



Revealing the use of dental indices to infer taxonomic variation in sauropod dinosaurs

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Abstract: Sauropod teeth are commonly categorized taxonomically by two well-established measurement indices: slenderness index (SI; apicobasal height/mesiodistal width), which quantifies breadth, and compression index (CI; labiolingual width/mesiodistal width), which quantifies cross-sectional circularity. Although both indices are used to infer high-level taxonomic affinities, little is known about the linear relationships between the constituent measurements or how the indices vary intra-cranially and at lower taxonomic levels. Here, we evaluate these relationships using a novel dataset of sauropod teeth ($N = 898$) spanning all major sauropod groups. Results for both indices indicate significant differential scaling within Sauropodomorpha, both in slope and elevation. Broad-crowned sauropods mostly display positive allometry in SI compared to isometry in narrow-crowned sauropods. However, this distinction is less clear with CI as most sauropods display isometry, whilst non-sauropod sauropodomorphs (e.g. Plateosauridae)

display positive allometry. An ANOVA reveals SI varies significantly with genus and tooth position. Specifically, jaw type (maxilla and dentary) is significant within Plateosauridae, whilst tooth position is significant within titanosaurs. Overall, variation within CI is restricted to genus. Our findings reveal that whilst indices have taxonomic utility, there are caveats. The measurements used to calculate the indices exhibit significant allometry, indicating that index values are size-dependent. Furthermore, the indices may not accurately reflect size heterodont conditions present among early-branching sauropodomorphs. Our study highlights the importance of quantifying taxonomic relationships of measurement data, which can be used to inform hypotheses regarding the physiological and palaeoecological drivers influencing tooth shape evolution.

Key words: sauropod, dinosaur, teeth, slenderness index, compression index, heterodonty.

THE teeth of most Mesozoic dinosaurs were continuously replaced throughout their lives, a condition referred to as polyphyodonty. Combined with a high resistance to post-mortem taphonomic processes, teeth have great preservational potential, leading to a comparatively richer fossil record than other skeletal elements (Argast *et al.* 1987), with implications for evaluating taxonomic diversity and ecology within given clades and over time (e.g. Chure *et al.* 2010; García & Zurriaguz 2016). Sauropodomorphs were the largest terrestrial vertebrates, reaching sizes of up to 30–40 m in length and masses of up to 90 tonnes (Benson *et al.* 2014). Such large bodies would have required large quantities of food to sustain metabolic processes, and the constant tooth–food and tooth–tooth interactions lead to rapid wear. In the long term, this is expected to create selection pressure for dental adaptations that reduce wear incurred during feeding (Hummel *et al.* 2008; Sander *et al.* 2011). However, unlike other terrestrial herbivores (e.g. mammals and ornithischian dinosaurs), which increase dental

complexity, sauropodomorphs are hypothesized to have simplified their teeth and increased replacement rates in association with gigantism (Sander *et al.* 2011; Melstrom *et al.* 2021). Accordingly, tooth shape should be generally linked to sauropodomorph evolution, making teeth an important proxy for inferring ecological and taxonomic diversity (Buffetaut *et al.* 2006; Vullo *et al.* 2007; Vullo & Néraudeau 2010; Ósi *et al.* 2017; Becerra *et al.* 2018; Frauenfelder *et al.* 2020; Poropat *et al.* 2022).

Taxonomic identification of sauropodomorph teeth has previously relied on a combination of two indices: the slenderness index (SI; Upchurch 1998) and the compression index (CI; Díez Díaz *et al.* 2013). The SI is the ratio of crown apicobasal height to mesiodistal width where low values describe ‘broad-crowned’ teeth, and increasingly larger values describe ‘narrow-crowned’ teeth. In its original description, an SI of 4 served as a general threshold between the two types, defined using two phylogenetic characters (Upchurch 1998): one denoting those taxa with the broadest crowns ($SI < 3$) from those with an SI of about 4, and

another denoting the narrowest crowns ($SI > 5$) from more generally broad morphologies ($SI < 4$) (Fig. 1). Since then, threshold values have varied, but nonetheless remain the predominant approach for defining the two tooth categories (Barrett *et al.* 1998, 2002; Chure *et al.* 2010; García & Cerda 2010; Saegusa & Tomida 2011; Díez Díaz *et al.* 2012, 2013; Tschopp *et al.* 2015). While the dichotomy is arbitrary (e.g. Fig. 1), there is evident taxonomic significance, as the teeth of diplodocids and some titanosaurs are regarded as apomorphically ‘narrow-crowned’ compared to earlier-branching groups that fall into the plesiomorphic ‘broad-crowned’ category (Chure *et al.* 2010).

However, using SI has several shortcomings, as is often the case when using a single continuous variable for taxonomic discrimination. The ‘broad’ and ‘narrow’ categories are end members of a unimodal continuum (as defined by Mannion *et al.* 2013; Fig. 1), and intermediate tooth morphologies exist, such as in brachiosaurids and early-branching somphospondylans (Chure *et al.* 2010;

Martínez *et al.* 2016). Accordingly, it may be unjustified to place any threshold between ‘broad’ and ‘narrow’ crowns. Secondly, slenderness describes only one aspect of variation in dental shape and so cannot always taxonomically discriminate between certain groups (e.g. ‘narrow-crowned’ sauropodomorphs; Calvo 1994; García *et al.* 2010). Thirdly, the amount of apical wear can greatly influence the measured SI values. For instance, 12–15% of the apicobasal height of a *Brachiosaurus* tooth can be obliterated by wear, and so taking only the unworn portion into account would result in a misleadingly low SI value (Christiansen 2000; Díez Díaz *et al.* 2012, 2013). Finally, interpreting SI at a taxonomic level requires further consideration of ontogenetic and positional variability (Wilson 2005; Chure *et al.* 2010; Díez Díaz *et al.* 2012, 2013; Royo-Torres & Upchurch 2012; Mocho *et al.* 2016, 2017; Averianov & Sues 2017; Britt *et al.* 2017; Holwerda *et al.* 2018; Moore *et al.* 2018; Royo-Torres *et al.* 2020).

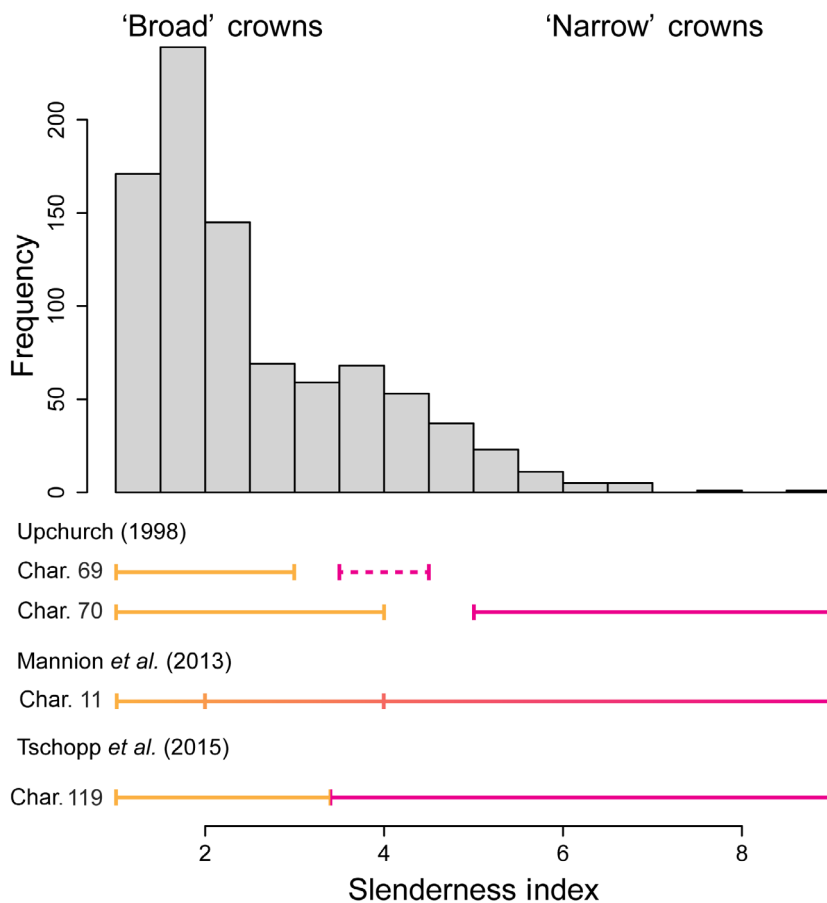


FIG. 1. Distribution of slenderness index values across Sauropodomorpha. Data are from the dataset compiled here. Figure highlights the lack of bimodal distribution between ‘broad’ and ‘narrow’ crowned sauropods, and examples of previously defined thresholds (Upchurch 1998; Mannion *et al.* 2013; Tschopp *et al.* 2015). Note that Mannion *et al.* (2013) treated the character as continuous, delineating three states to define synapomorphies. In all cases, yellow tones denote the plesiomorphic states, whereas pink tones denote apomorphic states.

The compression index (CI) is another shape proxy calculated from the ratio of labiolingual width to mesiodistal width of the crown at mid-height (Díez Díaz *et al.* 2013). The index measures circularity or eccentricity where CI values approaching one indicate teeth with sub-circular cross sections and those approaching zero represent labiolingually constricted teeth with sub-ovoid cross sections. In contrast to SI, no thresholds have been proposed that subdivide sauropodomorphs into groups based on the distribution of CI. However, CI has been primarily used to separate titanosaurs tooth morphotypes within a locality (Díez Díaz *et al.* 2013; Averianov & Sues 2017; Holwerda *et al.* 2018; Bindellini & Dal Sasso 2021). Accordingly, whether the CI is more broadly applicable taxonomically or ecologically is unknown.

There are limitations to the application of SI and CI for taxonomic discrimination of sauropodomorph teeth worth considering. For instance, Chure *et al.* (2010) examined the macroevolution of SI values across the Mesozoic, noting that whilst some sauropod groups differ (e.g. neosauropods and non-sauropod sauropodomorphs), many other groups overlap (e.g. non-sauropod sauropodomorphs and non-eusauropod sauropods). Furthermore, Holwerda *et al.* (2018) found that these indices could not differentiate between non-titanosaur titanosauriforms and titanosaurs. Given the overlap in SI values between sauropod groups and the unknown distribution of CI across all sauropodomorphs, these indices warrant further scrutiny. Critically, as with all ratios, the taxonomic utility of these indices depends on two major assumptions: (1) that the variables defining the ratio scale isometrically; and (2) that isometric scaling is true on both a general and group-specific level. By contrast, if allometry or differential scaling is found, index values will be size-dependent, and taxonomy cannot be interpreted directly.

This study aims to test the hypothesis that dental indices provide a robust and general proxy for sauropod taxonomic classification, filling in the aforementioned gaps in knowledge and addressing previously untested assumptions. We seek to: (1) evaluate the linear scaling relationship(s) of their constituent variables, testing for allometry and differential scaling; (2) determine the taxonomic accuracy of the indices as compared to the residuals obtained from the linear scaling analysis; and (3) identify and describe the variability of SI and CI along the maxillary and dentary tooththrows.

MATERIAL & METHOD

Dataset construction

The dataset comprises dental measurements taken from 898 sauropodomorph teeth. The three linear measurements that

define the indices include the maximum apicobasal length (ABL), maximum mesiodistal width (MDW), and maximum labiolingual width (LLW) (Fig. 2). Measurements were obtained from first-hand observations using a digital caliper or from published works (See Data S1). Data from published specimens were either extracted from tabulated data or descriptions where available or measured directly from scaled figures using Fiji v1.53f51 (Schindelin *et al.* 2012). As data were extracted from the literature, not all measurements could be obtained for every specimen: 887 teeth were used to evaluate ABL and MDW and 539 teeth were used to compare MDW and LLW.

Institutional abbreviations. NHMD, Natural History Museum of Denmark, Copenhagen, Denmark; SMA, Sauriermuseum Aathal, Aathal, Switzerland; USNM, National Museum of Natural History, Smithsonian Institute, Washington DC, USA; ZRC, Zoological Research Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore.

Sauropod classification

To explore the relationship between dental metrics and taxonomy, we classified each tooth into three classification schemes, each at a differing level of taxonomic inclusiveness and with a balance of monophyletic and paraphyletic groupings, following current understandings of family-level phylogenetic relationships (Fig. 3; see references below). Class assignments for each tooth were based on identifications from either the original publication, the Paleobiology Database (<https://paleobiodb.org>), or phylogenetic analyses (Gorscak *et al.* 2017; Sallam *et al.* 2018; Mannion *et al.* 2019; Royo-Torres *et al.* 2020; Schwarz *et al.* 2020; Beccari *et al.* 2021; Díez Díaz *et al.* 2021; Propat *et al.* 2021; Silva Junior *et al.* 2022).

