Paleobiology

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Another worm bites the dust: the Lilliput Effect in scolecodonts from the Late Devonian Biodiversity Crisis

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Article

Cite this article: Chilcoat, G., and P. Cohen (2026). Another worm bites the dust: the Lilliput Effect in scolecodonts from the Late Devonian Biodiversity Crisis. *Paleobiology*, 1–10. https://doi.org/10.1017/pab.2026.10093

Received: 28 February 2025
Revised: 17 December 2025
Accepted: 01 January 2026

Handling Editor:
Paul Harnik

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Abstract

The Lilliput Effect, wherein assemblages decrease in mean individual body size after mass extinctions, has not been documented at a wide geographic scale in any of the Late Devonian mass extinction pulses in invertebrate taxa. Based on a dataset of 800 scolecodonts (polychaete jaw elements) from the literature, museum collections, and newly presented data from the Appalachian Basin, we find that scolecodont size distribution per temporal bin decreases across the Frasnian/Famennian Kellwasser Events from a median length of 500 μm before the Kellwasser Events to a median length of 196 μm during the Kellwasser Events. The majority of the small scolecodonts documented during the extinction interval are newly measured specimens from the Kellwasser Events of the Appalachian Basin, although this size change is not unique to the Appalachian Basin. We interpret the reduction in body size as a hypoxia-driven occurrence of the Lilliput Effect because of the susceptibility of benthic invertebrates to hypoxia and the association of this extinction event with hypoxia. While previous studies have shown that polychaete community biomass decreases in response to oxygen stress, our study provides fossil evidence of individual size reduction, plausibly due to oxygen stress.

Non-technical Summary

Sometimes after mass extinction events, organisms get smaller. This is known as the Lilliput Effect. The Lilliput Effect has been observed in several mass extinctions, but has not been well documented in any of the Late Devonian mass extinction pulses in invertebrate taxa. Based on a newly assembled dataset of 800 scolecodonts (polychaete worm jaw microfossils) from the literature, museum collections, and newly presented data from the Appalachian Basin, we find that scolecodont size decreases during the extinction interval, then increases toward a pre-extinction baseline in the Carboniferous. The majority of the small scolecodonts documented during the extinction interval are newly measured specimens from the Appalachian Basin during the Kellwasser Events, but this pattern is not driven exclusively by the new specimens. We instead interpret the reduction in body size as a hypoxia-driven occurrence of the Lilliput Effect, because worms in the ocean mud are particularly sensitive to changes in oxygen concentrations, and this extinction event is associated with low oxygen levels. While previous studies have shown that polychaete worm community biomass decreases in response to oxygen stress, this is new fossil evidence of individual size reduction due to oxygen stress.

Introduction

The Late Devonian epoch was punctuated by the Late Devonian Biodiversity Crisis, one of the "big five" mass extinctions of the Phanerozoic. The main extinction pulses of this event, the Kellwasser Events (KWE), occurred near the Frasnian/Famennian (F/F; ca. 372 Ma) boundary, and an additional extinction pulse known as the Hangenberg occurred at the Devonian/Carboniferous boundary (D/C, also the Famennian/Tournaisian boundary; ca. 359 Ma) (Cohen et al. 2013).

The Late Devonian biocrisis is unique compared with the other major Phanerozoic extinctions in its apparent lack of a single point source; rather, it seems to have been caused by the culmination of deleterious environmental factors including sea-level change, temperature change, and carbon cycle perturbations (Bond et al. 2013; Becker et al. 2016; Kaiser et al. 2016; Qie et al. 2019). Paleogeographic conditions promoting restricted basins caused intensified localized environmental effects because seas were not well-mixed with global ocean systems (Carmichael et al. 2019). In addition, the extinction was protracted—it played out over both the Frasnian and Famennian stages, with major pulses at the F/F and D/C boundaries. Newly presented data in this study are from strata before, during, and after the F/F extinction events, known as the Lower and Upper Kellwasser Events (LKE and UKE).

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The primary kill mechanism during the Kellwasser Events has been identified as climate change coupled with oxygen stress characterized by intermittent anoxia and euxinia (Cohen et al. 2022, 2023; Pier et al. 2021). Sedimentological and geochemical records show global evidence of anoxia and eutrophication (Arthur and Sageman 1994; Hakenkamp and Palmer 2000; Kaiser et al. 2016; White et al. 2018; Carmichael et al. 2019; Boyer et al. 2021). However, these records do not indicate complete water column anoxia throughout the entire Late Devonian—rather, they indicate that the water column was intermittently anoxic, dysoxic, euxinic, and oxic, and variable across space and time (Carmichael et al. 2019; Boyer et al. 2021). The causes of variably low oxygen concentrations in the water column and eutrophication during the Kellwasser Events include basin isolation due to eustatic sea-level change (White et al. 2018; Carmichael et al. 2019) and nutrient input as a result of tectonic activity (Golonka 2020; Boyer et al. 2021), as well as nutrient input associated with the development of robust forest ecosystems (Rimmer et al. 2015; Pawlik et al. 2020).

The tendency of individuals within assemblages to decrease in mean body size during and after mass extinctions is known as the Lilliput Effect (Urbanek 1993). Harries and Knorr (2009) have proposed three mechanisms to explain the Lilliput Effect: the preferential survival of smaller lineages, heritable size change within lineages, and evolution of novel small morphotypes. In the first model, lineages of all sizes exist before the extinction boundary, but during the extinction and recovery interval, the smallest lineages have disproportionately high survival rates and dominate (Payne 2005; Harries and Knorr 2009). In contrast, the Lilliput Effect can also be caused by size change within lineages: the preferential survival of smaller individuals within a single lineage. In this case, the smallest *members* of each species are selected for, and thus the descendants of that species inherit small body size (Landman et al. 1991; Harries and Knorr 2009). Instead of or in combination with these processes, smaller morphotypes may preferentially speciate (Harries and Knorr 2009; Abbott et al. 2024).

