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Evidence of Parallel Evolution in the Dental Elements of *Sweetognathus* Conodonts

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Abstract

The repeated emergence of similar morphologies in the dental elements of Permian *Sweetognathus* conodonts has been a hypothesized example of parallel evolution. To test if morphological parallelisms occur between isolated *Sweetognathus* lineages, this study uses 2D-based geometric morphometrics combined with a revised and expanded phylogeny of Permian *Sweetognathus* conodonts to quantify dental element trait distributions and compare the phenotypic trajectories between lineages. A hierarchical clustering method was used to identify recurrent species pairs based on principal component scores describing their morphological variation, with the further incorporation of widely-used ecological metrics such as limiting similarity and morphological overlap. Our research implies that a major contributor to conodont diversity in Palaeozoic marine trophic networks is the emergence of recurrent parallel morphologies via disruptive and directional selection. This study illustrates the mechanisms through which conodonts achieved their status as hyper-diverse predators and scavengers, contributing substantially to the complexity of Palaeozoic marine communities.

Keywords: Parallel Evolution, Conodont Trophic Networks, *Sweetognathus*

Introduction

Conodonts are an extinct group of early marine vertebrates (~510 to 201 million years ago) that were the first to develop a biomineralized phosphatic dental skeleton, which consisted of tooth-like elements forming a complex feeding apparatus [1, 2, 3]. Phylogenetically, their position remains unresolved between cyclostomes and stem gnathostomes, with their closest living relative being lampreys [4, 3]. Based on wear and fracture patterns in their dental elements [5, 6], biomechanics [7], growth allometry [8], and microstructural adaptation [9], filter-feeding or parasitic habit can be excluded for most conodonts. They were most likely a free-swimming animal capable of actively pursuing their prey and of mechanical mastication of its tissues.

The *Sweetognathus* lineage evolved near the beginning of the Permian Period (298.9 Ma) within near-equatorial, shallow-water seas. Reconstructions of its evolutionary history are based on their P₁ elements, which were located in the pharynx of the animal and, as in many conodonts, developed food-processing adaptations analogous with mammalian molars [10]. Their adaptive radiation and dispersions followed numerous significant relative sea-level fluctuations controlled by the waxing and waning of continental ice-sheets during the Late Paleozoic Ice Age (LPIA), with derived populations becoming isolated during sea-level lowstands when Gondwana ice volume was at its greatest (figure 1) [11].

In this study, we test whether repeated episodes of morphological radiations in *Sweetognathus* conodonts [12, 13, 14] satisfy the definition of parallel evolution. With the advent of modern genomic techniques multiple definitions of parallel evolution have been proposed, which attempt to address the underlying genetic mechanisms that lead to parallelisms, as well as the affect environmental selective pressures have on phenotypic expression (reviewed in [15]). Since the underlying genetic mechanisms of parallel evolution cannot be tested in deep-time studies [16], we adopt a definition that enables us to directly address morphological parallelisms. Parallel evolution will thus be defined as the similarity in phenotypic trajectories between two closely related lineages ([17], reviewed in [18]).

The present study has two objectives. The first is to quantify the morphological variation in the oral surface of *Sweetognathus* species, including morphological overlap and limiting similarity, using geometric morphometric techniques [19, 20]. This provides a measure of intra- and interspecific morphological variation between populations and allows us to recognize potential species pairs. The second objective is to test if parallel evolution between

Sweetognathus lineages has occurred by computing and comparing their phenotypic trajectories [21, 16]. If significant similarities in the phenotypic trajectories among *Sweetognathus* populations exist, our goal will then be to evaluate the drivers of the parallel evolution by comparing our observations with the causes documented in extant fish species demonstrating the same phenomenon.

Methods

Three-dimensional (3D) surface models of *Sweetognathus* P₁ dental elements were created at Friedrich-Alexander University Erlangen-Nuremberg, GeoZentrum Nordbayern, Germany using a phoenix v|tome|x research edition computer tomographic scanner at a resolution of 1.362 μm^3 . Beam voltage was set to 80 kV, current at 100 μA , resulting in an 8 W beam. Images were taken with 400 ms exposure, averaging over 5 images, and skipping the initial image. 1500 images were taken from the 0° starting position. Image stacks as well as meshes are stored through the open source repository MorphoBank [22, 23] (<http://morphobank.org/permalink/?P3736will>), while R analysis code is stored through the open source repository GitHub [24] (<https://github.com/WyattSP/Evidence-of-Parallel-Evolution-in-the-Dental-Elements-of-Sweetognathus-Conodonts>). A total of 59 *Sweetognathus* P₁ dental elements were scanned for this study. They originated from 7 locations (supplementary information Locality Information; figure 1). *Sweetognathus* elements are curated at the University of Calgary.

Model Generation, Landmark Selection, and General Procrustes Analysis

3D models were rendered in VG Studio Max from the acquired image stacks. Elements not displaying dextral curvature (right-curving chirality) were inverted in the open source software IDAV Landmark ([25], Version 3.0).

Discrete cross sections ($n = 401$) were computed through individual denticles on the dorsal platform in the open source software Meshlab ([26], 64bit v2016.12] and imported into R Studio ([27], Version 1.1.423) running R Software ([28], Version 3.6.2) using the R package Momocs ([29], Version 1.2.9). For example, a specimen with nine dorsal platform denticles would yield nine discrete cross sections describing their individual shapes (figure 2a).

One crucial benefit in using 3D rendered models is for their ability to show subtle morphological characteristics since models can be easily reoriented. This is usually difficult when using an optical microscope or a scanning electron microscope as conodont elements tend to be quite small and difficult to physically manipulate. In the 3D models, we were able to identify a small anteriorly (ventrally) directed indentation (inside the basal cavity) on the aboral side of the conodont element that points to the first carinal denticle (figure 2b); compressed ventral denticles are on the free blade. For reference, all *Sweetognathus* P₁ elements essentially lack a true cusp that is clearly distinguishable from the other denticles, as it's not clear where the apex of the basal cavity points. With this discovery, the cusp can be consistently and confidently diagnosed between taxa, assuring correspondence in the assignment of denticle position in this study, as well as establishing a homologous character with species outside the *Sweetognathus* genus (figure 2c-k).