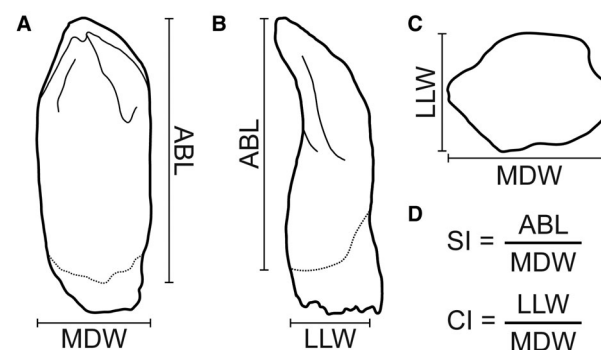
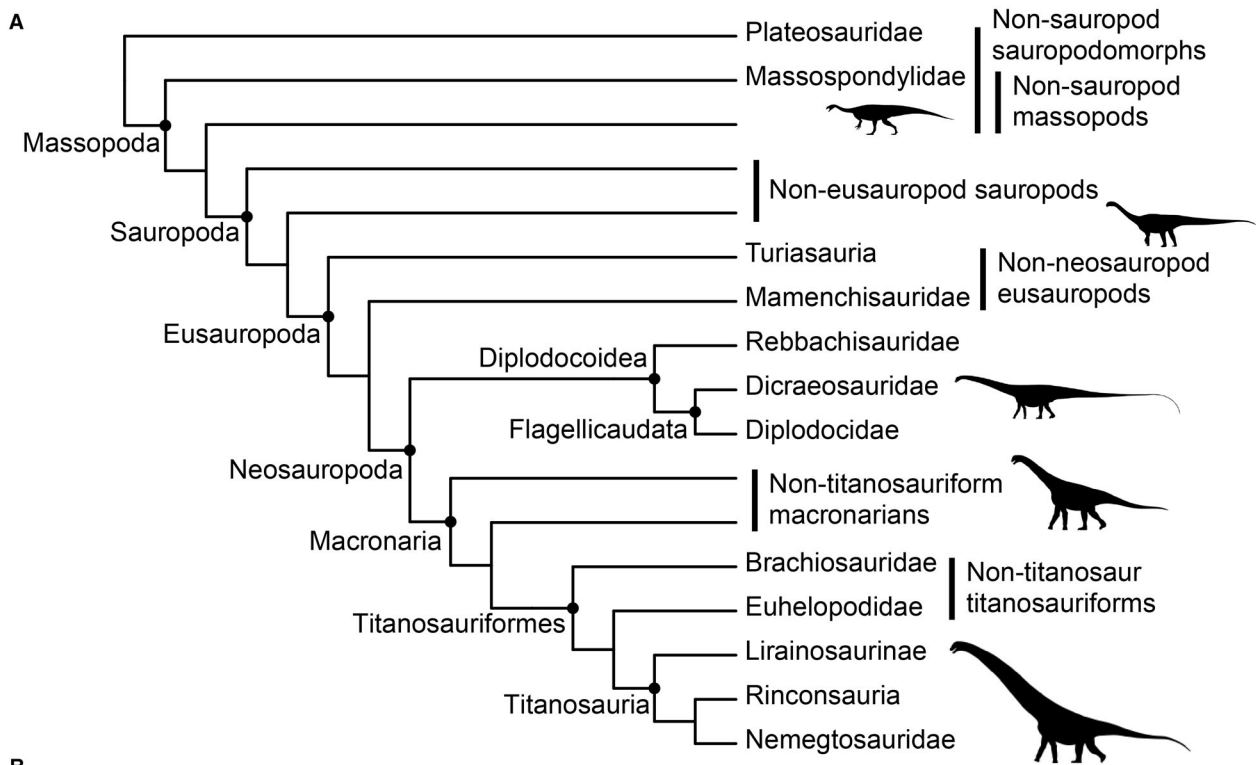


FIG. 2. Measurements and indices taken from the sauropodomorph tooth sample. Example based on *Camarasaurus* sp. (SMA 0002). Tooth in: A, lingual; B, profile; C, apical view. D, index calculations. **Abbreviations:** ABL, apicobasal length; CI, compression index; LLW, labiolingual width; MDW, mesiodistal width; SI, slenderness index.



B

Classification Scheme 1	Classification Scheme 2	Class. Scheme 3
Non-sauropod sauropodomorphs	Plateosauridae	
	Non-sauropod massopods	Massospondylidae
Non-eusauropod sauropods		
Non-neosauropod eusauropods	Mamenchisauridae	
	Turiasauria	
Diplodocoidea	Flagellicaudata	Diplodocidae
		Dicraeosauridae
Non-titanosauriform macronarians	Rebbachisauridae	
Titanosauriformes	Camarasauridae	
	Non-titanosaur titanosauriforms	Brachiosauridae
		Euhelopodidae
	Titanosauria	Lirainosaurinae
		Rinconsauria
Nemegtosauridae		

FIG. 3. Phylogenetic and taxonomic framework adopted in this study. A, general Sauropodomorpha phylogenetic relationships based on multiple phylogenetic analyses (see text for more details). B, the three taxonomic classification schemes (CS1, CS2 and CS3) used throughout. Sauropodomorph silhouettes are from Phylopic (<https://www.phylopic.org/>): *Plateosaurus*, *Diplodocus*, *Camarasaurus*, *Dreadnaughtus* by Scott Hartman (CC BY-NC-SA 3.0); *Patagosaur* by Smokeybjb (CC BY-SA 3.0).

Classification scheme 1 (CS1) contains the fewest and most inclusive groups, dividing all teeth into two clades and four grades. Classification scheme 2 (CS2) increases the number of monophyletic groups and reduces their inclusiveness, resulting in seven clades and two grades. Several taxa cannot be assigned to any of the classes defined in CS2, thereby excluding non-eusauropod sauropods (*Amygdalodon patagonicus* and *Pulanesaura eocollum*), non-neosauropod eusauropods (including *Bellusaurus sui*, *Jobaria* sp., *Lapparentosaurus* sp. and *Patagosaurus* sp.), non-sauropod sauropodomorphs (including *Pantyraco caducus*, *Saturnalia tupiniquim*, *Thecodontosaurus antiquus* and *Yimenosaurus youngi*), and non-titanosauriform macronarians, which could not be assigned beyond the levels defined by CS1. Consequently, 80 teeth with SI and 54 with CI values were excluded from CS2. Classification scheme 3 (CS3) further increases the number of monophyletic groups and restricts their inclusiveness, resulting in 13 clades. As in CS2, several taxa could not be assigned to one of the classes in CS3, thereby excluding non-sauropod massopods (including *Anchisaurus polyzelus*, *Leoneriasaurus taquetrensis*, *Melanorosaurus readi*, *Mussaurus patagonicus* and *Yunnanosaurus huangi*), non-titanosaur titanosauriforms (including *Europatitan eastwoodi*, *Ligabeusaurus* sp. and *Sibirotitan astrosacralis*), and titanosaurs (including *Alamosaurus* sp., *Karongasaurus* sp., *Malawisaurus dixeyi*, *Mongolosaurus haplodont*, *Petrobrasaurus peustohernandez*, *Pitekunsaurus macayai*, *Rapetosaurus* sp. and *Sarmientosaurus musachioi*). In total, 275 teeth with SI values and 251 with CI values were omitted from CS3.

The taxonomic groupings (and their composition) used in our classification schemes are defined as follows (see also Data S1): non-sauropod sauropodomorphs consist of those taxa traditionally referred to as 'prosauropods', including Plateosauridae and non-sauropod massopods (including Massospondylidae), as well as several non-sauropod sauropodomorphs not assigned to either clade. Given sampling limitations, LLW measurements of plateosaurids are limited to two specimens of *Issi saaneq* (NHMD 164741 and NHMD 164758). Non-eusauropod sauropods consist of *Amygdalodon patagonicus* and *Pulanesaura eocollum*. Non-neosauropod eusauropods include Mamenchisauridae, Turiasauria, and non-neosauropod eusauropods not assigned to either clade. Diplodocoidea includes Rebbachisauridae and Flagellicaudata (Diplodocidae and Dicraeosauridae). Non-titanosauriform macronarians include those teeth assigned to Camarasauridae and non-titanosauriform macronarians not assigned to a more exclusive clade. Titanosauriformes consist of titanosaurs and non-titanosaur titanosauriforms. The latter includes Brachiosauridae, Euhelopodidae, three species not assigned to either clade (*Europatitan eastwoodi*, *Ligabeusaurus leanzai* and *Sibirotitan astrosacralis*), and

isolated teeth referred to as indeterminate titanosauriform. Titanosauria includes Lirainosaurinae, Rinconsauria and Nemegtosauridae, eight species not assigned to the aforementioned clades, and any isolated teeth referred to an indeterminate titanosaur. Titanosaur phylogenetics can be highly unstable (e.g. Carballido *et al.* 2017; Mannion *et al.* 2019; Hechenleitner *et al.* 2020; Cerda *et al.* 2021; Navarro *et al.* 2022; Silva Junior *et al.* 2022), and rinconsaur monophyly and the positions of *Tapuiasaurus* and *Nemegtosaurus* require further clarification. While some previous analyses recovered a polyphyletic Rinconsauria (Mannion *et al.* 2019), most recent publications support its monophyly (e.g. Navarro *et al.* 2022; Silva Junior *et al.* 2022), but more importantly, they support the close relationship between the two rinconsaurs sampled here, relative to other taxa in the dataset: *Rinconsaurus* and *Maxakalisaurus*. *Tapuiasaurus* is here placed within Nemegtosauridae along with *Nemegtosaurus*, following Poropat *et al.* (2016). We acknowledge that the phylogenetic affinities of either taxon are volatile, and indeed the family may not be valid (see Cerda *et al.* 2021; Navarro *et al.* 2022). However, saltasaurs are represented by a single *Alamosaurus* tooth, and thus grouping *Tapuiasaurus* and *Nemegtosaurus* in CS3 is unlikely to affect the analysis as a whole.

Linear models and comparisons

All analyses were conducted in R v4.3.0 (R Core Team 2020; Appendix S1). To explore the linear scaling between each measurement, we used standardized major axis (SMA) scaling, implemented in the R package *smatr* v3.4-8 (Warton *et al.* 2012). This scaling approach was preferred as a dependent-independent relationship between the measurements cannot be assumed, and SMA will minimize the residual variation across both the x and y axes. Two broad-scale linear models were generated to compare tooth measurements:

$$SI_{SMA} = ABL \sim MDW$$

$$CI_{SMA} = LLW \sim MDW$$

All measurements were \log_{10} transformed, and residuals of each model were visually inspected to ensure a normal distribution. Henceforth, all linear models comparing MDW to ABL will be referred to as SI_{SMA} ; similarly, MDW to LLW linear models are called CI_{SMA} .

Standardized major axis coefficients (i.e. slope (m) and elevation (b)) were calculated according to the sample size of each model (SI_{SMA} : N = 901; CI_{SMA} : N = 542) and for each of the three aforementioned classification schemes. For each classification scheme, slopes were compared using the (Bartlett-corrected) likelihood ratio test,

and elevations were compared using the Wald statistic test, as implemented by *smatr* (Warton *et al.* 2006). The elevation comparisons assume a common slope across the sample, so comparisons were limited to those clades with non-differential slopes. Accordingly, elevation comparisons in the results section correspond to those following a common slope. In addition to coefficient comparisons, clades and grades within a classification scheme were compared using their residual values from the overall SI_{SMA} and CI_{SMA} linear models. Residuals were statistically compared using a one-way analysis of variance (ANOVA), followed by *post hoc* Tukey's tests to determine the significant differences between classification levels, and visualized using boxplots. Comparisons were only made between clades or grades with greater than five specimens. Accordingly, Dicraeosauridae was excluded from SI_{SMA} comparisons, and non-sauropod massopods and Massospondylidae were excluded from the CI_{SMA} comparisons. Camarasauridae is represented by only one specimen (SMA 0002), which is the same for both SI_{SMA} and CI_{SMA} . In CI_{SMA} the non-sauropod sauropodomorph sample is dominated by the plateosaurid *Issi saaneq* (c. 97%). Finally, to test the general fidelity of the indices against the comparisons established by the linear models, SI and CI were regressed against the residuals of their respective linear models (i.e. SI_{SMA} and CI_{SMA} , respectively). Correlations were determined by calculating the Pearson correlation coefficient (r) and testing them against a value of zero. If indices depict the same signal as the linear model residuals, then a 1:1 and high R^2 relationship is expected.