In addition to evolutionary pressures, epigenetics or phenotypic plasticity can also cause the members of assemblages to decrease in body size (Stearns et al. 1991; Urbanek 1993). Stressors, such as a lack of nutrients or low oxygen concentrations, can lead to lower average tissue mass in a population; as soon as the stressful conditions end, body size can increase again. In this scenario, there should be a direct and immediate relationship between environmental conditions and body size because there is no evolutionary lag time, but time-averaging likely makes it impossible to observe this on a generational scale (Harrison et al. 2010; Abbott et al. 2024). Under the transient signal of plasticity, we would expect to see a greater variation in sizes in the fossil record within a given species, as environmental conditions fluctuated rapidly and fossils are time averaged (Bush et al. 2002). Additionally, lineages should look morphologically very similar to their relatives outside the stress interval, apart from body size.

Of the "big five" mass extinctions, the Lilliput Effect is most extensively described at the Permian/Triassic Mass Extinction (e.g., Twitchett 2007; Zhang et al. 2016; Chen et al. 2019) and also often observed at the Cretaceous/Paleogene boundary (e.g., Wiest et al. 2018). Evolutionary miniaturization is also regularly described within individual taxa during regional extinctions and environmental perturbations, including in the Devonian (e.g., Bosetti et al. 2011; Aretz et al. 2014; Comniskey et al. 2016; Thuy et al. 2022; Prow-Fleischer et al. 2024). Often, the Lilliput Effect is characterized through studies of the period immediately following the extinction, demonstrating postcrisis opportunism (e.g., Sallan and Galimberti 2015); a strength of this study is the availability of material before, during, and after the extinction event. There are isolated accounts of miniaturization at every mass extinction (e.g., Huang et al. 2010; Sallan and Galimberti 2015; Schoepfer et al. 2022), but the data and synthesis on this topic in the Late Devonian are especially sparse.

In contrast to miniaturization records at other mass extinction events that rely heavily on the invertebrate fossil record, the most complete synthesis of miniaturization from the Late Devonian is a study of marine vertebrates. Sallan and Galimberti (2015) found that smaller, rapidly reproducing, opportunistic vertebrates (mostly fish) were more successful at diversifying after the Hangenberg Event than larger vertebrates, and smaller vertebrates remained dominant well into the Mississippian. These authors find that the body-size change in vertebrates was driven by long-term biotic/ecological factors, not environmental change such as temperature and hypoxia. Renaud and Girard (1999) catalogue the Lilliput Effect at centimeter-scale resolution with a detailed analysis of phenotypic change in the Kellwasser Event in France, also in chordates (conodonts). Some records of invertebrate miniaturization at the Late Devonian mass extinction exist (e.g., Harper and Yu 2001; Aretz et al. 2014; Boyer et al. 2019; Salamon et al. 2021; Pier et al. 2021); but these are taxonomically and/or geographically isolated reports.

Records of poorly preserved taxa are largely unresolved during this biologically important transition, which exacerbates scientific gaps in knowledge. Annelids are one of the most abundant metazoans of the Paleozoic and one of the most common macrobenthos in the modern, yet our understanding of their abundance over time is very poor, in large part due to their low preservation potential and nonspecific taxonomy (Fauchald and Jumars 1979; Eriksson et al. 2004). Scolecodonts, the fossilized organic jaws of polychaete annelids in family Eunicida, provide a unique opportunity to study annelid distribution over time. Eunicidans are an extant and ecologically diverse group of segmented, mandible-bearing worms that originated in the Cambrian (Fauchald 1977; Parry et al. 2014, 2015; Zanol et al. 2021). Scolecodont-bearing animals (hereafter "scolecodonts") are generally interpreted as benthic organisms, and likely at least partially infaunal (Eriksson et al. 2004; Nowaczewski 2011).

Global polychaete faunal turnovers have never been documented at a mass extinction, and scolecodont abundance over time has not been studied extensively. The majority of scolecodont research has been focused on the early–middle Paleozoic, which is reflected in the handful of occurrences recorded in the Paleobiology Database (PBDB). Most occurrences in the PBDB are not associated with high-resolution photomicrographs. Eriksson et al. (2004: p. 282) suggest that "preliminary results indicate that jawed polychaete faunas show some characteristics attributed to extinction events, e.g., possible 'lilliput' effects [*sic*], disaster and recovery faunas, and Lazarus taxa," yet those turnovers were incongruent with changes in other biota. In areas where taxonomy is resolved, changes in polychaete faunas seem to be gradual rather than abrupt (Hints et al. 2006). Other early Paleozoic extinction events had little to no effect on scolecodont lineages (Eriksson et al. 2004; Tonarová et al. 2025).

Here, we aim to enhance the record of the Late Devonian biocrisis, scolecodonts, and the Lilliput Effect by introducing new samples at high stratigraphic resolution around the Upper Kellwasser Event and contextualizing them with body size data in a newly created database of middle Paleozoic scolecodonts from the literature.

Materials and Methods

To study scolecodont size over time, we compiled a database of 838 mid-Paleozoic (Silurian through Carboniferous) scolecodonts belonging to 12 families. Specimens were sourced from the literature ($n = 465$), the Carnegie Museum of Natural History collections ($n = 297$), and Appalachian Basin samples described here ($n = 76$).

Appalachian Basin Sample Collection

Scolecodonts newly described in this study come from siliciclastic rocks sourced from four sites in the Appalachian Basin: 6 to 10 m sections below, within, and above the Pipe Creek Formation (Lower Kellwasser Event equivalent, upper *rhenana* conodont zone) at Pipe Creek (PC; New York), and below, within, and above a dark shale previously correlated with the Pipe Creek Formation at Tioga B (TGB; Pennsylvania), Cameron Creek (CAM; New York), and Big Creek (BCP; New York) in 2015 and 2018 (Bush et al. 2015; Beard et al. 2017; Fig. 1). The sampled shale at TGB, CAM, and BCP represents an extinction pulse and has been previously correlated with the Pipe Creek Formation, but new conodont data presented by Over (2025) suggest it may instead correlate with the Point Gratiot bed, which is temporally equivalent to the Upper Kellwasser Event. TGB is the most proximal to shore, followed by CAM and BCP, while PC is relatively distal and contains scarce scolecodonts (Cohen et al. 2022). Samples were prepared following standard hydrofluoric acid maceration protocol and separated with a 25 μm sieve (Pippenger 2020).