Shape variation in the denticle cross sections was then computed using 2D geometric morphometric (GM) methods [18, 19] (reviewed in [30, 31]) including the analysis of phenotypic trajectories between identified species pairs [21]. A 2D GM methodology was implemented in this paper for two reasons. The *Sweetognathus* genus has very few homologous anatomical structures that would allow for the assignment of landmarks, and as such an insufficient number of landmarks exist to define the boundaries of 3D semi-landmark patches. Additionally, differences in element taphonomy between specimens further limits the availability of homologous anatomical landmarks. Based upon this fact, a 2D approach could assure positional and functional homology between all of the specimens was followed, especially as this is the first attempt to quantify shape variation in *Sweetognathus* conodonts. Second, the usage of histological sections identical in orientation and morphology to the cross sections used in this study, and of which are being used in finite element analysis for other conodont taxa [32], make the results obtained between these different methods comparable and accommodating to a unified interpretation on functional adaptations.

A qualitative assessment of this method's ability to differentiate between different morphotypes as well as its ability to accommodate user error in cross section selection was assessed beforehand in the supplementary information (Denticle Cross Section Sensitivity Analysis). Type 1 (homology-based) landmarks could not be consistently defined on the elements to accurately recreate its shape [33], therefore 50 equally-spaced semi-landmarks were

placed around the circumference of the median vertical section through each denticle, with 2 landmarks positioned on either extremes of the cross section (start of the curve and end of the curve) (figure 2).

Conodont elements are known to record wear (e.g. scratches, flaking or spalling) as a result of their dental function [7, 10, 34], but their shape is periodically restored through a mechanism unique to conodonts [6]. Here, some degree of wear has likely changed the overall profile of the denticles (see D1 in figure 2d). To mitigate the possible affects wear has had on the analysis methods, species denticle averages (supplementary information figure S12) were computed and used as input parameters in the hierarchical clustering and in the other quantitative metrics (see below sections; denticle asymmetries seen in figure 2d are no longer present when species denticle means are taken). Increased within-species variance in shape may be caused by sampling individuals in different phases of the wear-repair cycle, as well as by the species-specific distribution of wear across the denticles. The inclusion of an occlusal model to help deduce the changes in denticle outlines incurred by wear would be beneficial, unfortunately only a handful of reconstructed occlusal models exist, as fossil preservation needs to be exceptional [5, 7, 34].

The assignment of landmarks along each cross section was done in the R package geomorph [35] (see R analysis code for detailed methods [24]). Semi-landmarks were placed at equidistant intervals along the curve, between a start and end point, of the denticle outline. Finally, a generalized Procrustes analysis [36, 37] was completed to calculate the shape differences between the 50 sliding semi-landmarks and 2 landmarks that defined the shape of each cross section [35]. For the GPA, bending energy was minimized as the optimization criterion during Procrustes superimposition [36, 37].

Sweetognathus Phylogenetic Hypothesis

The evolutionary relationships of the *Sweetognathus* phylogenetic hypothesis (figure 4) presented in this paper were formulated using a non-quantitative cladistic approach and considers the timing of introduction of interpreted shared derived characters, characters that have long been used to identify species of *Sweetognathus* (similar approaches can be found in [14] and [11]). This approach is possible thanks to abundant data on *Sweetognathus* occurrences in the fossil record, with consideration to the systematic distribution of gaps, due to its biostratigraphic

significance. The ranges of species are well constrained using numerous methods including radiometric age dating [38, 39], and astronomical tuning of 405 thousand-year cyclothem in the Canadian Arctic and mid-continent USA [40,11]. The topological relationships (branch pattern) are constrained by the relative timing of key character introductions and a pattern of two distinct lineages was considered most likely given the average 4-million-year separation of first occurrences of given characters.

Quantification of Morphological Variation in Sweetognathus Specimens

To visualize the morphological differences between specimens, Procrustes-aligned coordinates were then subjected to principal component analysis (PCA) [31]. Mean principal component (PC) values were then calculated for each denticle grouped by species and subjected to hierarchical clustering (HC) via a multiscale bootstrap resampling method as implemented by the R package pvclust ([41], Version 2.2; 1,000 bootstrap replications) to identify clusters of morphologically similar taxa. The mean PC values were used for HC as some specimens had fewer than eight denticles and missing values cannot be accommodated in the character matrix (first nine PC values included in HC and weighted by percent variance, this accounted for 99% of the overall variance). Denticle position was assessed based on an assumed functional homology as outlined above (i.e. the cusp on the platform will have a homologous function between all taxa). An additional assumption made during analysis is that all conodont specimens are adults, based on the comparable size between the specimens and their similar number of carinal denticles. A Euclidean distance measure and Ward's method was used for HC. The cutoff value for clustering was $\alpha = 0.05$.

A multivariate approach was then taken to assess if the identified clusters were statistically different from each other. First, a multivariate analysis of variance (MANOVA) was run to test for differences between the clustered groups, this was completed for both the overall species means as well as for each individual denticle (supplementary information table S5). Procrustes-aligned coordinates [18, 42, 43] were used in the analysis with the grouping term set to the clustered groups (trait spaces). If the results calculated for Pillai's trace test statistic in the MANOVA were significant, the same inputs were subjected to a pairwise comparison. All multivariate analysis was completed in the RRPP package [44, 45] (see R Analysis Code [24]).