Evaluating variation along the tooth row

To evaluate the SI and CI variation along the tooth row (i.e. intra-individual variation, corresponding to shape heterodonty), some teeth were assigned a position number within their associated bone (either maxilla or dentary) and designated as either right or left. Comparisons were made between teeth that could be assigned to a single specimen using a three-way non-parametric ANOVA, as implemented in the *geomorph* v4.0.5 package (Baken *et al.* 2021) to explore SI or CI as a function of tooth position, side, and jaw bone. For SI, positional data were sampled from specimens representing eight taxa:

Camarasaurus sp., *Issi saaneq*, *Losillasaurus giganteus*, *Mamenchisaurus youngi*, *Nemegtosaurus mongoliensis*, *Plateosaurus trossingensis*, *Sarmientosaurus musacchioi* and *Tapuiasaurus macedoi* (see Data S1 for specimen details). For CI, five taxa were sampled: *Bajadasaurus pronuspinax*, *Issi saaneq*, *Losillasaurus giganteus*, *Nemegtosaurus mongoliensis* and *Sarmientosaurus musacchioi*. A secondary one-way ANOVA was limited to dentary teeth using four specimens (three for SI and two for CI), including *Brachiosaurus altithorax*, an undescribed diplodocid, *Camarasaurus* sp. and *Pantyraco caducus*.

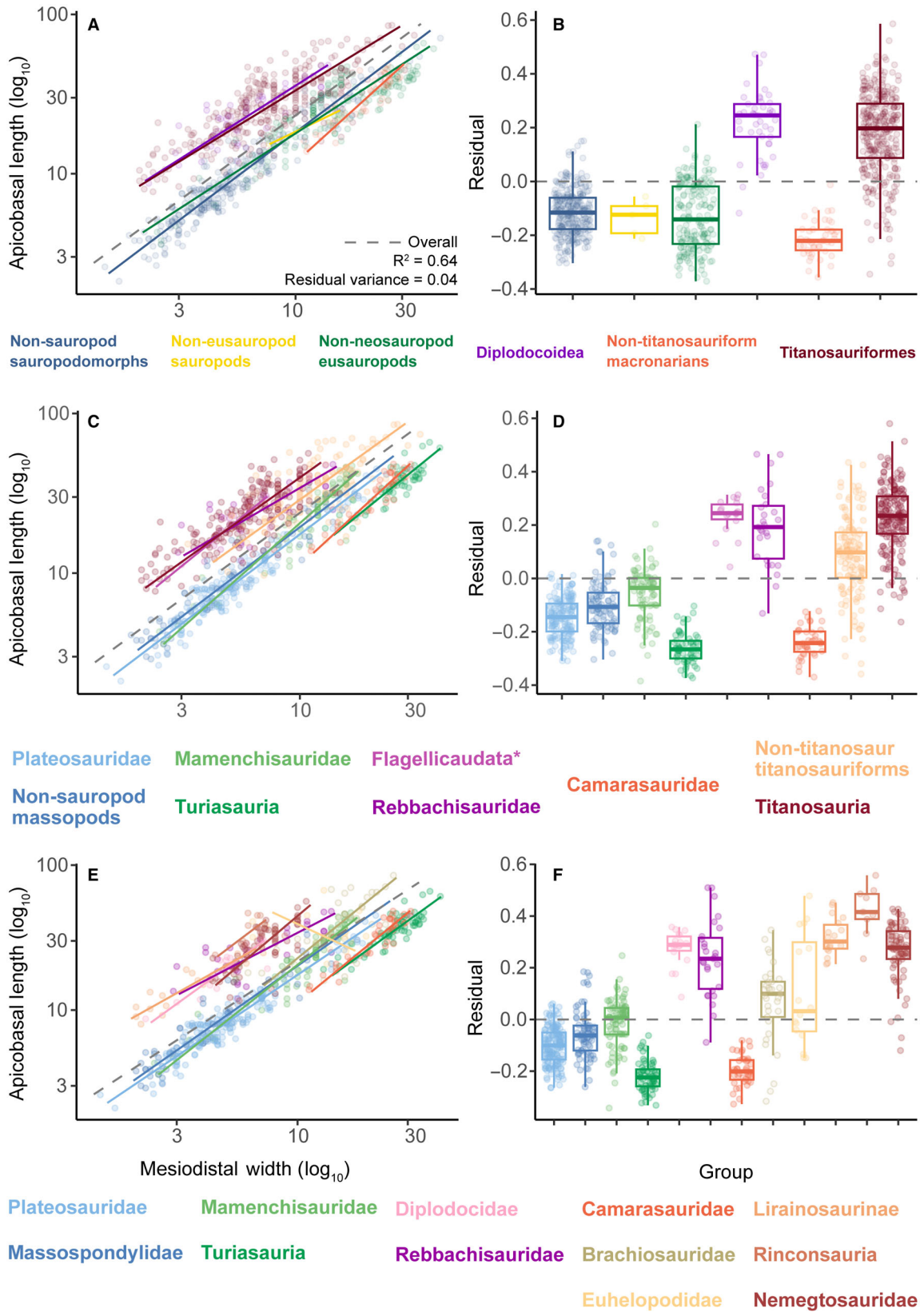
Finally, to test the relative importance of intra- and interspecific variation on SI and CI values, we conducted a clade/grade-level four-way non-parametric ANOVA. For SI, the aforementioned species were analysed together (i.e. Sauropodomorpha) or as part of Plateosauridae, non-neosauropod Eusauropoda or Titanosauria. For CI, all specimens were labelled as either Sauropodomorpha, Flagellicaudata or Titanosauria.

RESULTS

Linear models

Overall, a positive and significant relationship exists between mesiodistal width and both apicobasal length and labiolingual width (SI_{SMA} : $m = 1.03$, $R^2 = 0.64$; CI_{SMA} : $m = 1.13$, $R^2 = 0.81$, respectively; Figs 4, 5; Tables 1, 2). The relationship between ABL and MDW (i.e. SI_{SMA}) has a slope close to one that cannot be differentiated from isometry (Table 1). There is a positive allometric relationship for the CI_{SMA} model, suggesting that LLW increases at a faster rate relative to MDW (Table 2), although this is driven by the low LLW values relative to MDW observed in non-sauropod sauropodomorphs (Fig. 5). Despite the significant relationships, there is high residual variance, especially in the SI_{SMA} model, driven by high ABL values in diplodocoids and titanosauriforms relative to MDW (i.e. positive residuals) compared to other sauropodomorphs (Fig. 4). By contrast, residual variance in CI_{SMA} is largely driven by non-sauropod sauropodomorphs (Fig. 5), which have a higher slope than most other sauropods (Table 2), although this is possibly due to the sample being almost exclusively from a single species, *Issi saaneq*.

FIG. 4. Results of the linear models of apicobasal length and mesiodistal width (SI_{SMA}). A, C, E display the linear relationships; B, D, F display the residuals for each classification. A–B, classification scheme 1. C–D, classification scheme 2. E–F, classification scheme 3. Colours in A, C, E, correspond to those in B, D, F, and those used in Figure 3. The dashed grey lines illustrate the overall SI_{SMA} relationship of the entire sample. All measurements (in mm) were \log_{10} transformed. The negative relationship in euhelopodids is explored in Figure S4. *Abbreviation:* R^2 , coefficient of determination.



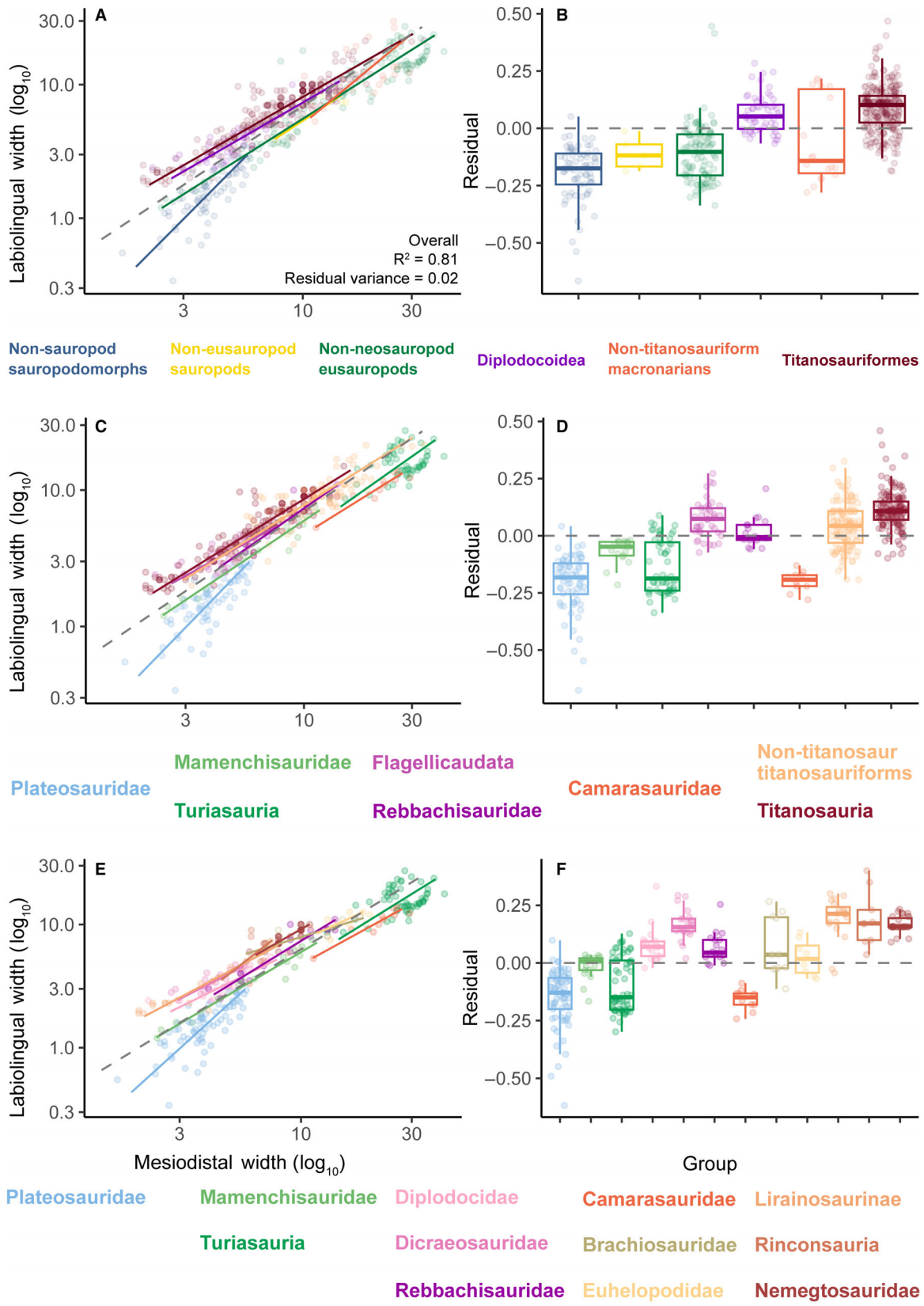


FIG. 5. Results of the linear models of labiolingual width and mesiodistal width (CI_{SMA}). A, C, E, display the linear relationships; B, D, F, display the residuals at each classification. A–B, classification scheme 1. C–D, classification scheme 2. E–F, classification scheme 3. Colours in A, C, E, correspond to those in B, D, F, and those used in Figure 3. The dashed grey lines illustrate the CI_{SMA} relationship of the entire sample. All measurements (in mm) were \log_{10} transformed. *Abbreviation:* R^2 , coefficient of determination.

Classification scheme 1. Group-level comparisons between the SI_{SMA} coefficients highlight six significantly different slopes and four allometric trajectories (Figs 4, S1; Table 1). Apicobasal length shows positive allometry with MDW (i.e. SI_{SMA}) in non-titanosauriform macronarians ($m = 1.27$) and has a significantly higher elevation than most other groups in this classification scheme (Fig. S1; Table 1). Positive allometry is also recovered in non-sauropod sauropodomorphs. By contrast, non-neosauropod eusauropods and titanosauriforms show negative allometry, with slopes significantly below other macronarians and non-sauropod sauropodomorphs. Of the compared elevations, all are significant except for non-eusauropod sauropods, which cannot be differentiated from non-neosauropod eusauropods and non-sauropod sauropodomorphs, and likewise, titanosauriforms cannot be differentiated from diplodocoids (Fig. S1).