Photomicrography

To determine which samples contained scolecodonts, we first took 100 photomicrographs of dried macerate slides of each horizon at each site and examined all images. For all fossiliferous localities, we measured all scolecodonts captured in the first round of photomicrography. Then, we examined one 50 ml tube of macerate from each fossiliferous sample under a stereoscope, photographing all additional scolecodonts. We took multiple photographs at varying foci and stacked the images using Helicon Focus or Photoshop. Scolecodonts were removed after being photographed to ensure none were photographed twice. Some scolecodonts were also photographed using a scanning electron microscope to obtain higher-resolution images.

To increase the sample size of Appalachian Basin lower Paleozoic scolecodonts, we also measured the scolecodonts from the extensive collections in the Carnegie Museum of Natural History (CMNH). These scolecodonts were collected, prepared, and described by former curator of the museum E. R. Eller in the mid-1900s, and have also been described by M. Eriksson and C. Bergman (Eller 1934a,b, 1941, 1955, 1961, 1963a,b, 1964, 1967; Eriksson and Bergman 1998). These were photomicrographed under 40× magnification at Williams College or at the CMNH using a ProScope EDU 300 Portable Standalone Digital Microscope.

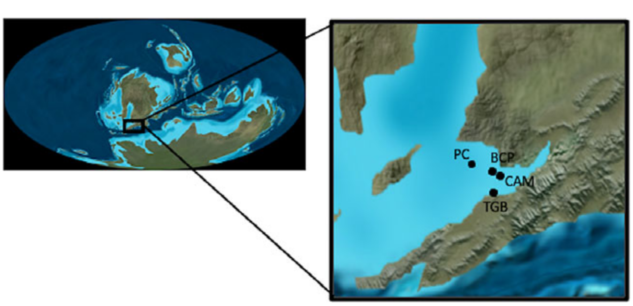

Figure 1. Global paleogeography of the Late Devonian, 370 Ma. Source map © 2020 Colorado Plateau Geosystems Inc. Box indicates the Appalachian Basin on the Laurussian continent, where new data in this study are introduced. PC, Pipe Creek; BCP, Big Creek; CAM, Cameron Creek; TGB, Tioga B (see "Materials and Methods").

Literature Review

We conducted an extensive literature review to collect data on all viable published images of Devonian and Carboniferous scolecodonts, as well as a large sampling of Silurian scolecodonts. We excluded from the dataset or excluded from most calculations some images that were unusable because the scolecodonts were obscured or images were too low quality; stratigraphic resolution was too poor; scale bars were absent and magnification could not be reliably determined; images were sketches rather than photomicrographs; or scolecodont affinity was uncertain. Scolecodonts in this literature search represent 73 global localities, where no one locality contributed more than 9.7% of individuals from the literature (Supplementary Fig. 1). Except for a few cases of obvious consensus revisions, we do not attempt to correct stratigraphic or taxonomic information reported in the literature. In this study, references to the Late Devonian extinction include the overall period of diversity depletion, while references to the Kellwasser Events refer specifically to the extinction events near the F/F boundary.

Photomicrographs taken at the Carnegie Museum were calibrated to a scale bar and directly measured (length and width) using ProScope software. Photomicrographs obtained from the literature were uploaded into ImageJ, calibrated using the scale bar provided in the publication, and measured in ImageJ (Fig. 2).

The Mid-Paleozoic Scolecodont Database

All data from this project are published in a publicly available repository (see "Data Availability Statement"). Compiling this database involved reconciling biological occurrences with stratigraphic information and geochemical records from the literature and adding in length and width measurements performed in this study (for scolecodont image and associated geochemical references, see the "Readme" within the Mid-Paleozoic Scolecodont Database on

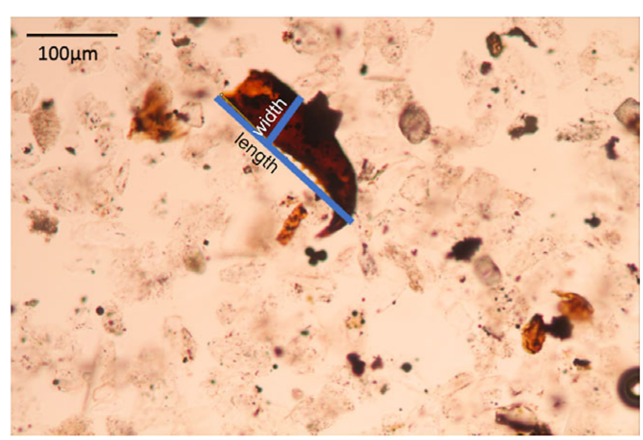

Figure 2. Screenshot showing length and width dimensions of a scolecodont in ImageJ. Following Jansonius and Craig (1971), length is the largest dimension of a jaw roughly parallel to the teeth, while width is the largest dimension of a jaw roughly perpendicular to the teeth. Length and width measurements need not be exactly perpendicular. Scale bar, 100 μm.

https://doi.org/10.1017/pab.2026.10093 Published online by Cambridge University Press

Data Dryad). Geochemical data (total organic carbon and Hg) for Appalachian Basin scolecodonts described in this study are taken from Pippenger et al. (2023). When lithology and geochemical data were not reported in the paper reporting scolecodonts, we cross-referenced these data from other papers at the highest stratigraphic resolution possible; when stratigraphy could not be definitely assigned, lithology and geochemistry were excluded from the database. Paleogeographic provinces were assigned based on general consensus in the literature.