Two other metrics were also calculated to quantify the intra- and interspecific variation between species. The ratio of the distance between trait means (μ_{mv} for PCs; mean) to their trait widths (σ_{mv} for PCs; standard deviation) was calculated for each species ([46], reviewed in [47]). This ratio is equivalent to MacArthur and Levins (1967) quotient of interspecific niche means to interspecific niche widths (limiting similarity). Limiting similarity is an idealized case of competitive exclusion whereby competitive selective pressures lead to the extinction of a species [46]. This can be understood in terms of the ‘competitive exclusion principle’, which states that species cannot coexist if they occupy identical niche spaces and are in complete competition with each other [48]. The coexistence of these closely related species will then be dependent on the degree of trait displacement between species that enable individuals to utilize different resources [49, 50]. By calculating the degree of similarity between closely related species we can get a quantitative metric on the degree of trait overlap. This can help us to understand the potential evolutionary pathways whereby morphological innovations could have arisen. This ratio is used as a metric to quantify niche similarity between species. Next, the species-wide variance (σ^2_{mv}) relative to the total variance of the genus (σ^2_{cv}) was assessed for each species [51, 47] to determine the degree of morphological overlap across the *Sweetognathus* phylogeny.

Analysis of Phenotypic Change between Sweetognathus Lineages

To test the evolutionary mechanisms at play in *Sweetognathus* diversification, phenotypic evolution needed to be quantified and compared between the different lineages in the *Sweetognathus* genus. Adams and Collyer (2009) define phenotypic evolution trajectories as an ordered sequence of estimated phenotypes along an evolutionary path. As such, the magnitude and direction of these phenotypic trajectories can be quantified and compared to examine the evolution of phenotypes through evolutionary time between species. Phenotypic trajectories were calculated and compared using the R package RRPP [44, 45] (trajectories calculated using Procrustes-aligned coordinates; see R analysis code for detailed methods [24]). The input requires an ordered sequence of phenotypes through evolutionary time as well as species groupings. Taking into account the phenotypic groupings found from the HC, species were split into four groups based on the hypothesized *Sweetognathus* phylogeny. Group one consisted of Early Asselian taxa, *Sw. cf. adenticulatus* and *Sw. aff. binodosus*. Group two consisted of Sakmarian taxa, *Sw. binodosus* and *Sw. anceps*. Group three consisted of Late Asselian taxa, *Sw.*

whitei and *Sw. obliquidentatus*. Finally, group four consisted of Artinskian taxa, *Sw. asymmetricus* and *Sw. clarki*. Based on the results obtained from HC, the *Sweetognathus* phylogeny, and relationship in morphospace (figure 3), it was hypothesized that group one and two as well as group three and four contained parallel species pairs, respectively. Phenotypic trajectories were then plotted and compared to evaluate the potential divers of evolutionary change between the identified parallel species pairs (figure 5).

Results

Element Morphospace

The first and second principal components (PC 1 and PC 2) described 79 and 9 percent of the denticle shape variance respectively, encompassing a total 88 percent of the total variance (supplementary information Supporting Figures and Tables). Most of the species in the morphospace, grouped by denticle position, plot closely with each other and have a large amount of overlap, with *Sw. obliquidentatus* and *Sw. clarki* having the highest degree of separation from the other species (figure 3; supplementary information figure S9, S10, S11).

To aid in the characterization and description of the shape differences between the denticle morphologies, thin-plate spline deformation grids of the mean denticle shape warped from the global mean (consensus configuration) in each species were generated (supplementary information figure S8, S12; [19]; reviewed in [31]).

Sw. whitei, *Sw. aff. binodosus*, *Sw. binodosus*, and *Sw. anceps* have the first and second denticles elongated in the oral direction, with an overall triangular appearance. Denticles 3 to 5 are all fairly equidimensional, with a slight asymmetry in the denticle apex (medial ridge) depending on the species. Denticles 6 and 7 for *Sw. whitei* and *Sw. aff. binodosus* maintain the equidimensional denticle form, while *Sw. binodosus* and *Sw. anceps* begin to elongate orally and form a rounded/hemi-spherical upper surface. Denticles 8 and 9 for *Sw. whitei*, *Sw. aff. binodosus*, *Sw. binodosus*, and *Sw. anceps* continue with the trend of oral elongation, but to varying degrees. *Sw. clarki*, *Sw. obliquidentatus*, and *Sw. cf. adenticulatus* have a more equidimensional first denticle, though still orally elongated, as compared to *Sw. whitei*, *Sw. aff. binodosus*, *Sw. binodosus*, and *Sw. anceps*. *Sw. asymmetricus* has an orally elongated first denticle constricted at the base, with a rounded/hemi-spherical upper surface. Denticles 2, 3, 4, and 5 of *Sw. clarki* and *Sw. obliquidentatus* are laterally elongated (orally compressed). A

prominent axial groove is present in *Sw. obliquidentatus* and weakly in *Sw. clarki*. In denticles 6 and 7 of *Sw. clarki*, the denticle upper surface becomes rounded/hemi-spherical. Denticle 8 in *Sw. clarki* and denticle 9 in *Sw. obliquidentatus* are equidimensional, as denticle 9 in *Sw. clarki* is elongated orally, medially constricted, and has a rounded/ hemi-spherical upper surface while denticle 8 in *Sw. obliquidentatus* retains the axial groove. *Sw. asymmetricus* and *Sw. cf. adenticulatus* tend to have slightly orally compressed denticles. A faint medial ridge can be seen on the upper surface of the denticles, but all are much more rounded/hemi-spherical than the other species. *Sw. asymmetricus* diverges in morphology from *Sw. cf. adenticulatus* as the posterior denticles tend to be slightly more rounded/hemi-spherical on the upper surface.

Along the positive direction of the first PC axis, denticles tend to elongate orally (supplementary information figure S8). Along the negative direction of the first PC axis, denticles are elongated laterally, having a prominent axial groove. Along the positive direction of the second PC axis, denticles tend to be orally constricted at their base, be laterally elongated at the top of the denticle, and have a flat upper oral surface. Finally, along the negative direction of the second PC axis, denticles tend to be triangular.