Comparisons between groups within CS1 for CI_{SMA} (i.e. $LLW \sim MDW$) identify four significantly different slopes, ten different elevations, and two groups that show positive allometric scaling (Fig. S2; Table 2). Titanosauriforms are indistinguishable from diplodocoids in slope but can be differentiated in elevation, where titanosauriforms have a higher LLW than diplodocoids on average ($b = -0.11$ and -0.15 , respectively). Non-sauropod sauropodomorphs exhibit the highest slope ($m = 1.72$), which is positively allometric and significantly different from most other groups, excluding non-eusauropod sauropods and non-titanosauriform macronarians. The latter two share high slope coefficients, but isometry cannot be rejected (Table 2). Despite similar slopes, non-sauropod sauropodomorphs can be differentiated by elevation from non-eusauropod sauropods and non-titanosauriform macronarians ($b = -0.43$, -0.29 and -0.22 , respectively; Fig. S2). Non-neosauropod eusauropods follow a positive allometric pattern ($m = 1.08$) that can be differentiated from non-sauropod sauropodomorphs and titanosauriforms (Fig. S2). Its elevation ($b = -0.27$) significantly differs from diplodocoids ($b = -0.15$).

One-way ANOVA finds significant relationships between groups within CS1 and the residuals of SI_{SMA} and CI_{SMA} (Table 3). Across both models, a *post hoc* Tukey test finds that diplodocoids and titanosauriforms are different from all other groups except each other (Fig. S3), and the residuals of the remaining groups were indistinguishable, except for non-titanosauriform macronarians. Taxa within this group have lower MDW than ABL for a given tooth

size compared to non-neosauropod eusauropods and non-sauropod sauropodomorphs. Furthermore, non-sauropod sauropodomorphs have significantly lower CI_{SMA} residuals than non-titanosauriform macronarians and non-neosauropod eusauropods (Fig. S3).

Classification scheme 2. Taxonomic groups within CS2 reveal fewer significant slope differences than elevation for SI_{SMA} (11 and 32 differences, respectively; Fig. S1). Five groups show positive allometry (Table 1; Fig. 4C–D). Slopes for non-sauropod massopods and platesosaurids show positive allometry consistent with those calculated under CS1 (i.e. non-sauropod sauropodomorphs; Table 1). However, non-sauropod massopods exhibit significantly narrower teeth (i.e. higher elevation) than platesosaurids ($b = 0.2$ and 0.15 , respectively; Fig. S1). Subdivision of non-neosauropod eusauropods into mamenchisaurids and turiasaurs reveals indistinguishable positive allometry but significantly different elevations. Turiasaurs exhibit the lowest elevation sampled in this study ($b = -0.01$), significantly below all other sauropodomorphs, including camarasaurids ($b = 0.02$), indicating they have the broadest teeth overall. Diplodocoid subclades (Diplodocidae and Rebbachisauridae) do not differ in slope or elevation. When comparing narrow-crowned sauropods, there are no differences in the slopes of titanosauriform and diplodocoid groups. However, non-titanosaur titanosauriforms have a significantly lower elevation ($b = 0.35$) when compared to diplodocoids, rebbachisaurids, and titanosaurs ($b = 0.53$, 0.48 , and 0.52 , respectively; Fig. S1).

In CI_{SMA} , there are 7 slope and 23 elevation differences and one allometric relationship (Fig. S2; Table 2). Mamenchisaurids and turiasaurs do not differ in slope or elevation. However, mamenchisaurids are shifted negatively compared to turiasaurs along their common slope and elevation (Wald statistic = 110, $p \approx 0$). Flagellicaudatans and rebbachisaurids cannot be differentiated from each other, nor can they be differentiated from non-titanosaur titanosauriforms in slope. However, both diplodocoid clades differ in elevation ($b = -0.17$ and -0.22 , respectively) from titanosaurs ($b = -0.13$; Fig. S1; Table 2). Camarasaurids ($b = -0.42$) differ in elevation from all sauropodomorph groups, including turiasaurs ($b = -0.35$). Turiasaurs and camarasaurids have the lowest elevation of all sauropods, indicative of their labiolingually narrow teeth. Notably, some turiasaur teeth are broader labiolingually compared to other known turiasaurs (Fig. 5C; see Discussion). If these teeth are removed,

TABLE 1. Linear scaling and allometric relationships of SI_{SMA} .

Group	n	Linear model results			Common-slope elevation (b)		Allometry
		Slope (m) (95% CI)	Intercept (95% CI)	R^2	Intercept (95% CI)		
Sauropodomorpha	887	1.025 (0.985 to 1.066)	0.341 (0.302 to 0.38)	0.643	NA	0	
Classification scheme 1							
Non-sauropod sauropodomorphs	284	1.059 (1.022 to 1.098)	0.201 (0.172 to 0.23)	0.905***	0.243 (0.221 to 0.265)	+	
Non-eusauropod sauropods	5	0.672 (0.314 to 1.436)	0.592 (-0.025 to 1.209)	0.793*	0.233 (0.117 to 0.349)	0	
Non-neosauropod eusauropods	184	0.909 (0.849 to 0.974)	0.344 (0.269 to 0.418)	0.777***	0.239 (0.202 to 0.276)	-	
Diplodocoidea	45	0.89 (0.736 to 1.076)	0.663 (0.528 to 0.798)	0.616***	0.578 (0.536 to 0.621)	0	
Non-titanosauriform macronarians	45	1.274 (1.128 to 1.438)	-0.203 (-0.41 to 0.005)	0.842***	0.161 (0.117 to 0.204)	+	
Titanosauriformes	324	0.858 (0.802 to 0.918)	0.665 (0.612 to 0.718)	0.621***	0.541 (0.511 to 0.571)	-	
Classification scheme 2							
Plateosauridae [†]	162	1.073 (1.022 to 1.127)	0.17 (0.131 to 0.209)	0.901***	0.15 (0.125 to 0.176)	+	
Non-sauropod massopods	90	1.076 (1.011 to 1.145)	0.212 (0.162 to 0.263)	0.914***	0.195 (0.165 to 0.225)	+	
Mamenchisauridae [†]	84	1.259 (1.165 to 1.36)	0.054 (-0.048 to 0.156)	0.876***	0.216 (0.177 to 0.255)	+	
Turiasauria [†]	62	1.151 (1.012 to 1.31)	-0.085 (-0.297 to 0.127)	0.75***	-0.013 (-0.062 to 0.035)	+	
Diplodocidae [†]	18	1.152 (0.913 to 1.452)	0.494 (0.303 to 0.684)	0.805***	0.528 (0.485 to 0.572)	0	
Rebbachisauridae [†]	27	0.824 (0.621 to 1.091)	0.71 (0.509 to 0.91)	0.52***	0.481 (0.412 to 0.55)	0	
Camarasauridae [†]	40	1.307 (1.164 to 1.467)	-0.259 (-0.462 to 0.056)	0.876***	0.016 (-0.031 to 0.064)	+	
Non-titanosaur titanosauriforms	132	1.022 (0.899 to 1.162)	0.438 (0.296 to 0.58)	0.451***	0.354 (0.31 to 0.398)	0	
Titanosauria	192	1.012 (0.926 to 1.106)	0.586 (0.517 to 0.655)	0.614***	0.52 (0.49 to 0.55)	0	
Classification scheme 3							
Massospondylidae	73	1.116 (1.029 to 1.21)	0.19 (0.127 to 0.252)	0.882***	0.178 (0.145 to 0.211)	+	
Brachiosauridae	33	1.297 (0.986 to 1.706)	0.061 (-0.366 to 0.488)	0.425***	0.252 (0.179 to 0.325)	0	
Euhelopodidae	16	-0.74 (-1.277 to 0.429)	2.334 (1.865 to 2.804)	0.001	0.3 (0.167 to 0.434)	NA	
Lirinosaurinae	18	0.893 (0.721 to 1.106)	0.691 (0.585 to 0.797)	0.835***	0.565 (0.517 to 0.612)	0	
Rinconosauria	9	1.205 (0.575 to 2.524)	0.583 (-0.208 to 1.373)	0.182	0.64 (0.548 to 0.732)	0	
Nemegtosauridae	71	1.347 (1.137 to 1.596)	0.303 (0.108 to 0.497)	0.495***	0.48 (0.439 to 0.521)	+	

[†]Groups that are in both CS2 and CS3; p-values associated with the slope significance (i.e. different from zero): *0.05 > p > 0.01, ***p < 0.001. Presence and direction of allometry are determined by the location of 1 relative to the slope 95% CI.

TABLE 2. Linear scaling and allometric relationships of CI_{SMA}.

Clade/Grade	n	Linear model results		R ²	Common-slope elevation (b)		Allometry
		Slope (m) (95% CI)	Intercept (95% CI)		Intercept (95% CI)		
Sauropodomorpha	539	1.132 (1.091–1.175)	–0.291 (–0.332 to –0.251)	0.808	NA	NA	+
Classification scheme 1							
Non-sauropod sauropodomorphs	71	1.719 (1.476–2.001)	–0.827 (–0.982 to –0.671)	0.596***	–0.426 (–0.462 to 0.389)	–0.426 (–0.462 to 0.389)	+
Non-eusauropod sauropods	5	1.129 (0.507–2.512)	–0.399 (–1.501 to 0.704)	0.767 [‡]	–0.289 (–0.418 to 0.159)	–0.289 (–0.418 to 0.159)	0
Non-neosauropod eusauropods	113	1.082 (1.01–1.159)	–0.337 (–0.429 to 0.245)	0.865***	–0.274 (–0.321 to 0.226)	–0.274 (–0.321 to 0.226)	+
Diplodocidea	58	0.987 (0.889–1.095)	–0.121 (–0.199 to 0.043)	0.848***	–0.152 (–0.184 to 0.119)	–0.152 (–0.184 to 0.119)	0
Non-titanosauriform macronarians	18	1.418 (0.915–2.198)	–0.713 (–1.537 to 0.112)	0.271*	–0.216 (–0.321 to 0.111)	–0.216 (–0.321 to 0.111)	0
Titanosauriformes	274	0.979 (0.937–1.023)	–0.071 (–0.111 to 0.032)	0.864***	–0.114 (–0.147 to 0.082)	–0.114 (–0.147 to 0.082)	0
Classification scheme 2							
Plateosauridae [†]	69	1.708 (1.464–1.992)	–0.823 (–0.979 to 0.666)	0.598***	–0.457 (–0.497 to 0.417)	–0.457 (–0.497 to 0.417)	+
Mamenchisauridae [†]	17	1.113 (0.991–1.25)	–0.337 (–0.441 to 0.234)	0.955***	–0.31 (–0.357 to 0.264)	–0.31 (–0.357 to 0.264)	0
Turiasauria [†]	57	1.17 (0.919–1.491)	–0.481 (–0.892 to 0.07)	0.18***	–0.349 (–0.42 to 0.279)	–0.349 (–0.42 to 0.279)	0
Flagellicaudata	40	0.905 (0.74–1.107)	–0.06 (–0.183 to 0.063)	0.619***	–0.174 (–0.213 to 0.135)	–0.174 (–0.213 to 0.135)	0
Rebbachisauridae [†]	18	1.16 (0.99–1.359)	–0.293 (–0.465 to 0.122)	0.91***	–0.219 (–0.273 to 0.165)	–0.219 (–0.273 to 0.165)	0
Camarasauridae [†]	10	1.034 (0.784–1.365)	–0.36 (–0.748 to 0.029)	0.881***	–0.418 (–0.494 to 0.342)	–0.418 (–0.494 to 0.342)	0
Non-titanosaur titanosauriforms	123	1.032 (0.938–1.136)	–0.141 (–0.245 to 0.038)	0.716***	–0.189 (–0.237 to 0.141)	–0.189 (–0.237 to 0.141)	0
Titanosauria	151	1.032 (0.972–1.094)	–0.097 (–0.145 to 0.05)	0.867***	–0.133 (–0.168 to 0.097)	–0.133 (–0.168 to 0.097)	0
Classification scheme 3							
Diplodocidae	18	0.921 (0.709–1.197)	–0.11 (–0.283 to 0.062)	0.75***	–0.251 (–0.314 to 0.189)	–0.251 (–0.314 to 0.189)	0
Dicraeosauridae	22	0.967 (0.729–1.281)	–0.067 (–0.243 to 0.109)	0.625***	–0.166 (–0.219 to 0.114)	–0.166 (–0.219 to 0.114)	0
Brachiosauridae	11	0.575 (0.384–0.859)	0.323 (0.069 to 0.577)	0.699***	–0.257 (–0.377 to 0.137)	–0.257 (–0.377 to 0.137)	–
Euhelopodidae	8	0.887 (0.434–1.81)	–0.021 (–0.832 to 0.79)	0.397 [‡]	–0.301 (–0.419 to 0.182)	–0.301 (–0.419 to 0.182)	0
Lirainosaurinae	19	1.001 (0.82–1.222)	–0.071 (–0.193 to 0.051)	0.846***	–0.142 (–0.202 to 0.081)	–0.142 (–0.202 to 0.081)	0
Rinconosauria	9	1.475 (0.694–3.135)	–0.42 (–1.411 to 0.57)	0.143	–0.138 (–0.256 to 0.019)	–0.138 (–0.256 to 0.019)	0
Nemegtosauridae	31	1.072 (0.898–1.279)	–0.11 (–0.29 to 0.069)	0.781***	–0.16 (–0.225 to 0.095)	–0.16 (–0.225 to 0.095)	0

[†]Groups that are in both CS2 and CS3; p-values associated with the slope significance (i.e. different from zero). [‡]0.1 > p > 0.05; *0.05 > p > 0.01; ***p < 0.001. Presence and direction of allometry are determined by the location of 1 relative to the slope 95% CI.