The length of a scolecodont is the greatest dimension of a jaw approximately parallel to the dentary, while the width is the greatest dimension of a jaw roughly perpendicular to the length (Jansonius and Craig 1971; Fig. 2). Multiple independent systems of classification have arisen from different schools of polychaete taxonomists, and these have yet to be fully reconciled (Eriksson et al. 2004). In this research, we are most interested in higher-order size patterns rather than differences between specific taxonomic groups, so the problematic scolecodont taxonomy is not a significant barrier. However, we compare these generalized findings with trends in identifiable subgroups when possible (i.e., fossils identifiable as members of the same family of fossils that represent the same jaw element type) to test whether the patterns we observe are representative.

Data Analysis

After filtering out low-quality records, we included 800 scolecodonts in our statistical calculations. To achieve a relatively high resolution while maintaining sufficient sample size per bin, we binned samples by age (Fig. 3): Silurian (n = 112, 443–420 Ma), Early Devonian (Lockhovian, n = 38, 420–413 Ma; Pragian, n = 22, 413–411 Ma; Emsian, n = 63, 411–393), Middle Devonian (Eifelian, n = 171, 393–388 Ma; Givetian, n = 165, 388–382 Ma), Frasnian Epoch of the Late Devonian excluding the Kellwasser Events (n = 98, 382–373 Ma), the Frasnian Epoch during and after the Kellwasser Events (n = 68, ca. 372 Ma), Famennian Epoch (in other words, the Late Devonian after the Kellwasser Events) (n = 43, 372–357 Ma), and Carboniferous (n = 18, 357–299 Ma). We focus our size analyses on length, which can reasonably be used as a proxy for overall body size (Abbott et al. 2024). We tested whether our measurement of lengths binned to the selected time bins was appropriate by comparing our length results with width measurements, and by subsampling our results based on well-sampled families, components, and basins. We performed 1000 iterations of bootstrap resampling on each of these subsets. For ease of visualization and increased sample size, subsetted data are binned to the epoch level, but the different trends shown in stage-level data should be noted.

Family was determined based on information reported in publications and verified or updated using the World Register of Marine Species (WoRMS Editorial Board 2025). When possible, families were assigned to individuals newly described in this publication based on published taxonomic guides (i.e., Jansonius and Crag 1971). Geographic provenance at the basin level was determined based on reported information from the literature, and width was measured as described earlier. Most of the smallest individuals are not assigned to a family (most "Other" individuals are "Unknown" or *incertae sedis*), making it impossible to determine whether a particular family drives the overall size trends. Therefore, this study focuses on size distribution shift at the family level.

Data management, analysis, and organization were done in R (Wickham 2011, 2023; Becker et al. 2022, 2025; Neuwirth 2022; Kassambara 2023, 2025; Wickham et al. 2019, 2023, 2025; Garnier et al. 2024; Gearty 2024; R Core Team 2024; Lang 2025; Robinson et al. 2025; Wilke 2025).

Results

Mean lengths range from 41 μm (Famennian) to 5778 μm (Carboniferous), and widths range from 10 μm (Frasnian) to 2644 μm (Eifelian). The dataset represents 671 individuals before the Kellwasser Events (KWE; median length = 500 μm), 68 individuals during the KWE (median length = 196 μm), and 61 individuals after the

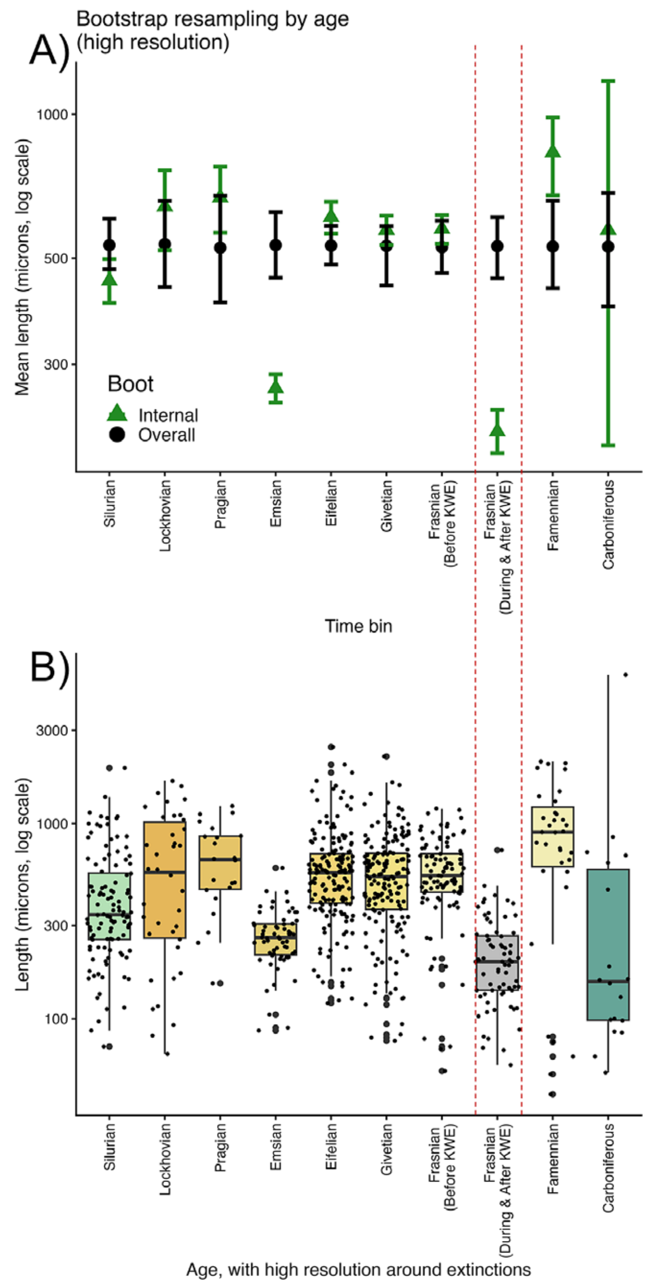

Figure 3. A, Bootstrap mean length of the entire dataset (black circles) and of each time bin (green triangles) with the number of data points (filled circles) and 90% confidence intervals (μm, logarithmic scale). Values from all bins were pooled, and distributions were resampled up to the sample size that characterizes each bin. **B,** Box-and-whisker plot showing length of all individual scolecodonts (μm, logarithmic scale) over time in the Silurian, Devonian, and Carboniferous; with Devonian data separated by stage, including the Kellwasser Events (KWE) (n = 797). KWE.