Cluster Analysis

Hierarchical clustering (HC) using a multiscale bootstrap resampling method yielded two statistically significant clusters using the first nine principal component scores (accounting for 99% of the variance) weighted using percent variance (supplementary information figure S9). Clustered species consisted of *Sw. binodosus*, *Sw. whitei*, and *Sw. aff. binodosus* (p-value = 0.05), and *Sw. clarki* and *Sw. obliquidentatus* (p-value < 0.01). *Sw. asymmetricus* and *Sw. cf. adenticulatus* (p-value = 0.19) were associated together, but not significantly. *Sw. anceps* was least associated to *Sw. clarki* and *Sw. obliquidentatus*.

Analysis of Sweetognathus Species in Trait Space

Principal component plots of the first and second PCs are presented in figure 3, grouped by potential evolutionary sequences as hypothesized by the *Sweetognathus* phylogeny and the cluster analysis results. Species were classified *a priori* into five groups based on the HC results, referred to as trait spaces as they encompass the full range of trait variation and as such allow for the identification of recurrent morphotypes (species pairs) (trait space 1: *Sw. cf. adenticulatus*;

trait space 2: *Sw. aff. binodosus*, *Sw. binodosus*, *Sw. whitei*; trait space 3: *Sw. anceps*; trait space 4: *Sw. asymmetricus*; trait space 5: *Sw. clarki*, *Sw. obliquidentatus*).

When trait spaces were compared for the entire data set (not filtering data based on denticle position) MANOVA revealed significant variation among the trait spaces (Phillai's trace = 0.62, $Z = 7.73$, $P = 0.0001$). Pairwise comparisons were then made between each trait space revealing a continuum of trait spaces in morphospace, with trait space 5 being different from all the others (supplementary information table S5). The same multivariate analysis was also completed on trait spaces filtered by denticle position (shape data for each denticle position run independently) with similar results, apart from slight denticle specific variations (supplementary information table S5). For example, trait spaces were less defined for anterior carinal denticles than posterior carinal denticles.

Next, the ratio of the distance between species trait means to trait widths was calculated (limiting similarity). In all cases, the ratio of limiting similarity was smallest for species that inhabited similar trait spaces (supplementary information table S3). Finally, species-wide variance (σ^2_{MV}) relative to the total variance of the genus (σ^2_{CV}) was calculated for each species ($\sigma^2_{MV} / \sigma^2_{CV}$) (table 1). Trait spaces all maintained low values, that gradually increased from trait space 1 to trait space 5 (table 1).

Based on the above results, it appears that the trait spaces inhabit different regions in morphospace and likely represent recurrent morphotypes or species pairs between the *Sweetognathus* lineages.

Evolutionary Trajectories between Sweetognathus Lineages

Morphological parallelisms were assessed by examining species in morphospace (figure 3) and comparing phenotypic trajectories between identified species pairs in the *Sweetognathus* lineages (figure 5). The null hypothesis in the model assumed the angle theta between the phenotypic trajectories is 0° , indicating parallel phenotypic trajectories. Between the Early Asselian and Sakmarian evolutionary sequences the angle theta between the two phenotypic trajectories was 28.42° ($P\text{-value} = 0.18$) and differences in magnitude of 0.02 ($P\text{-value} = 0.71$). This indicates that the direction between the two phenotypic trajectories was similar and that the magnitude of phenotypic evolution between the two lineages was similar. In the case of the Late Asselian and Artinskian evolutionary sequences the angle theta between the two phenotypic

trajectories was 24.65° (P-value = 0.25) and differences in magnitude of 0.20 (P-value = 0.0002). This indicates that the direction between the two phenotypic trajectories was similar but the magnitude of phenotypic evolution between the two lineages was significantly different.

Discussion

Parallel Species Pairs and Evolutionary Trajectories in Sweetognathus Conodonts

In our study we demonstrated the occurrence of recurrent parallel species pairs that follow similar phenotypic trajectories (figure 3, figure 5). The strongest evidence for morphological parallelisms is observed in the analysis of phenotypic trajectories that found two instances of parallel evolution in *Sweetognathus* populations (figure 5). The first example is observed between the Early Asselian and Sakmarian populations, where trajectories indicated a shift towards more symmetrical anterior carinal denticles and orally elongated posterior carinal denticles, laterally constricted at their base. The second example is observed between the Late Asselian and Artinskian populations, where trajectories indicated the repeated tendency of the denticles to elongate laterally and compress orally, as well as to form a distinct axial groove, losing the denticle apex. The catalyst for the emergence of these recurrent parallel morphologies in both examples of parallel phenotypic evolution is likely some form of repeated directional selection brought on by similarities in environmental selective pressures.

The differences in the trajectory direction between the Early Asselian and Sakmarian populations and the Late Asselian and Artinskian populations could be the result of strong environmental selective pressures leading to disruptive and directional selection on extreme phenotypes [52, 53]. The selective regimes occurring between these geographically isolated populations might have been an important mechanism in trophic diversification, which contributed to *Sweetognathus* species adapting to divergent niches in terms of their food base.

No direct interpretation of functional morphology exists for these morphological trends as only a few conodont taxa have been found in preservation that allow for the reconstruction of their occlusion [e.g. 14]. Broad, laterally expanded P_1 elements have been reconstructed to have repeatedly evolved to allow higher loads generated during mechanical food digestion [7], whereas sharp, laterally flattened elements were adapted to have a cutting function [34]. The morphological variation has been in all cases associated with expansion to new trophic niches [7, 54].