TABLE 3. One-way ANOVAS of SI_{SMA} and CI_{SMA} residuals as a function of classification scheme.

Linear model	Classification scheme	Term	Degrees of freedom	Sum of squares	Mean squares	F-value
SI_{SMA}	CS1	Data	5	21.538	4.308	292.708***
		Residuals	881	12.965	0.015	–
	CS2	Data	8	23.889	2.986	259.633***
		Residuals	798	9.178	0.012	–
	CS3	Data	11	18.104	1.646	172.916***
		Residuals	601	5.720	0.010	–
CI_{SMA}	CS1	Data	5	6.339	1.268	105.438***
		Residuals	533	6.409	0.012	–
	CS2	Data	8	6.748	0.843	90.058***
		Residuals	477	4.468	0.009	–
	CS3	Data	11	5.101	0.464	48.067***
		Residuals	277	2.672	0.010	–

*** $p < 0.001$

the turiasaur trajectory reveals a higher, positively allometric slope ($m = 1.24$ (95% CI: 1.03–1.5), $b = -0.68$).

As with CS1, one-way ANOVAS of the residuals using CS2 were significant (Table 3). A *post hoc* Tukey test using the SI_{SMA} residuals shows that the following groups cannot be differentiated statistically (Fig. S3): (1) camarasaurids and turiasaurs; (2) diplodocids, rebbachisaurids and titanosaurs; and (3) mamenchisaurids and non-sauropod massopods. The *post hoc* Tukey test of the CI_{SMA} residuals found significant differences between plateosaurids and all other groups except camarasaurids (Fig. S3). The plateosaurid representatives in this model, two specimens of *Issi saaneq* (NHMD 164741 and NHMD 164758), have the lowest residuals in our sample (Fig. 5D). Rebbachisaurids can be differentiated from titanosaurs but not flagellicaudatans or non-titanosaur titanosauriforms. Finally, there is a significant difference between non-titanosaur titanosauriforms and titanosaurs, despite the substantial residual overlap (Figs 5D, S3). Across both SI_{SMA} and CI_{SMA} , camarasaurids and turiasaurs have the lowest residuals of all sauropod groups, characteristic of their broad and labiolingually compressed teeth. By contrast, rebbachisaurids, flagellicaudatans, non-titanosaur titanosauriforms and titanosaurs have tall, narrow teeth with subcircular crowns and display the highest residuals (Figs 4D, 5D).

Classification scheme 3. Most non-titanosauriform clades represented in CS3 correspond to groupings used in CS2 and do not need to be redescribed here. Of the five titanosauriform subclades, euhelopodids exhibit negative slopes in the SI_{SMA} model (i.e. $m < 0$), although the slope coefficient is not significant (Table 1), and further inspection indicates that the apparent negative slopes are driven by a combination of intergeneric slenderness variation (i.e. *Huabeisaurus* has comparatively narrower teeth than *Euhelopus*), low sampling,

and low range in measurements (Fig. S4). Accordingly, we do not compare this slope; elevation can be compared as it shares the common slope with other clades.

In the SI_{SMA} models, brachiosaurids and lirainosaurines cannot be differentiated from isometry. However, they have weakly differential slopes. Brachiosaurids also differ in slope from rebbachisaurids (Fig. S1; Table 1) and have the lowest elevation of all sauropods ($b = 0.25$). Brachiosaurids differ in elevation from diplodocids ($b = 0.53$), nemegtosaurids ($b = 0.48$), and rinconsaurs ($b = 0.64$), but not euhelopodids ($b = 0.3$; Fig. S1). Rinconsaurs are poorly sampled compared to other clades, yet possess the highest elevation ($b = 0.64$), differing from all other sauropodomorph clades (Fig. S1). Nemegtosaurids are the only titanosauriforms showing positive allometry (Table 1) and can be differentiated from lirainosaurines. Nemegtosaurids are also significantly different in elevation compared to most other groups and differ in slope from rebbachisaurids. However, nemegtosaurids are indistinguishable from diplodocids in slope and elevation (Fig. S1; Table 1).

In the CI_{SMA} model, all three diplodocoid clades have slopes indistinguishable from isometry (Table 2). Only the dicraeosaurids, limited to *Bajadasaurus pronospinax*, differ in elevation from rebbachisaurids and diplodocids ($b = -0.17$, -0.22 and -0.25 , respectively; Fig. S2). Among titanosauriforms, rinconsaurs exhibit a non-significant slope that cannot be interpreted. However, once forced to a common slope, its elevation ($b = -0.14$) is different from all non-titanosauriform sauropodomorphs, except for the dicraeosaurid *Bajadasaurus pronospinax* (Fig. S2). Brachiosaurids show negative allometry (Table 2), significantly different from all other sauropodomorphs except euhelopodids. There are no significant differences in slope or elevation among titanosaurs, and none can be differentiated from the dicraeosaurid *Bajadasaurus pronospinax*. However, lirainosaurines and nemegtosaurids ($b = -0.14$ and -0.16) can be

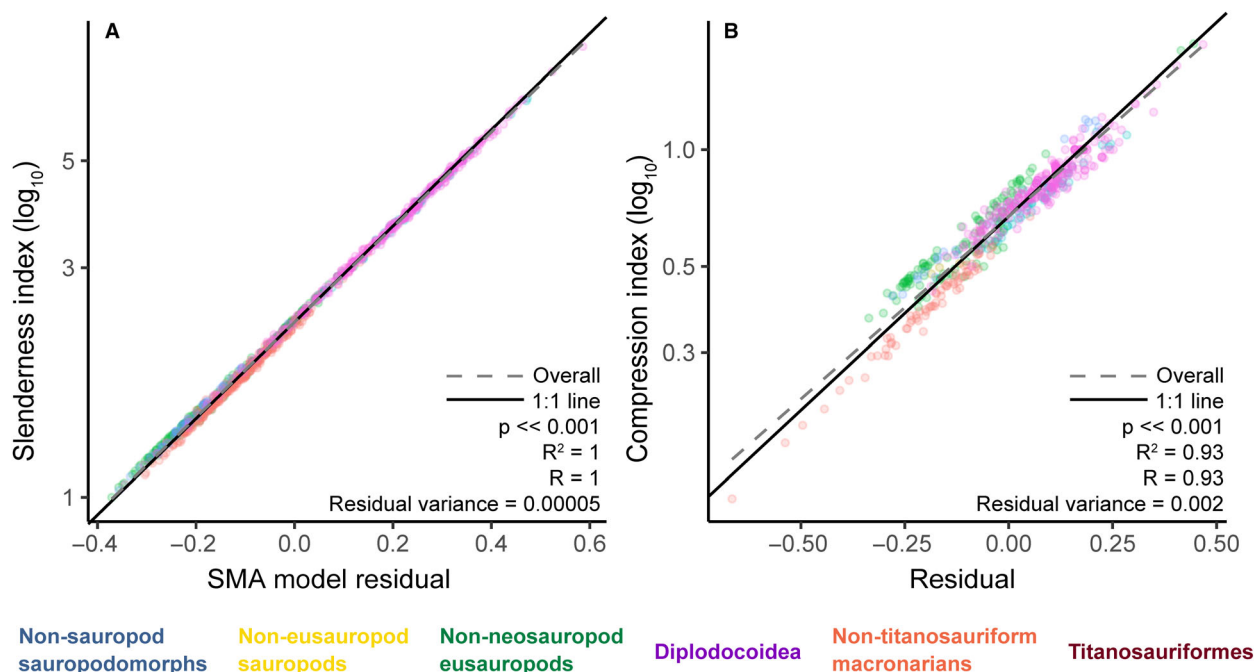


FIG. 6. Correlation between linear model residuals and their respective indices. A, SI_{SMA} residuals vs SI (\log_{10}). B, CI_{SMA} residuals vs CI (\log_{10}). The colour scheme follows CS1 (Fig. 3). The black solid line represents the 1:1 line; the dashed grey lines are those of best-fit under a standardized major axis model. *Abbreviations:* p, probability value; R, adjusted coefficient of correlation; R^2 , coefficient of determination.

differentiated in elevation from rebbachisaurids and diplodocids (Fig. S2).

Residuals of the SI_{SMA} and CI_{SMA} models are significantly related to CS3 (Table 3). *Post hoc* Tukey tests of the SI_{SMA} residuals indicate significant differences across almost all clades used in CS3 (Fig. S3). Mamenchisaurids cannot be differentiated from massospondylids, nor can the broad-crowned turiasaurs and camarasaurids. Brachiosaurids are similar to euhelopodids, but significantly different from all other clades. ‘Narrow-crowned’ sauropods (i.e. titanosaurs and diplodocoids) cannot be differentiated based on residual values except for rinconsaurs (Figs 5F, S3). On average, rinconsaurs exhibit the highest residual values and differ significantly from other ‘narrow-crowned’ clades except for lirainosaurines. Of the CI_{SMA} model residuals, no significant differences are recovered between diplodocoids (Fig. S3) despite seemingly higher residual values in *Bajadasaurus pronuspinax* compared to diplodocids and rebbachisaurids (Fig. 5F). As was the case in SI_{SMA} , the CI_{SMA} residuals cannot differentiate between brachiosaurids and euhelopodids. Similarly, titanosaurs are also indistinguishable from each other. In contrast, euhelopodids significantly differ from all titanosaur clades (Fig. S3). Of the ‘narrow-crowned’ clades, lirainosaurines are different from rebbachisaurids and diplodocids, and rebbachisaurids are different from nemegtosaurids.

Sauropod tooth indices vs residuals

A correlation between the SI_{SMA} residuals and the $\log_{10} SI$ reveals a very strong relationship ($m = 0.99$, standard error = 0.001). In addition, the residual variance is exceedingly low, with no outliers (Fig. 6A). Notably, the relationship is significantly different from a perfect 1:1 line ($r = -0.31$, $p \approx 0$). Teeth with high residuals (i.e. >0) tend towards lower SI values compared to their residuals, whereas teeth with lower residuals (i.e. <0) tend towards larger SI values (Fig. 6A).

A strong linear correlation exists between CI_{SMA} residuals and $\log_{10} CI$ ($m = 0.94$, standard error = 0.01), but with a substantially higher residual variance than the SI patterns described above. For instance, data points corresponding to non-sauropod sauropodomorphs (corresponding largely to *Issi saaneq*) are consistently below the best-fit line, indicating lower CI values given their residuals. In contrast, non-titanosauriform macronarians and most non-neosauropod eusauropods occur above the best-fit line, suggesting higher CI values than expected from their CI_{SMA} residuals. A 1:1 relationship between CI and CI_{SMA} residuals can be rejected ($r = -0.22$, $p = 0.0000001$), indicative of lower CI values corresponding to relatively high residuals and vice-versa.

TABLE 4. Results of the Procrustes ANOVA quantifying the variation of SI as a function of tooth position, side, bone of attachment, and genus for 16 taxa/grades.