KWE (median length = 630.5 μm). Euramerica is the most-sampled province (n = 540), and Gondwana is the least-sampled province (n = 13).

Analysis of variance (ANOVA) and Tukey's test are appropriate to test the variance of lengths between time bins (Supplementary Fig. 2, Supplementary Table 1). Tukey's test shows significantly different mean lengths between many sets of time bins; the only time bin that is significantly different from all other time bins is the KWE. We conducted a bootstrap resampling with 1000 iterations in which all bins were pooled and distributions were resampled up to the sample size that characterizes each bin to account for some of the large differences in sample size between time bins. With bootstrap resampling taken into account we found, similarly, that the most prominent deviations from bootstrapped means were in the KWE and Famennian. The Carboniferous true mean is within 90% confidence interval of the bootstrapped mean, indicating that the size difference between the Carboniferous and other time bins may have been exaggerated by ANOVA and Tukey's testing due to a small sample size. This analysis also emphasizes that the Early Devonian mean length is driven contradictorily by the Emsian (smaller) and Lockhovian–Pragian (larger), making Middle Devonian specimens appear to represent a size increase relative to the Early Devonian (Fig. 3).

We tested whether our measurement of lengths binned to the selected time bins was appropriate by subsampling our results by comparing our length results with width measurements, and by subsampling our results based on well-sampled families, components, and basins. We performed 1000 iterations of bootstrap resampling on each of these subsets. Maxilla I (MI), components, the largest component of the scolecodont jaw apparatus, are relatively evenly distributed across time intervals, which indicates that preferential preservation or description of smaller jaw components does not drive the size trends (Fig. 4, Supplementary Fig. 3). When width is measured instead of length, the overall trend is again very similar, with the exception of a shorter tail on the Carboniferous (Fig. 5, Supplementary Fig. 4). Basins are differentially preserved and exposed across time bins, with most occurrences from the Kellwasser Events being from the Appalachian Basin (Fig. 6, Supplementary Fig. 5). Many of the largest individuals across all time bins are from the Michigan Basin. The decrease in mean length during the KWE is still present when excluding newly introduced Appalachian Basin samples, but in this case, smaller individuals exist outside the extinction interval than within it.

Mean scolecodont length shows statistically significant changes across the study interval. In sum, mean scolecodont length decreases in the Emsian, increases during the Middle Devonian, stabilizes in the Frasnian, decreases significantly during the KWE, rebounds in the Famennian, and stabilizes in the Carboniferous (Fig. 3). These patterns hold when controlling for sample size by bootstrapping and subsetting well-sampled families, basins, and lithofacies, and they are not driven exclusively by newly introduced samples. Although the Carboniferous and Devonian each represent 60 Myr, this literature search yielded 594 Devonian individual scolecodont specimens and only 18 Carboniferous scolecodonts.

Geographically, most samples come from Europe, Japan, and the United States, indicating undersampling in the Global South. The only basins with more than 50 individuals distributed across more than two time bins are the Appalachian Basin (n = 213), Michigan Basin (n = 144), and Iowa Basin (n = 97). A decrease in mean scolecodont length during the extinction interval is most notable in the Iowa Basin (Fig. 6, Supplementary Fig. 5). The size difference between the Frasnian and KWE is far less pronounced in

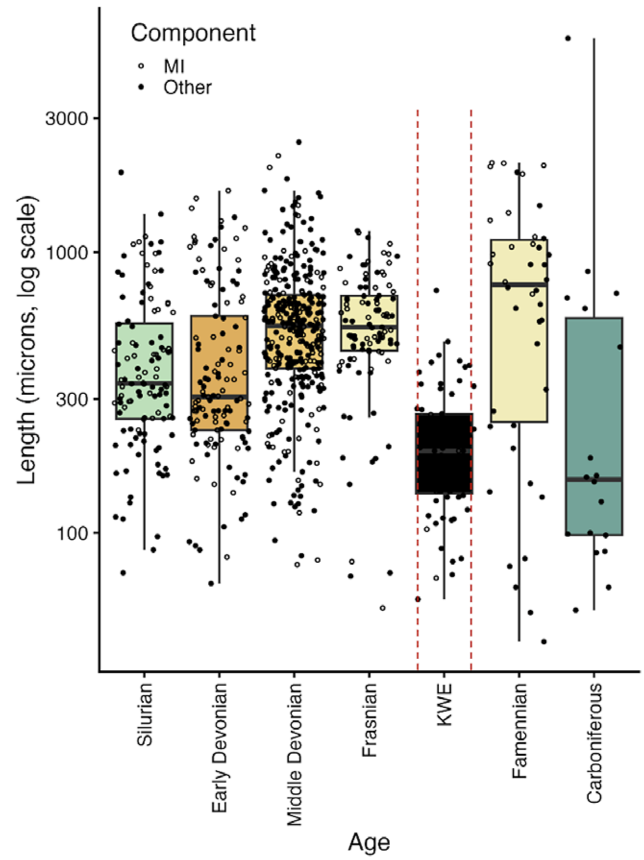

Figure 4. Box-and-whisker plot showing length of all individual scolecodonts (μm, logarithmic scale) over time, with points coded to scolecodont apparatus component (maxilla I [MI], n = 276, vs. all others, n = 524). This shows that size change over time is not driven by difference in sampling or preservation of the largest component of the apparatus. KWE refers to the Kellwasser Events.