It appears that the ancestral type morphology in this study is represented by *Sw. cf. adenticulatus*, as it occupies the initial trait space in the phenotypic evolutionary sequence between the Early Asselian and Sakmarian populations (figure 3, figure 4, figure 5). *Sw. binodosus* and *Sw. aff. binodosus* likely represent intermediary morphologies in the phenotypic evolutionary sequence, before the appearance of *Sw. anceps* (figure 5). Based on prior biostratigraphic studies (see [14]), *Sw. expansus*, *Sw. merrilli*, and *Sw. aff. merrilli* likely represent equivalent ancestral type morphologies in the *Sweetognathus* lineage to that of *Sw. cf. adenticulatus*, though they are not included in this study. Not sampled in this study but recognized in previous biostratigraphic studies is *Sw. aff. obliquidentatus*, which likely represents trait space 5 missing from the Early Asselian lineage. Other species such as *Sw. huecoensis* and *Sw. bucamangus* also likely represent an undefined trait space for each lineage (figure 4).

Potential Causes of Recurrent Parallel Species Pairs in Sweetognathus Conodonts

Empirical neontological studies have recognized parallel species pairs to emerge as a result of similar selective pressures [55, 56]. Threespine sticklebacks inhabiting coastal lakes in British Columbia [57, 58, 59, 60, 61, 62, 63] provide an analogue, as do Nicaraguan cichlid fish [64, 65 66], to the emergence of parallel species pairs in *Sweetognathus* conodonts. In each case, isolated populations derived from a single ancestral population repeatedly radiated in lake environments to optimize feeding ecology, limit competition, and increase fitness, demonstrating the importance of natural selection in shaping morphological parallelisms [64]. The calculated values for limiting similarity (supplementary information table S3) further support this idea, as species inhabiting equivalent niches (values approaching 0) tend not to coexist in the same lineage or region. Instead, adaptive responses (directional or disruptive selection) to new environmental pressures resulted in phenotypic shifts in the direction of a new phenotypic optima [52, 53], facilitating the diversification of new species to new trophic positions resulting in recurrent morphologies under similar selective pressures.

The extent of deviations in the magnitude and direction (figure 5) of the evolutionary trajectories between the *Sweetognathus* lineages from strict parallelism might reflect local environmental differences [17], developmental constraints [67], or differences in time available for diversification that changed both the order of occurrence in morphotypes and the rate at

which they emerged. The incorporation of T-statistics (reviewed in [60]) and other measures of variation when comparing the intra- and interspecific variation in morphospace has provided more basis to infer on the selective pressures that may have led to deviations in evolutionary trajectories.

Community-wide variance ($\sigma_{\text{env}}/\sigma_{\text{cv}}$) is used as a measure of the strength of external filters on a population, with values that approach 0 representing strong environmental selective pressures, and values that approach 1 representing high degrees of internal selective pressures (i.e. competition) [60]. In all the cases of trait spaces presented, environmental selective pressures appear to be exerting the greatest force on community assembly (table 1). For species inhabiting trait space 1, 2, and 3 it appears that environmental selective pressures exerted the highest degree of pressure on community assembly (table 1; $\sigma_{\text{env}}/\sigma_{\text{cv}}$ ranging from 0.16 to 0.18), while more derived forms experienced higher degrees of internal selective pressures (competition) (table 1; $\sigma_{\text{env}}/\sigma_{\text{cv}}$ ranging from 0.20 to 0.22). When taken in context with the ratio of trait overlap, it appears that species inhabiting initial trait spaces quickly specialized to new environmental conditions. Later, trait spaces then began to become more generalist retaining both ancestral traits as well as evolving new traits. Comparable analogues of this phenomenon are observed in Nicaraguan cichlid fish [64, 65]. Furthermore, recent studies examining *Gondolellid* evolution have found evidence for parallel evolution between lineages that experienced similar environmental selective pressures [67]. It therefore seems that the occurrence of recurrent parallel species pairs is the product of similar environmental selective pressures on dental morphologies.

Conclusion

Quantification of *Sweetognathus* dental element morphologies using geometric morphometrics and analyzed in association with phylogeny revealed morphological parallelisms and recurrent parallel species pairs in multiple isolated populations. The outstanding fossil record and rapid morphological radiation of *Sweetognathus* during the Early Permian provide a long-term evolutionary perspective on parallel evolution and its role in shaping trophic diversifications in late Palaeozoic shallow marine ecosystems. Based on comparisons with cases analyzing morphological variability in extant species, both intraspecific competition arising from repeated colonisation of similar environments and strong environmental selective pressures

leading to disruptive and directional selection drove parallelisms in *Sweetognathus*. Deviations in the magnitude and direction of evolutionary trajectories as well as differences in trait overlap, community-wide variance, and limiting similarity between species indicate the strong role both environmental selective pressures and community assembly play in shaping *Sweetognathus* diversity.

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References Cited

1. Donoghue PCJ. 1998. Growth and patterning in the conodont skeleton. *Phil. Trans. R. Soc. Lond. B.* 353 (1998): 633-666. doi: 10.1098/rstb.1998.0231.
2. Murdock DJE, Dong XP, Repetski JE, Marone F, Stamponi M, Donoghue PCJ. 2013. The origin of conodonts and of vertebrate mineralized skeletons. *Nature.* 502: 546-549.
3. Terrill DF, Henderson CM, Anderson JS. 2018. New applications of spectroscopy techniques reveal phylogenetically significant soft tissue residue in Paleozoic conodonts. *J. Anal. At. Spectrom.* doi: 10.1039/c7ja00386b.
4. Donoghue PCJ and Keating JN. 2014. Early Vertebrate Evolution. *Palaeontology.* 57(5): 879-893. doi: 10.1111.pala.12125.
5. Martínez-Pérez C, Rayfield EJ, Purnell MA, Donoghue PCJ. 2014. Finite element, occlusal, microwear and microstructural analyses indicate that conodont microstructure is adapted to dental function. *Palaeontology.* 57 (5): 1059-1066. doi: 10.1111/pala.12102.