Taxon/Grade	n	Partial R^2 values				
		Genus	Bone of attachment	Side	Tooth position	Residuals
Sauropodomorpha	347	0.722***	0.001	0.001	0.025***	0.151
Plateosauridae	92	0.002	0.269***	0.012	0.002	0.635
<i>Plateosaurus trossingensis</i>	26	–	0.182*	0	0.092 [‡]	0.609
<i>Issi saaneq</i>	30	–	0.164*	0.073 [‡]	0.011	0.602
<i>Pantydraco caducus</i>	9	–	–	–	0.525*	0.475
Non-neosauropod eusauropods	97	0.65***	0.003	0.001	0.206***	0.269
<i>Mamenchisaurus youngi</i>	62	–	0.064**	0.001	0.387***	0.448
<i>Mamenchisaurus sinocanadorum</i>	11	–	–	–	0.851***	0.149
<i>Losillasaurus giganteus</i>	24	–	0.652***	0.007	0.223**	0.279
Diplodocidae indet.	15	–	–	–	0.321*	0.679
<i>Camarasaurus</i> sp.	33	–	0.09*	0.127*	0.305***	0.427
<i>Brachiosaurus altithorax</i>	10	–	–	–	0.07	0.93
<i>Sarmientosaurus musacchioi</i>	30	–	0.269**	0.067 [‡]	0.205**	0.5
Titanosauria	87	0.292***	0	0.026 [‡]	0.082**	0.556
<i>Tapuiasaurus macedoi</i>	36	–	0.054	0.017	0.161*	0.7
<i>Nemegtosaurus mongoliensis</i>	21	–	0	0.004	0.068	0.929

p-values relative to an R^2 value of zero: [‡]0.1 > p > 0.05; *0.05 > p > 0.01; **0.01 > p > 0.001; ***p < 0.001.

Tooththrow variation

Across sauropodomorphs, SI varies significantly with genus and tooth position, but not bone of attachment or side (Table 4). In order of explanatory power, genus explains c. 72% of the SI variance, followed by tooth position (2.5%). In plateosaurids, genus does not explain SI variance, and jaw type significantly explains 27% of the variance with a large outstanding residual variance. At the species level, tooth position is not a significant factor driving SI in this group (Fig. 7A). By contrast, a weakly significant negative relationship exists between tooth position and SI in *Pantydraco caducus*, indicating an overall posterior decrease in SI along the dentary (Fig. 7B).

Among non-neosauropod eusauropods, genus significantly explains most of the variance (c. 65%), followed by tooth position (c. 21%). At the species level, tooth position is significant across all three studied taxa. Tooth position in both *Mamenchisaurus* species significantly explains much of the SI variance (Table 4), where SI decreases from approximately 3 in anterior teeth to nearly 1 in posterior teeth (Fig. 7). Bone of attachment is also significant within *Mamenchisaurus youngi* (c. 6%), with dentary teeth exhibiting lower SI values on average than maxillary teeth (Table 5). Differences between maxillary and dentary teeth were particularly strong in *Losillasaurus giganteus*, accounting for 65% of the SI variance. Dentary teeth exhibit significantly higher SI values than maxillary teeth (Table 5).

Slenderness index changes significantly along the dentary of an undescribed diplodocid (cast of ZRC 2.7076), with

lower SI values posteriorly. In the macronarian *Camarasaurus* sp. (SMA 0002), c. 31% of the SI variance is explained by tooth position, decreasing along the jaw. By contrast, c. 9% of the variance is explained by the bone of attachment, with the dentary exhibiting slightly higher SI values (Table 5). *Camarasaurus* sp. (SMA 0002) is the only specimen to produce significant differences in SI between left and right jaws (c. 13%), with teeth from the right jaw having higher SI values on average ($SI_{\text{left}} = 1.31 \pm 0.13SD$ vs $SI_{\text{right}} = 1.52 \pm 0.22SD$). Slenderness index does not vary as a function of tooth position in the dentary of *Brachiosaurus altithorax*. Within Titanosauria, genus explains c. 29% of the SI variance, followed by tooth position (c. 8%). Slenderness index significantly decreases posteriorly along the tooth rows of *Sarmientosaurus musacchioi*. Bone of attachment also explains a significant component of SI variance, with dentary teeth possessing higher SI values on average (Table 5). Tooth position only significantly explains c. 16% of the variance in SI of *Tapuiasaurus macedoi*, with values decreasing along the tooth row. Finally, in *Nemegtosaurus mongoliensis*, combined factors explain a non-significant component of variance (c. 7%), indicating highly consistent SI values in its mouth (Table 5).

The CI in sauropodomorphs varies mostly as a function of generic diversity (c. 72%; Table 6). Similar patterns are observed across flagellicaudatans and titanosaurs. The remaining three explored factors explain comparatively minimal CI variance (Table 6). Compression index variance is significantly related to sidedness within non-neosauropod sauropodomorphs (i.e. *Issi*

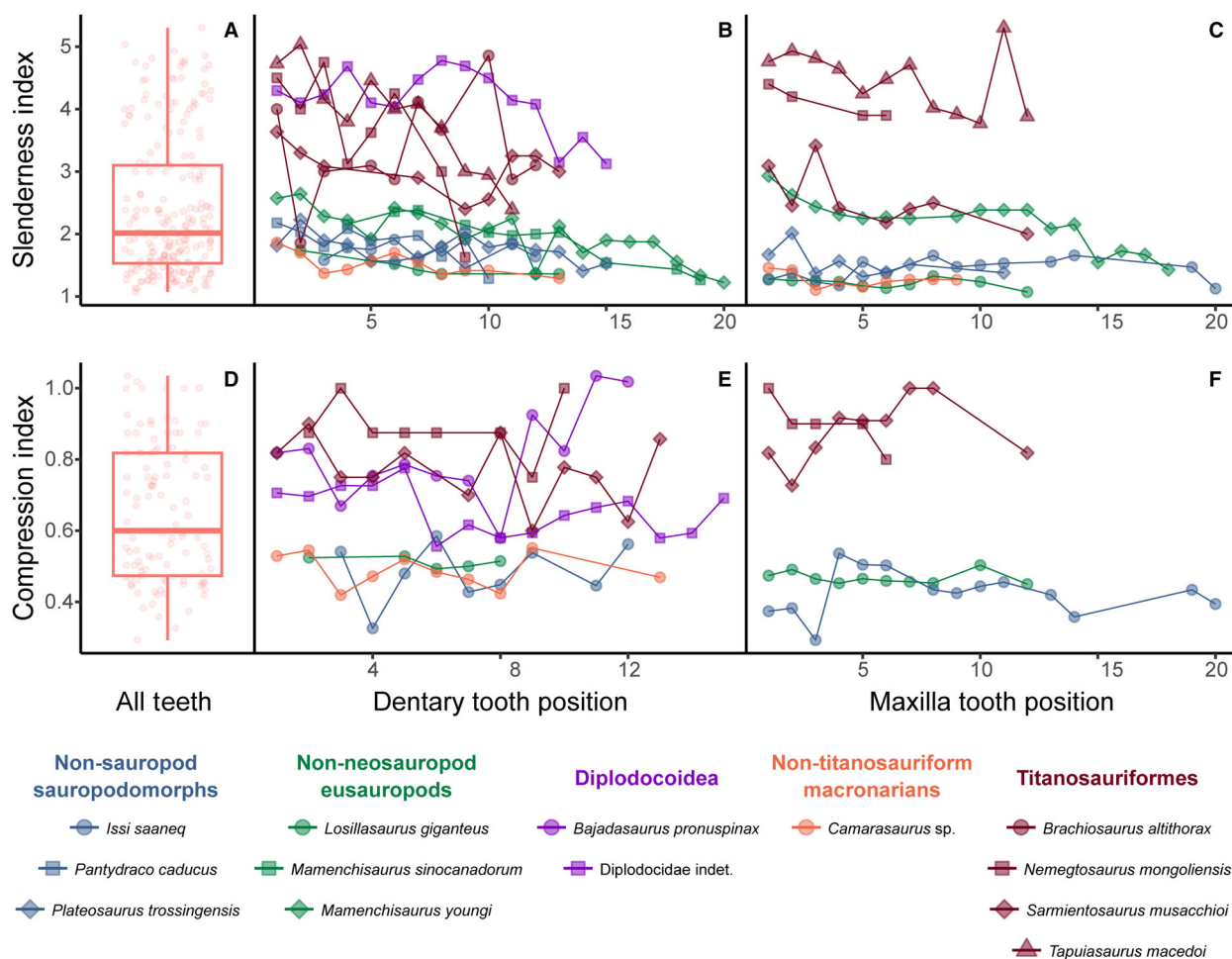


FIG. 7. Variation in the slenderness and compression indices along the tooththrow across a sample of sauropodomorphs. Index values: A, D, entire sample; B, E, dentary; C, F, maxilla. Colour scheme follows that of CS1 (Fig. 3).

TABLE 5. Maxilla and dentary slenderness index comparisons.

Species	Maxillary	Dentary
<i>Plateosaurus trossingensis</i>	1.53 ± 0.23	1.78 ± 0.2
<i>Issi saaneq</i>	1.43 ± 0.17	1.64 ± 0.15
<i>Mamenchisaurus youngi</i>	2.29 ± 0.36	2.02 ± 0.38
<i>Losillasaurus giganteus</i>	1.21 ± 0.07	1.43 ± 0.15
<i>Camarasaurus</i> sp.	1.34 ± 0.24	1.45 ± 0.18
<i>Sarmientosaurus musacchioi</i>	2.73 ± 0.47	3.14 ± 0.41
<i>Tapuiasaurus macedoi</i>	4.34 ± 0.9	3.81 ± 0.6
<i>Nemegtosaurus mongoliensis</i>	3.83 ± 0.67	3.75 ± 0.84

Values are average slenderness index (SI) values, with standard deviation (±).

saaneq and *Losillasaurus giganteus*). In *Issi saaneq*, sidedness explains *c.* 18% of the CI variance, with teeth on the right side having higher CI values on average than teeth on the left side (CI = 0.48 ± 0.07 and 0.41 ± 0.06, respectively). In *Losillasaurus giganteus*, sidedness accounts for *c.* 18% of the variance in CI, with teeth on the right side

having slightly higher CI values on average compared to teeth on the left side (CI = 0.49 ± 0.03 and 0.47 ± 0.02, respectively). In addition, the bone of attachment accounts for the highest explained variance of CI in *Losillasaurus giganteus* (*c.* 22%), with dentary teeth having higher CI values on average. Otherwise, no other significant factors were observed at the species level (Table 6).

DISCUSSION

Utility of sauropodomorph dental indices

Ratios or indices have a long history of use in biological sciences (see Atchley *et al.* 1976). Their appeal lies in the synthesis of bivariate relationships into a single univariate and relative proxy, facilitating comparisons across a sample. In palaeontology, ratios are commonly used as proxies for shape when constructing phylogenetic characters. This was the motivation behind the

TABLE 6. Results of the Procrustes ANOVA quantifying the variation of CI as a function of tooth position, side, bone of attachment, and genus for 10 taxa.

Taxon	n	Partial R^2 values				
		Genus	Bone of attachment	Side	Tooth position	Residuals
Sauropodomorpha	196	0.719***	0	0.002	0	0.152
<i>Issi saaneq</i>	30	–	0.005	0.179*	0.005	0.742
<i>Losillasaurus giganteus</i>	22	–	0.216*	0.181*	0.083	0.53
Flagellicaudata	37	0.358***	–	0.009	0.009	0.545
<i>Bajadasaurus pronuspinax</i>	22	–	–	0.029	0.187*	0.797
Diplodocidae indet.	15	–	–	–	0.19 [‡]	0.81
<i>Camarasaurus</i> sp.	10	–	–	–	0.044	0.956
<i>Sarmientosaurus musacchioi</i>	37	–	0.083 [‡]	0.047	0.056	0.859
Titanosauria	61	0.102*	0.023	0.02	0.012	0.861
<i>Nemegtosaurus mongoliensis</i>	24	–	0.044	0.004	0.091	0.893

p-values relative to an R^2 value of zero: [‡]0.1 > p > 0.05; *0.05 > p > 0.01; ***p < 0.001.

sauropodomorph tooth slenderness index: the ‘broad-crowned’ trait defined by lower SI values was considered primitive, whereas the ‘narrow-crowned’ trait defined by higher SI values was the derived trait, evolving independently at least twice within neosauropods (i.e. diplodocoids and titanosaurs; Upchurch 1998). The phylogenetic signal expressed by broad- and narrow-crowned dental morphologies is mirrored on a temporal scale. During the Late Triassic to Late Jurassic, sauropodomorph teeth were broader with lower SI values, whereas narrow teeth with higher SI values appeared later, and are well described in sauropods from the Late Jurassic through to the end-Cretaceous (Wilson 2005; Chure *et al.* 2010). Our results support a general separation between broad- and narrow-crowned sauropodomorphs, represented as two clusters above and below the SMA line for all sauropodomorphs (Fig. 4; Chure *et al.* 2010). However, there are considerable areas of overlap representing specimens with intermediate tooth morphologies, indicating caution when defining a specific threshold between broad- and narrow crowns (see Fig. 1; Yates & Kitching 2003; Chure *et al.* 2010; Mannion *et al.* 2013). The overlap in tooth morphology also has a temporal component; sauropodomorphs with narrow and broad crowns co-existed during the Late Jurassic to Early Cretaceous, and even within the same stratigraphic horizon (Yates & Kitching 2003; Knoll 2004; Chure *et al.* 2010; Mocho *et al.* 2017). If these general shape designations (i.e. broad vs narrow) are to be supported, it must be acknowledged that few differences exist between residuals. For example, among typically narrow-crowned taxa, Flagellicaudata differs from Titanosauria but not from Rebbachisauridae, and Rinconsauria differs from diplodocids, nemegtosaurids, and rebbachisaurids but not lirainosaurines. Our results indicate that only sometimes can indices support differences among sauropod groups, and that factors such as

allometry and size need to be considered. Consequently, can taxonomic affinities be determined based purely on these indices, and if so, to what level?