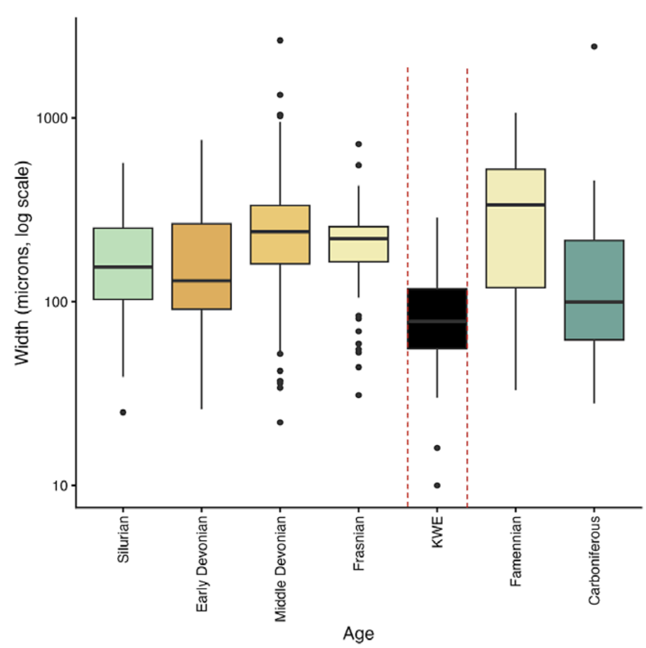

Figure 5. Box-and-whisker plot showing width of all individual scolecodonts (μm, logarithmic scale) over time. Width shows similar trends to length over time. KWE refers to the Kellwasser Events.

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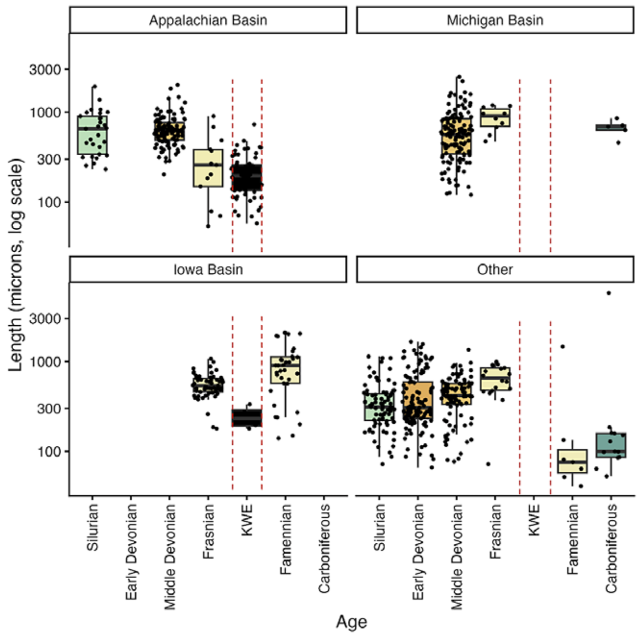

Figure 6. Box-and-whisker plots showing length of individual scolecodonts (μm, logarithmic scale) for the three basins representing more 50 individuals total in more than two time bins (Appalachian Basin, n = 213; Michigan Basin, n = 144; Iowa Basin, n = 97). KWE refers to the Kellwasser Events.

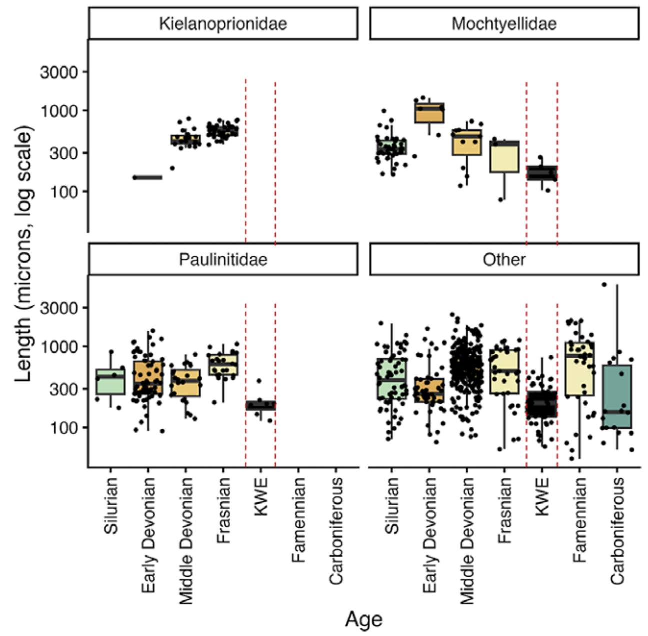

Figure 7. Box-and-whisker plots showing length of individual scolecodonts (μm, logarithmic scale) for the three families representing more than 50 individuals (Kielanoprionidae, n = 57; Mochtyellidae, n = 68; Paulinitidae, n = 127). KWE refers to the Kellwasser Events.

the Appalachian Basin, which may indicate protracted stress throughout the Frasnian. These data distributed across multiple Euramerican basins also support that the pattern of size decrease during the KWE is not specific to newly presented specimens, although the size change may have been temporally asynchronous across basins.

Three families have more than 50 individuals recorded in this dataset: Kielanoprionidae (n = 57), Mochtyellidae (n = 68), and Paulinitidae (n = 127). Each family records different size trends over time: an increase over time in Kielanoprionidae, where no post-Frasnian data are available; a peak in size during the Early Devonian and decrease into the KWE in Mochtyellidae, and overall stability before the KWE in Paulinitidae (Fig. 7, Supplementary Fig. 6). It is possible that individual lineages at a more specific taxonomic level drive some size changes in the overall pool, but this is impossible to determine without more detailed taxonomy. Family diversity is lower postextinction, but this is likely driven by a lack of specimens assigned to a family in the Famennian and Carboniferous, so it is difficult to assess whether community diversity is actually lower postextinction (Supplementary Fig. 7).