6. Shirley B, Grohgan M, Bestmann M, Jarochowska E. 2018. Wear, tear and systematic repair: testing models of growth dynamics in conodonts with high-resolution imaging. *Proc. R. Soc. B.* 285. doi: 10.1098/rspb.2018.1614.
7. Martínez-Pérez C, Rayfield EJ, Botella H, Donoghue PCJ. 2016. Translating taxonomy into the evolution of conodont feeding ecology. *Geology*. 44 (4): 247-250. doi: 10.1130/G37547.1.
8. Purnell MA, 1993. Feeding mechanisms in conodonts and the function of the earliest vertebrate hard tissues. *Geology*. 21: 375-377.
9. Donoghue PCJ and Sansom JJ. 2002. Origin and early evolution of vertebrate skeletonization. *Microsc Rec Tech.* 59: 352-372.
10. Donoghue PCJ, Purnell MA. 1999. Mammal-like occlusion in conodonts. *Paleobiology*. 25: 58-74.
11. Henderson CM. 2018. Permian conodont biostratigraphy in Lucas SG, Shen SZ. (eds) 2018. *The Permian Timescale*. Geological Society, London, Special Publications. 450: 119-142. doi: 10.1144/SP450.9.
12. Wang CY, Ritter SM, Clark DL. 1987. The *Sweetognathus* complex in the Permian of China: implications for evolution and homeomorphy. *Journal of Paleontology*. 61 (5): 1047-1057.
13. Sweet WC. 1988. The Conodonta: Morphology, Taxonomy, Paleoecology, and evolutionary history of a long-extinct animal phylum. *Oxford Monographs on Geology and Geophysics*, No. 10, 212 p. Clarendon Press, New York, Oxford.
14. Mei S, Henderson CM, Wardlaw BR. 2002. Evolution and distribution of the conodonts *Sweetognathus* and *Iranognathus* and related genera during the Permian, and their implications for climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 180 (2002): 57-91.
15. Elmer KR, Meyer A. 2011. Adaptation in the age of ecological genomics: insights from parallelism and convergence. *Trends Ecol. Evol.* 26, 298–306.
16. Monnet C, De Beats K, Klug C. 2011. Parallel evolution controlled by adaptation and covariation in ammonoid cephalopods. *BMC evolutionary Biology*. 11(1), 115. <https://doi.org/10.1186/1471-2148-11-115>.
17. Kaster J, Berger J. 1977. Convergent and parallel evolution: A model illustrating selection, phylogeny and phenetic similarity. *Biosystems*. 9: 195-200.
18. Oke KB, Bukhari M, Kaueffer R, Rolshausen G, Räsänen K, Bolnick DI, Peichel CL, Hendry AP. 2016. Does plasticity enhance or dampen phenotypic parallelism? A test with

- three lake-stream stickleback pairs. *Journal of Evolutionary Biology*. 29: 126-143. doi: 10.1111/jeb.12767.
19. Bookstein FL. 1991. *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, New York, New York, USA.
 20. Rohlf FJ, Marcus LF. 1993. A revolution in morphometrics. *Trends in ecology and evolution*. 8: 129-132.
 21. Adams DC, Collyer ML. 2009. A general framework for the analysis of phenotypic trajectories in evolutionary studies. *Evolution*. 63(5): 1143-1154. doi: 10.1111/j.1558-5646.2009.00649.x.
 22. O'Leary MA, Kaufman SG. 2012. MorphoBank 3.0: Web application for morphological phylogenetics and taxonomy. <http://www.morphobank.org>.
 23. Petryshen W, Henderson C, De Baets K, Jarochowska E. Data from: Evidence of Parallel Evolution in the Dental Elements of *Sweetognathus* Conodonts. MorphoBank. (<http://morphobank.org/permalink/?P3736will>)
 24. Petryshen W, Henderson C, De Baets K, Jarochowska E. 2020. R Analysis Code from: Evidence of Parallel Evolution in the Dental Elements of *Sweetognathus* Conodonts. v.1.0.0. Zenodo. doi: 10.5281/zenodo.4117371. (<https://github.com/WyattSP/Evidence-of-Parallel-Evolution-in-the-Dental-Elements-of-Sweetognathus-Conodonts>)
 25. Wiley DF, Amenta N, Alcantara DA, Ghost D, Kil YJ, Delson E, Harcourt-Smith W, Rohlf FJ, St. John, K, Hamann B. 2005. Evolutionary morphing. *IEEE Visualisation*. 2005: 431-438.
 26. Cignoni P, Callieri M, Corsini M, Dellepiane M, Ganovelli F, Ranzuglia G. 2008. Meshlab: an open-source mesh processing tool. *Sixth Eurographics Italian Chapter Conference*. 2008: 129-136.
 27. RStudio Team. 2020. *RStudio: Integrated Development for R*. RStudio, PBC, Boston, MA. URL <http://www.rstudio.com/>.
 28. R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
 29. Bonhomme V, Picq S, Gaucherel C, Claude J. 2014. Momocs: Outline Analysis Using R. *Journal of Statistical Software*, 56(13), 1-24. URL <http://www.jstatsoft.org/v56/i13/>.
 30. Adams DC, Rohlf FL, Slice DE. 2013. A field comes of age: geometric morphometrics in the 21st century. *Hystrix It. J. Mamm.* 24(1): 7-14. doi: 10.4404/hystrix-24.1-6283.