One of the fundamental issues of ratios or indices is that they are ignorant of scaling patterns between the variables used to define them and, particularly, differential scaling (i.e. differences in slopes) when comparing groups (Atchley *et al.* 1976). When these groups are functional (e.g. feeding guilds), these issues may be largely irrelevant as ratios may be linked to specific shapes, given a form–function relationship (Goswami & Polly 2013). However, taxonomic groups can span a suite of shapes, which often vary as a function of size (i.e. allometry). Accordingly, ratios can only discriminate between two taxa if constituent measurements scale isometrically and similarly between said taxa. Our results showed that allometric patterns appear to decrease as a function of taxonomic resolution. For SI_{SMA} , 4 out of 6 groups (c. 67%) were allometric when using CS1, whereas only 5 of 12 (c. 42%) were allometric when considering clades (i.e. CS3). Similarly, for CI_{SMA} 2 of 6 groups (c. 33%) were allometric when using CS1, whereas 2 of 12 (c. 17%) were allometric when considering clades. Although decreases in the relative amount of allometric patterns may be due to comparatively lower sample sizes, it suggests that indices are better indicators of clade-level taxonomies than paraphyletic grades.

Except for CS1, there is a general pattern for more significant differences between intercepts than between slopes (see Figs S1, S2). This indicates that most taxa compared here follow consistent scaling trajectories and that differences between intercepts, which also follows those differences observed between residuals, provide support to the taxonomic utility of both SI and CI. However, there are some notable and significant differential scaling patterns in the measurements used to define SI and CI

between different sauropodomorph groups which requires further discussion.

The apicobasal length of mamenchisaurid teeth shows positive allometry relative to mesiodistal width and differs significantly from many other sauropodomorph taxa we compared. As a result, the smaller mamenchisaurid teeth with low SI values would be considered broad crowned, whereas the larger teeth with high SI values would be considered narrow crowned (Fig. 4C). The mamenchisaurid sample consists of teeth associated with *Mamenchisaurus youngi* and isolated indeterminate mamenchisaurid teeth, which were described as pertaining to a single taxon (Averianov *et al.* 2019). The indeterminate teeth are slightly broader (mean SI = 2) than those of *M. youngi* (mean SI = 2.2) and they are also smaller overall. Regardless, they follow a common linear trend (Fig. 5S). As discussed later, the variation in SI resulting in positive allometry within Mamenchisauridae is related to position within the jaw, where larger and more narrow-crowned teeth are placed anteriorly and smaller, and more broad-crowned teeth are positioned posteriorly.

Brachiosaurids also appear to exhibit a size-dependent shift from broad to narrow-crowned teeth, although the relationship between the SI measurements for the sampled taxa could not be differentiated from isometry. Some smaller brachiosaurid teeth overlap with typically broad-crowned taxa such as camarasaurids and turiasaurs, whereas others approach relative values seen in typically narrow-crowned sauropods such as diplodocoids and titanosaurs (Fig. 4). Scrutiny of the data indicates that smaller teeth pertain to replacement teeth in *Brachiosaurus altithorax*, and their removal reduces the slope from 1.3 to 1.1, supporting a generally isometric relationship among brachiosaurids. Accordingly, replacement teeth are here shown to exhibit lower SI compared to fully grown erupted teeth, suggesting their SI values are of limited taxonomic use. Rebbachisaurids do not exhibit significant allometry, yet qualitatively suggest a size-dependent shift from smaller narrow-crowned teeth (e.g. *Nigersaurus taqueti*; Holwerda *et al.* 2018) to larger broad-crowned teeth (e.g. *Demandsaurus darwini*; Fernández-Baldor *et al.* 2011) (Fig. 4C). Together, rebbachisaurids, brachiosaurids and mamenchisaurids exhibit a wide range of possibly size-dependent variation, suggesting caution when using relative slenderness as an indicator of clade-level membership; other features need to be considered (e.g. Averianov *et al.* 2019).

Unlike apicobasal length, labiolingual width is positively allometric relative to mesiodistal width across all Sauropodomorpha. This pattern is driven by platesaurids, which exhibit stronger positive allometry compared to other sauropodomorphs (Fig. 5). However, this subsample is limited to sets of teeth from two specimens of a single species, *Issi saaneq* from the Late Triassic of

Greenland (Beccari *et al.* 2021). Notably, the teeth from one of the specimens (NHMD 164741) are substantially larger and are more circular in cross-section than teeth from the other specimen (NHMD 164758). Although our dataset does not permit a comprehensive exploration of growth-related patterns, these results suggest that CI, and to some extent also SI, values can be ontogenetically variable. It is likely that intra- and interspecific patterns of tooth shape variation may not be consistent across sauropodomorphs, but further consideration of this is outside the scope of the present study. Brachiosaurid teeth exhibit negative allometry, indicating that teeth become more labiolingually compressed as they get larger (Fig. 5E). This pattern is particularly noticeable in the teeth of *Vouivria damparisensis* (Mannion *et al.* 2017), which have lower CI values compared to the other brachiosaurids in our dataset. Despite the limited sample size, this variation suggests that CI may be useful for identification at lower taxonomic levels among brachiosaurids at least, although size dependence should nonetheless be considered first. Finally, turiasaurs are conspicuously grouped in two clusters (Fig. 5). The first cluster consists of labiolingually compressed teeth with correspondingly low CIs that pertain to named turiasaur species (e.g. *Turiasaurus riodevensis* and *Losillasaurus giganteus*). The second cluster consists of teeth with high CIs that pertain to isolated, unnamed teeth from numerous formations of Jurassic age in Portugal (Mocho *et al.* 2016). These specimens can be separated into three morphotypes and all are tentatively referred to Turiasauria based on their heart-shaped morphology in labial view, a pointed and asymmetrical apex, relative labiolingual compression (i.e. low CI values), and a convex labial surface with a bulge extending labiolingually (Mocho *et al.* 2016). However, both the average SI and CI values of the Portuguese sample are higher (SI = 1.38, CI = 0.76) than those of other turiasaurs (e.g. *L. giganteus*: SI = 1.3, CI = 0.48 (Royo-Torres *et al.* 2020); *T. riodevensis*: SI = 1.26, CI = 0.43 (Royo-Torres & Upchurch 2012)). These shape differences, and particularly the difference in CI, suggest that turiasaurs may be expected to exhibit a range of tooth shapes, which may conflate them other taxonomic groups. For instance, features such as apical asymmetry and shape variability along the tooth row (assuming they represent a single taxon) are also shared with *Camarasaurus* and *Giraffatitan* (Mocho *et al.* 2016; Royo-Torres *et al.* 2020).

The utility of the CI as initially conceived was to differentiate between different narrow-crowned sauropods, specifically titanosaurs (Díez Díaz *et al.* 2013). However, subsequent studies have noted an overall lack of significant differences between titanosaur teeth and even concluded that neither SI nor CI could distinguish between titanosaur morphotypes (Holwerda *et al.* 2018). Furthermore, even when differences are observed there are

substantial overlaps in the range of CI values, with the ‘Massecaps’ morphotype (CI = 0.72–0.84) more similar to *Atsinganosaurus* (CI = 0.75–0.9), despite the overlap with *Lirainosaurus* (CI = 0.82–1; Holwerda *et al.* 2018). Our results support previous observations that CI measurements (i.e. LLW and MDW) cannot differentiate between titanosaurs clades (Figs 5, S2). However, we note that lirainosaurine and nemegtosaurid titanosaurs can be differentiated from rebbachisaurids and diplodocids (but not dicraeosaurids) using CI, offering support for its use when SI fails (Fig. 5F).

The nature of tooth variation in Sauropodomorpha

Our results largely corroborate the hypothesis that dental indices indicate taxonomy, at least at higher levels (i.e. family and above). However, the results discussed above and those of previous studies (Chure *et al.* 2010; Holwerda *et al.* 2018) do not explore other sources of variation beyond taxonomy. For instance, sauropod teeth can decrease in size distally along the jaw, such that the premaxillary teeth are often the largest (i.e. size heterodonty; Wilson 2005; Britt *et al.* 2017; Mocho *et al.* 2017; Royo-Torres *et al.* 2017; Wiersma & Sander 2017; Moore *et al.* 2018, 2023). However, no attempt has been made to test for variation of dental indices along the tooth row (i.e. shape heterodonty) and to what extent taxonomy or shape heterodonty explain dental variation.

Strictly speaking, heterodonty refers to variation in dental function along the tooth row that allows animals to compartmentalize food processing (such as chewing, grasping, etc.) thereby increasing the efficiency with which nutrients are extracted (Shimada 2001; Smith 2005; D’Amore *et al.* 2019). Such functional differences are most often associated with omnivorous, insectivorous, and herbivorous vertebrates (Edmund 1969; Hungerbühler 2000; Smith 2005; Butler *et al.* 2009; Reichel 2010; Norman *et al.* 2011; Zanno & Makovicky 2011; D’Amore 2015; Becerra *et al.* 2018; Clack *et al.* 2019; Melstrom & Irmis 2019), with the notable exception of sauropod sauropodomorphs, in which heterodonty is purportedly absent (Chure *et al.* 2010). However, heterodonty has been described for most non-sauropod sauropodomorphs (e.g. Galton 1985; Barrett 2000; Button *et al.* 2017), the non-neosauropod eusauropods *Bellusaurus* (Moore *et al.* 2018) and *Mamenchisaurus sinocanadorum* (Moore *et al.* 2023), and discussed in turiasaurs (Royo-Torres *et al.* 2020). Despite a supposed lack of functional variation in sauropodomorph teeth, variation in tooth size and possibly shape suggests that hypotheses of heterodonty require further scrutiny.

Our results reveal significant shape variation within the jaws of specific sauropodomorphs, particularly in terms

of slenderness (Table 4; Fig. 7). This indicates that taxonomic interpretations using dental indices should also consider variation resulting from dental positions and occurrence in different dentigerous bones (i.e. premaxilla, maxilla and dentary). For instance, >23% of the SI variance in plateosaurids relates to the dentigerous bone in which the teeth are implanted and is a stronger source of variance than generic designation (c. 0.4%); variance due to relative tooth position was effectively zero. In contrast, >30% of the SI variance in *Mamenchisaurus sinocanadorum* and *Camarasaurus* relates to position along the jaw; both taxa display significant decreases in slenderness distally along the dentary (Fig. 7B). Overall, almost all genus- or species-level comparisons return significant decreases in SI along the jaw, especially for teeth that occur in the dentary. The largest shifts occurred in titanosaurs, where the dentary teeth of *Tapuiasaurus macedoi* are highly elongated mesially (SI \approx 4.2) but less so distally (SI \approx 3.2), also observed in *Mamenchisaurus* (Fig. 7B). Despite these patterns, we nonetheless find support for the assertion that taxonomy can be interpreted from SI values based on generic assignment contributing to a large proportion of SI variance (e.g. c. 74% of the variance across sauropodomorphs sampled herein).

Compared to tooth slenderness, circularity (as quantified by CI) varies less as a function of tooth position or dentigerous bone, but shows significant variance associated with generic designation (c. 71%), supporting its use in taxonomy. However, there are notable exceptions such as the dicraeosaurid *Bajadasaurus pronuspinax* which shows a slight increase in CI distally that barely crosses the threshold of statistical significance (c. 12% of the variance, $p = 0.08$) and the turiasaur *Losillasaurus giganteus*, in which c. 40% of the variance can be explained by the dentigerous bone or sidedness.

Overall, linear models reveal substantial residual variance across both SI and CI (Tables 4, 5), indicating variance unexplained by any of the factors explored here and suggesting that other factors (e.g. function) should be explored (Christiansen 2000; Chure *et al.* 2010; Mallon & Anderson 2014). The following discussion will explore the evolution of dental variation within major groups of sauropodomorphs.