Scolecodonts are present in many different lithological settings. The Kellwasser Events are expressed as a black shale interval, so if small scolecodonts were associated with shales, the taphonomy of source lithology could lead to the pattern of size decrease in the KWE. When binning scolecodonts by source rock lithology, it is clear that shales preserve small and large scolecodonts, and that small scolecodonts are also found in other lithologies, although they are infrequent in limestones (Fig. 8, Supplementary Fig. 8).

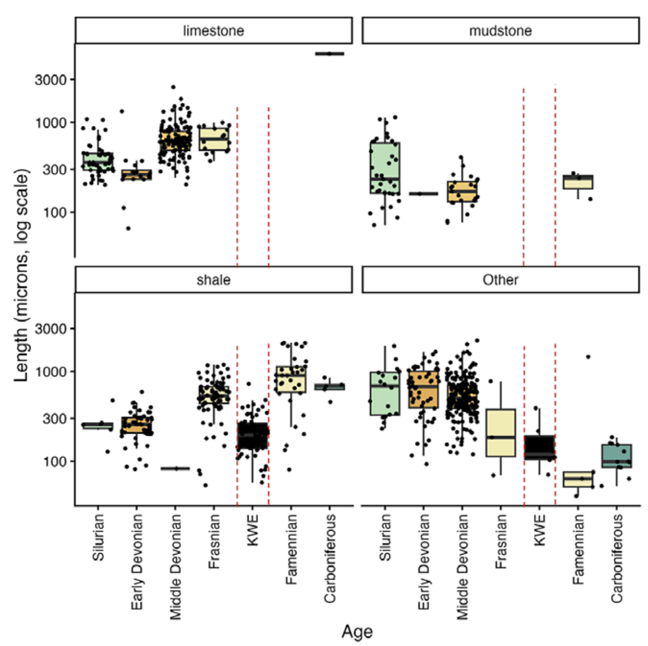

Figure 8. Box-and-whisker plots showing the length of individual scolecodonts (μm, logarithmic scale) for the three lithologies representing more than 50 individuals (limestone, n = 205; mudstone, n = 62; shale, n = 241). KWE refers to the Kellwasser Events.

Discussion

Our analyses reveal two statistically significant changes: scolecodonts increase in size from the Early Devonian to the Givetian–Frasnian, which appears more dramatic at coarse temporal resolution than fine resolution due to a size decrease in the Emsian, and decrease in size during the Kellwasser Event–associated black shale interval. The most significant change in this interval is the size decrease from before to during the Kellwasser Events, where median size declined from 500 μm to 196 μm.

https://doi.org/10.1017/pab.2026.10093 Published online by Cambridge University Press

Scolecodont size decreases substantially during the Kellwasser Events, reaching its lowest average value during this interval (Fig. 3). Size varies with geography, family, and lithology, but none of these factors alone can explain the size change over time. Because restricted basins that formed due to Late Devonian geography and sea level led to drastic interbasinal variation in climate and ecology, body-size patterns vary between basins (Fig. 6). The Michigan/Illinois/Iowa Basins and Poland record positive $\delta^{13}C$ excursions during the Kellwasser Events, but in the Appalachian Basin, this positive excursion is interrupted by a sharp decrease at the beginning of the Kellwasser Events; the Appalachian Basin negative anomaly occurs in black shales that are devoid of macrofossils (Uveges et al. 2019). This indicates it may have been a restricted basin that was more susceptible to reducing conditions, which could have driven the particularly dramatic, protracted size decrease in scolecodont size we observe in the Appalachian Basin (Cohen et al. 2022).

The size decrease observed in the Emsian is also relevant, although not the focus of this study. Most of the Emsian individuals in this study are derived from the Prague Basin near the Daleje Event, a transgressive regional event that is associated with oxygen stress (Tonarová et al. 2017). Future work should focus on improving global sampling of scolecodonts from the Emsian, as well as high-resolution sampling around the Daleje Event, to test whether this is an oxygen stress–driven diminutization paralleling the Kellwasser Events.

Mechanism of Miniaturization

As discussed in the "Introduction," several mechanisms can cause evolutionary miniaturization: the preferential survival of smaller lineages, heritable size change within lineages, and evolution of novel small morphotypes. Transient ecophenotypic plasticity can also drive miniaturization during periods of stress (Harrison et al. 2015). Determining the exact mechanism(s) of the miniaturization described here is challenging, because this study does not integrate species-level taxonomy, scolecodont taxonomic frameworks are not globally integrated, and some stratigraphy is relatively unconstrained.

Many scolecodont genera that existed in the lower Paleozoic extend stratigraphically to at least the Mississippian (Sylvester 1959), indicating they did not go extinct in the Devonian (i.e., the preferential survival of smaller lineages/extinction of larger lineages), but this is an imprecise measurement, particularly because phylogeny between the middle Paleozoic and the Recent is not well resolved (Edgar 1984). Although this pattern likely cannot account for the changes observed at a family level, it could at a lower taxonomic level. We also observe that maximum size decreases during the extinction interval, which could be interpreted as selective extinction of larger taxa. Lack of more detailed information about scolecodont lineages after the Devonian also prevents us from determining if the patterns in our data could be caused by the evolution of novel small morphotypes.

Generally, polychaete jaw size varies with body size (Ieno et al. 2000). Therefore, we assume that neoteny—the evolutionary retention of juvenile characteristics in the adult individual—cannot explain the size changes we observe. Beyond this, we do not have enough taxonomic resolution to determine whether heritable size change within lineages drives the miniaturization effect.