31. Mitteroecker P, Gunz P. 2009. Advances in geometric morphometrics. *Evol Biol.* 36: 235-247. doi: 10.1007/s11692-009-9055-x.
32. Martínez-Pérez C, Rayfield EJ, Purnell MA, Donoghue PCJ. 2014. Finite element, occlusal, microwear and microstructural analyses indicate that conodont microstructure is adapted to dental function. *Palaeontology.* 57 (5): 1059-1066. doi: 10.1111/pala.12102.
33. Zelditch ML, Swiderski DL, Sheets HD, 2012. *Geometric morphometrics for biologists: a primer.* Academic Press.
34. Jones D, Evans AR, Siu KK, Rayfield EJ, Donoghue PC. The sharpest tools in the box? Quantitative analysis of conodont element functional morphology. *Proceedings of the Royal Society B: Biological Sciences.* 2012 Jul 22;279(1739):2849-54.
35. Adams DC, Collyer ML, Kaliontzopoulou A. 2018. Geomorph: Software for geometric morphometric analyses. R package version 3.0.6. <https://cran.r-project.org/package=geomorph>.
36. Gower JC. 1975. Generalized Procrustes analysis. *Psychometrika.* 40: 33-51.
37. Rohlf FL, Slice DE. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology.* 39: 40-59.
38. Schmitz, M.D. and Davydov, V.I., 2012, Quantitative radiometric and biostratigraphic calibration of the global Pennsylvanian – Early Permian time scale: *Geological Society of America Bulletin*, 124:549-577.
39. Henderson CM. 2009. Chair note. *Permophiles.* 53:2.
40. Beauchamp B, Calvo Gonzalez D, Henderson CM, Baranova DV, Wang HY, Pelletier E. In press for 2020. Late Pennsylvanian–early Permian tectonically-driven stratigraphic sequences and carbonate sedimentation along northern margin of Sverdrup Basin (Otto Fiord Depression), Arctic Canada. In Henderson, C.M., Ritter, S., and Snyder, W.S. (Eds.), *Late Paleozoic Tectonostratigraphy and Biostratigraphy of western Pangea. SEPM Special Publication No. 113.* doi: 10.2110/sepmssp.113.
41. Suzuki R, Shimodaira H. 2006. Pvcust: an R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics.* 22(12): 1540-1542. doi: 10.1093/bioinformatics/btl117.
42. Dryden IL, Mardia KV. 1998. *Statistical shape analysis.* John Wiley & Sons, New York, New York, USA.
43. Rohlf FL. 1999. Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification.* 16: 197-223.

44. Collyer ML, Adams DC. 2019. RRPP: Linear model evaluation with randomized residuals in a permutation. R package version 0.5.1. [Procedure.https://CRAN.R-project.org/package=RRPP](https://CRAN.R-project.org/package=RRPP).
45. Collyer ML, Adams DC. 2018. RRPP: An R package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution*. 9(2): 1772-1779. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.123029>.
46. MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*. 101(921): 377-385.
47. Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Cell Press*. 27(4): 244-252. doi: 10.1016/j.tree.2011.11.014.
48. Gause GF. 1934. *The Struggle for existence*. Baltimore: Williams & Wilkins.
49. Turcotte MM, Levine JM. 2016. Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*. 31(10): 803-813. doi: 10.1016/j.tree.2016.07.013.
50. Albert CH, Thuiller W, Yoccoz NG, Douzet R, Aubert S, Lavorel S. 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Methods in Ecology and Evolution*. 1192-1201. doi: 10.1111/j.1365-2435.2010.01727.x.
51. Holsinger K, Weir B. 2009. Genetics in geographically structured populations: defining, estimating and interpreting F_{ST} . *Nat. Rev. Genet.* 10: 639-650.
52. Price TD, Qvarnström A, Irwin DE. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B*. 270: 1433-1440. doi: 10.1098/rspb.2003.2372.
53. Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*. 21(3): 394-407. doi: 10.1111/j.1365-2435.2007.01283.x.
54. Ginot S, Goudemand N. Conodont size, trophic level, and the evolution of platform elements. *Paleobiology*. 2019 Aug 1;45(3):458-68.
55. Clark BC. 1975. The contribution of ecological genetics to evolutionary theory: detecting the direct effects of natural selection on particularly polymorphic loci. *Genetics* 79(suppl.): 101-113.
56. Endler JA. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, N.J.

57. McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Bulletin of the Fisheries Research Board of Canada 173:1–381.
58. Bell MA. 1974. Reduction and loss of the pelvic girdle in *Gasterosteus* (Pisces): a case of parallel evolution. Natural History Museum of Los Angeles County Contributions in Science 257:1–36.
59. Bell MA. 1976. Evolution of phenotypic diversity in *Gasterosteus aculeatus* superspecies on the Pacific coast of North America. Systematic Zoologica 25:211–227.
60. Bell MA. 1987. Interacting evolutionary constraints in pelvic reduction of threespine sticklebacks, *Gasterosteus aculeatus* (Pisces, Gasterosteidae). Biological Journal of the Linnean Society. 31:347–382.
61. Bell MA, Foster SA. 1994. The evolutionary biology of Threespine Stickleback. Oxford University Press, Oxford, UK.
62. Walker JA, Bell MA. 2000. Net evolutionary trajectories of body shape evolution within a microgeographic radiation of threespine sticklebacks (*Gasterosteus aculeatus*). Journal of Zoology, London. 253: 293–302.
63. Schluter D, Clifford EA, Nemethy M, McKinnon JS. 2004. Parallel evolution and inheritance of quantitative traits. The American Naturalist. 163(6): 809–820.
64. Elmer KR, Shaohua F, Kusche H, Spreitzer ML, Kautt AF, Franchini P, Meyer A. 2014. Parallel evolution of Nicaraguan crater lake cichlid fishes via non-parallel routes. Nature Communications. 5: 5168. doi: 10.1038/ncomms6168.
65. Elmer KR, Kusche H, Lehtonen TK, Meyer A. 2010. Local variation and parallel evolution: morphological and genetic diversity across a species complex of neotropical crater lake cichlid fishes. Phil Trans R Soc B. 365: 1763–1782. doi: 10.1098/rstb.2009.0271.
66. Villa J. 1976. Ichthyology of the lakes of Nicaragua: historical perspective. In Investigations of the ichthyology of Nicaraguan lakes (ed. T. B. Thorson), pp. 101–113. Lincoln, NE: University of Nebraska Press.
67. Guenser P, Souquet L, Dolédec S, Mazza M, Rigo M, Goudemand N. 2019. Deciphering the roles of environment and development in the evolution of a Late Triassic assemblage of conodont elements. Paleobiology. 45(3): 440–457. doi: 10.1017/pab.2019.14.
68. Purnell MA, Donoghue PCJ, Aldridge RJ. 2000. Orientation and anatomical notation in conodonts. Journal of Paleontology. 75(1): 113–122.

