophonid *Kapes bentoni:* computed tomography of the skull and skeleton: *Papers in Palaeontology*, **v. 5**, p. 111–138.

Zahradnicek, O., Buchtova, M., Dosedelova, H., and Tucker, A.S., 2014, The development of complex tooth shape in reptiles: *Frontiers in Physiology*, **v. 5**, n. 74.

Zheng, D., Chang, S.-C., Wang, H., Fang, Y., Wang, J., Feng, C., Xie, G., Jarzembowski, E. A., Zhang, H., and Wang, B., 2018, Middle–Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China: *Science Advances*, **v. 4**, n. eaat1380.

https://doi.org/10.1017/jpa.2025.10195 Published online by Cambridge University Press