If the miniaturization effect is solely phenotypic plasticity (epigenetic stunting), we would still expect to see some scolecodonts in the normal size range during the extinction interval because dysoxia was not constant and ubiquitous (Boyer et al. 2021). There is some overlap between the size range of pre-extinction and within-extinction scolecodonts, and the smallest Euramerican scolecodonts are not found during the extinction interval—in fact, the smallest individuals from within the extinction interval are larger than the smallest individuals from any other time bin. In other words, the driver behind a smaller-sized assemblage is a decrease in the abundance of larger individuals (Fig. 3).

The smallest scolecodonts that exist outside the extinction interval could represent juveniles, stunted individuals, or mature individuals within the regular size distribution. A study taking more detailed morphology and taxonomy into account might be able to resolve whether one of these factors is strongest, and whether relative abundance of taxa of different median sizes varies across the extinction. Due to limited knowledge of scolecodont ontogeny, it is often not possible to determine whether scolecodonts are juvenile forms (Eriksson et al. 2004), although small individuals in the literature are sometimes speculatively labeled as juveniles (e.g., Jansonius and Craig 1971: p. 284; El Shamma et al. 2019). If a greater understanding of scolecodont taxonomy and ontogeny is achieved, it might be possible to tell what—if any—evolutionary mechanism was at play during the Late Devonian (Abbott et al. 2024).

Known Causes of Small Body Size in Annelids

Environmental factors such as dissolved oxygen concentrations, temperature, salinity, food availability, life history, sediment characteristics, and organic matter concentration all likely play a role in the size distribution of benthic infaunal invertebrates (Neuhoff 1979; Soltwedel 1996; Quiroga et al. 2005; Levin 2003). It can be difficult to distinguish which environmental factor is controlling body size in natural experiments, because oxygen availability often correlates with depth, and therefore food availability and organic matter concentration (Soltwedel et al. 1996). Further, some variables have contradictory effects depending on other conditions: for example, increased temperature can decrease body size by decreasing dissolved oxygen concentration, or increase body size by improving the efficiency of metabolic reactions (Neuhoff 1979; Massamba-N'Siala et al. 2012; Ohlberger 2013).

Assuming scolecodonts are benthic animals, the benthic oxygen crisis of the Kellwasser Events should be considered as a cause of miniaturization. Annelid body-size responses to hypoxia are poorly constrained at the individual level, although there are records of community biomass decreasing and individuals changing morphology under oxygen stress (i.e., Warren 1981; Forbes et al. 1994; Lamont and Gage 2000; Qu et al. 2015; Briggs et al. 2017; Grimes et al. 2020). Smaller organisms that passively respire are more successful under oxygen stress because they have a higher surface area to volume ratio for acquiring oxygen and distributing it to their tissues, providing a possible physiological mechanism for miniaturization (Tung et al. 2023).

Devonian marine dissolved oxygen concentration and marine temperature are poorly constrained, but some general trends have been identified (e.g., Cannell et al. 2022; Mills et al. 2023). Scolecodont size presented in this study follows an inverse pattern with recent sea-surface temperature reconstructions across the Devonian: temperatures are higher in the Early Devonian, lowest in the Middle Devonian, and higher in the Late Devonian (Chen et al. 2021). Temperature is inversely correlated with dissolved oxygen concentration, and indeed, the Middle Devonian is a period of high dissolved oxygen concentrations, while the Late Devonian extinction is associated with bottom-water anoxia (Carmichael et al. 2019). In

https://doi.org/10.1017/pab.2026.10093 Published online by Cambridge University Press

comparison, scolecodont sizes increase between the Early and Middle Devonian and decrease between the Middle and Late Devonian. Thus, without further examination, this size trend could be driven by temperature, oxygen availability, or both (Ohlberger 2013). However, lab studies on modern annelids have shown that oxygen stress has a stronger effect on annelids than temperature (Massamba-N'Siala et al. 2012).

Stunting from food loss is also a possible driver of reduced body size. Insufficient food can lead to stunting through the same evolutionary/physiological pathways as oxygen stress: preferential survival of smaller species (if smaller prey species, too, preferentially survived, therefore enabling smaller scolecodont species to survive); or phenotypic plasticity, that is, malnutrition causing organisms not to reach full mature adult body size. However, some eunicidan annelids are detritus feeders (Parry et al. 2014), and detrital organic matter would have been more available during the KWE interval than outside the interval (Pippenger et al. 2023). In addition, the size reduction we observe here across the extinction is found across the entire scolecodont assemblage, which could represent a wide range of feeding habits such as predators and detritus feeders. Ecological variables such as food availability, oxygen availability, and temperature will covary to an extent, making it difficult to parse out exactly which stressor causes each response. We prefer an interpretation that the pattern of decreasing body size is driven by the coupled environmental effects of oxygen and temperature changes.

Conclusions

Scolecodonts provide a rare insight into the behavior of soft-bodied metazoans in the Paleozoic fossil record. Scolecodont body-size data from the middle–late Paleozoic provide evidence for the Lilliput Effect occurring in marine invertebrates across the Late Devonian Biodiversity Crisis. With relatively high-resolution data on body size before, during, and after the extinction event globally, we find that the size change happens before and within the extinction event and rebounds in the Famennian. We suggest that oxygen stress, which is characteristic of the Kellwasser Events, is likely to be a contributing factor to this stress response, although we cannot discern a specific mechanism of miniaturization without an improved taxonomic and phylogenetic framework for scolecodonts.

Acknowledgments. The authors thank A. A. Kelly, E. K. Phillips, K. H. Pippenger, and members of the Williams College Cohen Lab for field work, sample preparation, and data analyses that supported this research. This article was improved by comments from D. L. Boyer and A. M. Bush, as well as the *Paleobiology* editorial board and two anonymous reviewers. Collections-based work was made possible by the Invertebrate Paleontology staff and volunteers at the Carnegie Museum of Natural History, with special thanks to the late A. D. Kollar. This work was supported by an American Chemical Society Petroleum Research Fund grant and National Science Foundation Sedimentary Geology and Paleobiology grant no. 2044223 to P.A.C.

Competing Interests. The authors declare no competing interests.

Data Availability Statement. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tqjq2bw72.

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