Early sauropodomorphs. Non-sauropod sauropodomorphs were the first dinosaurs capable of feeding at heights >1 m, with a potential for high-browsing (Vidal *et al.* 2020). However, an omnivorous diet was hypothesized based on an elongated snout with teeth extending across the whole jaw, mostly leaf-shaped teeth with denticles, varied tooth shapes (recurved to elongate), differing number of alveoli between the maxillary and dentary, and fast jaw closure speeds (Button *et al.* 2016, 2017;

Lautenschlager *et al.* 2016; Bronzati *et al.* 2019). Both plateosaurids in our sample, *Plateosaurus trossingensis* and *Issi saaneq*, have significantly broader maxillary teeth compared to those in the dentary. Tooth shape variation between dentigerous bones mimics other dental differences in *P. trossingensis*, as the maxillary teeth are recurved whereas the dentary teeth are vertically oriented (Prieto-Márquez & Norell 2011). However, no shape differences were noted in *Issi saaneq* (Beccari *et al.* 2021), the massospondylid *Lufengosaurus huenei*, or the non-massospondylid massopod *Yunnanosaurus huangi* (Barrett *et al.* 2005, 2007), suggesting that SI values are not necessarily related to other features of the teeth. Interestingly, *Pantydraco caducus* was the only non-sauropod sauropodomorph to show significant differences in slenderness along the tooth row (dentary), with narrow mesial teeth (SI of the first tooth is 2.1) compared to broader distal teeth (SI of the tenth tooth is 1.2; Fig. 7B). The middle maxillary and dentary teeth are the largest along the tooth row (Galton & Kermack 2010), a feature also described in *Bagualosaurus agudoensis* (Pretto *et al.* 2018). However, no corresponding variation was recovered in SI values, with middle teeth (positions 5–9) exhibiting values between 1.6 and 2 (Fig. 7B). Size heterodonty has not been observed within plateosaurids. However, differing tooth size along the tooth row has been described in multiple non-sauropod sauropodomorphs such as *Saturnalia tupiniquim* (Bronzati *et al.* 2019), *Bagualosaurus agudoensis* (Pretto *et al.* 2018), *Massospondylus carinatus* (Chapelle & Choiniere 2018), *Yunnanosaurus huangi* (Barrett *et al.* 2007), *Lufengosaurus huenei* (Barrett *et al.* 2005), *Pampadromaeus barberenai* (Cabreira *et al.* 2011), and *Saharhsaurus aurifontanalis* (Marsh & Rowe 2018). Whether the size differences are statistically significant is currently unknown and requires further scrutiny. Size heterodonty may have been lost in plateosaurids but retained in non-plateosaurid, non-sauropod sauropodomorphs, indicating that size heterodonty may have been the primitive condition within Sauropodomorpha.

Early-diverging eusauropods. Among non-neosauropod eusauropods (e.g. Mamenchisauridae and Turiasauria) sources of tooth slenderness variation shift from associations with the dentigerous bone to increased variation along the tooth row. These patterns are consistent with previous observations in non-neosauropod eusauropods such as *Bellusaurus sui* (Moore *et al.* 2018), mamenchisaurids (Pi *et al.* 1996; Zhang *et al.* 1998; Moore *et al.* 2023), and turiasaurs (Royo-Torres & Upchurch 2012; Royo-Torres *et al.* 2017, 2020). Despite similarities in the SI values between maxillary and dentary teeth, dentary teeth in *Bellusaurus* are distinct in lacking lingual convexity or denticles (Moore *et al.* 2018). This difference is also described in teeth putatively referred to

Patagosaurus (Rauhut 2003) and isolated *Mamenchisaurus* teeth (He *et al.* 1996). *Losillasaurus giganteus* was the only sauropodomorph in our dataset that showed a significant difference in tooth circularity associated with the dentigerous bone (Table 6). Maxillary teeth were slightly less circular (CI = 0.44–0.51) than dentary teeth (CI = 0.45–0.53), which is reflected by differences in the tooth morphology where the maxillary teeth are more labiolingually compressed than either premaxillary or dentary teeth (Royo-Torres *et al.* 2020). Higher labiolingual compression of the maxillary teeth has previously been described in other turiasaurs such as *Turiasaurus riodevensis* and *Meirasaurus bobyongi* (Royo-Torres *et al.* 2006, 2017, 2020; Royo-Torres & Upchurch 2012). Turiasaurs developed complex dentition similar to that of the non-titanosauriform macronarian *Camarasaurus*, suggesting that size and shape heterodonty may have allowed for feeding on tough woody material (Fiorillo 1998; Whitlock 2011; Button *et al.* 2016; Wiersma & Sander 2017). However, whether this hypothesized feeding ecology can be applied to other turiasaurs and mamenchisaurids is currently unknown.

Diplodocoidea. Diplodocoid dentition differed from earlier sauropodomorphs in having both narrow-crowned teeth (SI > 4) and teeth that are restricted to the anterior portion of the jaw in adults (Whitlock *et al.* 2010; Woodruff *et al.* 2018). Although the shapes of diplodocoid teeth are similar along the tooth row, they vary in size, which is the primitive condition in Sauropodomorpha. We were unable to compare SI and CI values between different diplodocoid genera and dentigerous bones due to lack of available data. However, we observed a significant decrease in tooth slenderness along the tooth row in an unknown diplodocoid (replica of ZRC 2.7076), with the distalmost three teeth having SI < 4 (SI = 3.1 for the mesialmost tooth). Although tooth circularity did not scale significantly with tooth position, the CI of the mesialmost five teeth ranged from 0.7 to 0.78, while the CI of the succeeding ten teeth ranged from 0.55 to 0.69. Tooth circularity in *Bajadasaurus pronuspinax* also did not differ along the tooth row or between left and right dentaries. However, the range of CI values in *Bajadasaurus* was larger than in the diplodocoid; values of the mesialmost five teeth ranged from 0.67 to 0.9, and the remaining distal teeth ranged from 0.58 to 1. Dicraeosaurid teeth are more circular than diplodocids overall and become more circular distally with a CI of 1 for the distalmost tooth. This suggests that tooth circularity may be a distinction between diplodocoid and dicraeosaurid teeth, which have an otherwise almost identical morphology.

Early-diverging macronarians. The dentition of early (i.e. non-titanosauriform) macronarians is represented here by *Camarasaurus* sp. The dentition of *Camarasaurus* is best

described as homodont, with broader-crowned teeth in the upper jaws compared to the lower jaws, and which decreases in size distally (McIntosh *et al.* 1996; Chatterjee & Zheng 2005). The consistent tooth circularity of the dentary corroborates previous descriptions of shape homodonty (Fig. 7E). However, we recovered significant variation in tooth slenderness associated with sidedness and tooth position, but no significant difference in slenderness between the maxillary and dentary teeth. A few dentary teeth (positions 1, 2, 6) are narrower than those of the maxilla (Fig. 7E), but these are rare exceptions. As such, the difference between teeth of the upper and lower jaws may relate to other features, such as lingual recurvature of the maxillary teeth but not crown slenderness. Interestingly, *Camarasaurus* sp. exhibits significant variation in size between left and right jaws, with the right dentary teeth larger than the left, although this variation may be due to post-burial taphonomic deformation (Wiersma & Sander 2017). Regardless, our results suggest that *Camarasaurus* (or at least this individual, SMA 0002) displays greater shape heterodonty than previously considered. Furthermore, based on its hypothesized dietary preference of woody and abrasive plant matter (Fiorillo 1998; Christiansen 2000; Whitlock 2011), complex feeding apparatus (e.g. strong bite force; Button *et al.* 2016, 2017) and a potential 'beak-like' structure (Wiersma & Sander 2017), it is likely that the shape heterodonty recovered here related to a functional compartmentalization of the mouth.

Titanosauriformes. Titanosauriforms spanned over 100 million years from the Jurassic to the Cretaceous and represent the only major sauropod group to survive until the end of the Mesozoic (D'Emic 2012; Mannion *et al.* 2019; Cashmore *et al.* 2020; Poropat *et al.* 2022). Across this interval, titanosauriforms exhibited almost the entire observed range of sauropod tooth slenderness, with broad/intermediate crowns found in non-titanosaur titanosauriforms (e.g. *Brachiosaurus altithorax*) and narrow crowns in late-branching titanosaurs (e.g. *Nemegtosaurus mongoliensis*). Among non-titanosaurs, Brachiosauridae had variable tooth morphologies along the toothrow, whilst little to no variation was noted in *Euhelopus zdanskyi* (Wilson & Upchurch 2009). *Brachiosaurus altithorax* is the only non-titanosaur titanosauriform in which variation along the tooth row was explored. No significant trends were observed along the dentary and the variation is seemingly random with respect to position. However, the range of observed variation is large; for instance, teeth at positions 1, 7 and 10 are very narrow ($SI \geq 4$) compared to the much broader second tooth ($SI = 1.9$), with teeth in the remaining positions of intermediate slenderness ($SI \approx 3$). This random variation in SI values along the tooth row is unique to *Brachiosaurus altithorax* (or at

least this specimen, USNM 5730), compared to other species studied here, but whether such variability is typical of all brachiosaurids remains to be tested.

Titanosauria convergently evolved narrow-crown tooth morphologies similar to those of diplodocoids. As in other non-plateosaurid sauropodomorphs, titanosaurs also displayed a significant decrease in slenderness distally overall, specifically within *Sarmientosaurus* and *Tapuiasaurus*. By contrast, the typically narrow-crowned *Nemegtosaurus* showed little variation along the tooth row, suggesting that size heterodonty was lost in *Nemegtosaurus*, possibly reflecting a novel feeding strategy, whereby teeth undergo greater shear forces with less precise tooth-to-tooth occlusion and involving softer food (Upchurch & Barrett 2000; Wilson 2005). This strategy and associated morphologies may be unique to *Nemegtosaurus*, as closely related taxa, *Sarmientosaurus* and *Tapuiasaurus*, have much larger teeth than *Nemegtosaurus*, exhibit significant SI heterodonty, and were possibly consuming tougher material (Martínez *et al.* 2016). However, sampling of teeth from this part of the Titanosauria tree remains poor, and such evolutionary hypotheses are speculative at this time.

CONCLUSION

This study examined the distribution of two sauropodomorph tooth measurement indices, the slenderness (SI) and compression (CI) indices, across an inclusive sampling of taxa and tested the assumption that they are effective tools for taxonomic classification. While we found statistical support for their utility in this instance, we recommend keeping in mind the following considerations:

1. When using indices for taxonomic purposes, it is assumed that scaling is consistent across the taxonomic groups of interest and follows (or approaches) isometry. Both assumptions were generally supported in our study; however, we nonetheless found significant deviations.
2. The use of indices may need prior consideration of tooth size. In cases where isometry is rejected (e.g. non-sauropod sauropodomorphs, non-neosauropod eusauropods, non-titanosauriform macronarians, and titanosauriforms), indices cannot be interpreted taxonomically at face value.
3. Positional variation within the jaw cannot be ignored. We provide the first statistical analysis of variation in SI and CI values along the toothrow in a large sample of sauropodomorphs, recovering significant shifts in slenderness (i.e. SI). For instance, narrow-crowned taxa (i.e. diplodocoids and titanosaurs) can nonetheless have broad-crowned ($SI < 4$) distal teeth.

Sauropodomorphs have historically been considered as homodont with little or no functional variation along the jaw, largely due to the ‘simple’ nature of their teeth compared to other herbivorous animals. Our overview and analyses of shape variation within sauropods shows that shape often varies, especially among ‘broad-crowned’ taxa, with evolutionary losses only in narrow-crowned titanosaurs. Therefore, ‘broad-crowned’ sauropodomorphs may exhibit more functional compartmentalization of the jaw than previously thought.

While our study serves to demonstrate the taxonomic utility of dental indices in sauropods, we noted significant unexplained residual variance, which may be functional in nature. Future exploration of these indices should focus on correlating tooth shape and tooth functionality to better understand ecomorphology within Sauropodomorpha.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12725>):

Appendix S1. R code.

Data S1. Measurements and specimen data.

Figure S1. SI_{SMA} group-level pairwise comparisons.

Figure S2. CI_{SMA} group-level pairwise comparisons.

Figure S3. Tukey’s HSD group-level pairwise comparisons of linear model residuals.

Figure S4. Exploration of the negative slope found in Euhelopodidae (Fig. 4E).

Figure S5. Detailed relationship in the mamenchisaurid sample.

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