Table 1. Values of the first principal component score trait means, variance, community-wide variance ($\sigma^2_{MV}/\sigma^2_{CV}$), overlap (species trait width / total trait width), and trait spaces found from hierarchical clustering.

Figure 1: Paleogeographic map of sampled *Sweetognathus* populations during sea-level lowstands [14]. Colours correspond to time of diversification; Green: Early Asselian, Red: Late Asselian, Blue: Sakmarian and Artinskian. The numbered localities refer to the locations of *Sweetognathus* populations used in this study; 1: Apillapampa Section, Bolivia, 2: Florence Limestone, Kansas, 3: Carlin Canyon, Nevada, 4: Tensleep, Wyoming, 5: Tingmissut Gorge Section, Melville Island, 6: East Blind Fiord, Ellesmere Island, 7: Dalny Tulkas Section, Russia. Species of *Sweetognathus* have a wider paleogeographic range during sea-level highstands.

Figure 2: *Sweetognathus* P₁ elements (a) Terminology used to describe *Sweetognathus* P₁ morphology (for more information on element orientation refer to [68]). The red line is an example of a cross section taken through the denticle. The oral surface of the element contains the denticles. b) 3D rendered model of aboral surface illustrating the basal cavity indentation. c) SEM image of *Sw. whitei* from the Tensleep Section in Wyoming, small nodes cover the surface of the denticles; the element displays left curvature. 3D rendered models of *Sw. whitei* (d), *Sw. asymmetricus* (e), *Sw. clarki* (f), *Sw. cf. adenticulatus* (g), *Sw. aff. binodosus* (h), *Sw. obliquidentatus* (i), *Sw. binodosus* (j), and *Sw. anceps* (k).

Figure 3: Principal component plots of *Sweetognathus* species grouped by time of diversification (evolutionary lineage; figure 4). In each of the plots, the initial phenotype expressed in the evolutionary lineage is indicated by the arrow. The Early Asselian and Sakmarian taxa are hypothesized to follow parallel phenotypic trajectories, as well as the Late Asselian and Artinskian taxa. Parallel species pairs (recurrent morphotypes) between the two hypothesized parallel lineages can be found in table 1. Open points represent the average values per species denticle, while closed points represent individual values for each denticle. The most likely parallel species pairs identified by cluster analysis are *Sw. aff. binodosus*, *Sw. binodosus*, and *Sw. whitei* (trait space 2), and *Sw. obliquidentatus* and *Sw. clarki* (trait space 5). The other species fall along trajectories of phenotypic evolution (trait spaces 1, 3, 4).

Figure 4: *Sweetognathus* phylogenetic hypothesis. The numbered nodes refer to character transitions (supplementary information Phylogenetic Hypothesis). Sea level fluctuations are indicated by the blue and red lines which represent transgressive system tracts (TST) and regressive system tracts (RST) (in press [40]). Colours correspond to species in figure 3. Evolutionary lineages examined in this study are Early Asselian taxa, *Sw. cf. adenticulatus* and *Sw. aff. binodosus*, Late Asselian taxa, *Sw. whitei* and *Sw. obliquidentatus*, Sakmarian taxa, *Sw. binodosus* and *Sw. anceps*, and finally Artinskian taxa, *Sw. asymmetricus* and *Sw. clarki*.

Figure 5: Phenotypic trajectories between species of *Sweetognathus* grouped by time of diversification and geographic location (evolutionary lineages). Principal components were calculated from the covariation matrix of mean shapes using the RRPP package [44,45]. The blue points represent the initial phenotype expressed by a population in an evolutionary sequence, while the green points represent the end phenotype expressed. Species were grouped into evolutionary sequences based on their degree of relatedness (figure 4), time and location of diversification, and HC results. *Sw. cf. adenticulatus* and *Sw. aff. binodosus* were tested against *Sw. binodosus* and *Sw. anceps* as having parallel evolutionary sequences (gold lines). *Sw. whitei* and *Sw. obliquidentatus* were tested against *Sw. asymmetricus* and *Sw. clarki* as having parallel evolutionary sequences (dark blue lines).

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Figure 2: Sweetognathus P1 elements (a) Terminology used to describe Sweetognathus P1 morphology (for more information on element orientation refer to [68]). The red line is an example of a cross section taken through the denticle. The oral surface of the element contains the denticles. b) 3D rendered model of aboral surface illustrating the basal cavity indentation. c) SEM image of Sw. whitei from the Tensleep Section in Wyoming, small nodes cover the surface of the denticles; the element displays left curvature. 3D rendered models of Sw. whitei (d), Sw. asymmetricus (e), Sw. clarki (f), Sw. cf. adenticulatus (g), Sw. aff. binodosus (h), Sw. obliquidentatus (i), Sw. binodosus (j), and Sw. anceps (k).

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PC 1	Variance	Mean		Overlap	Trait Space
<i>Sw. cf. adenticulatus</i>	0.03	-0.01	0.16	0.64	1
<i>Sw. aff. binodosus</i>	0.02	0.06	0.16	0.55	2
<i>Sw. binodosus</i>	0.03	0.1	0.17	0.72	2
<i>Sw. whitei</i>	0.03	0.06	0.18	0.76	2
<i>Sw. anceps</i>	0.03	0.14	0.18	0.7	3
<i>Sw. asymmetricus</i>	0.04	-0.1	0.2	0.77	4
<i>Sw. clarki</i>	0.05	-0.19	0.22	0.77	5
<i>Sw. obliquidentatus</i>	0.05	-0.24	0.21	0.85	5

Lineage
Early Asselian
Early Asselian
Sakmarian
Late Asselian
Sakmarian
Artinskian
Artinskian
Late Asselian