


Rise and diversification of chondrichthyans in the Paleozoic

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Article

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Non-technical Summary

Chondrichthyans (cartilaginous fishes, including sharks, rays, skates, and chimaeras) first appeared more than 450 million years ago in the Ordovician and diversified into many of the groups that still exist today. However, their biodiversity patterns across the rest of the Paleozoic (Silurian–Permian) are obscured by gaps in their fossil record, caused by several biases. For example, chondrichthyan skeletons are predominantly made of cartilage, which rarely fossilizes, therefore limiting the quality of their fossil record. In our study, we use a newly created dataset of chondrichthyan fossil occurrences and apply statistical methods that aim to estimate patterns of diversity from incomplete fossil samples. Through this approach, we found that chondrichthyan diversity was initially low in the Ordovician and Silurian, then increased substantially in the Early Devonian, about halfway through the Paleozoic. Diversity peaked in the middle Carboniferous before decreasing across the remainder of the Paleozoic. This peak in diversity is dominated by stem-holocephalan chondrichthyans (a major group of Paleozoic chondrichthyans). Conversely, acanthodian chondrichthyan (early shark-like fish) diversity is highest in the Early Devonian before declining rapidly by the end of the Devonian. This suggests that there were two radiations in chondrichthyan diversity during the Paleozoic: the first in the earliest Devonian, led by acanthodian chondrichthyans, and the second in the earliest Carboniferous, led by holocephalans. Early in the Paleozoic, chondrichthyans lived in shallower waters, but after the Devonian, they increasingly branched out into deeper waters. This transition coincides with the Hangenberg extinction event at the end of the Devonian, suggesting that the dispersal of chondrichthyans, specifically holocephalans, into deeper-water environments and expansion of their niches was a response to the impacts of the Hangenberg extinction event on other species in the oceans.

Abstract

The Paleozoic represents a key time interval in the origins and early diversification of chondrichthyans (cartilaginous fishes), but their diversity and macroevolution are largely obscured by heterogeneous spatial and temporal sampling. The predominantly cartilaginous skeletons of chondrichthyans pose an additional limitation on their preservation potential and hence on the quality of their fossil record. Here, we use a newly compiled genus-level dataset and the application of sampling standardization methods to analyze global total-chondrichthyan diversity dynamics through time from their first appearance in the Ordovician through to the end of the Permian. Subsampled estimates of chondrichthyan genus richness were initially low in the Ordovician and Silurian but increased substantially in the Early Devonian. Richness reached its maximum in the middle Carboniferous before dropping across the Carboniferous/Permian boundary and gradually decreasing throughout the Permian. Sampling is higher in both the Devonian and Carboniferous compared with the Silurian and most of the Permian stages. Shark-like scales from the Ordovician are too limited to allow for some of the subsampling techniques. Our results detect two Paleozoic radiations in chondrichthyan diversity: the first in the earliest Devonian, led by acanthodians (stem-group chondrichthyans), which then decline rapidly by the Late Devonian, and the second in the earliest Carboniferous, led by holocephalans, which increase greatly in richness across the Devonian/Carboniferous boundary. Dispersal of chondrichthyans, specifically holocephalans, into deeper-water environments may reflect a niche expansion following the faunal displacement in the aftermath of the Hangenberg extinction event at the end of the Devonian.

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Introduction

The early fossil record of chondrichthyans (cartilaginous fishes, including sharks, rays, skates and chimaeras) likely dates back to the Late Ordovician (Young 1997; Sansom et al. 2001, 2012; Andreev et al. 2015, 2016; Sansom and Andreev 2017). However, undoubted chondrichthyans first appeared in the early Silurian (Andreev et al. 2022a,b; Zhu et al. 2022) and rapidly diversified during the Devonian and early Carboniferous (Coates et al. 2018), alongside other major jawed vertebrate groups such as actinopterygians, sarcopterygians, and placoderms (Janvier 1996; Sepkoski 2002; Turner 2004; Brazeau 2009; Ginter et al. 2010; Sallan and Coates 2010). The recognition of the acanthodians, a group of Paleozoic spiny fusiform fishes, as a grade within the chondrichthyan stem-group has added considerable data to the earliest chondrichthyan fossil record (e.g., Brazeau 2009; Davis et al. 2012; Coates et al. 2018; Dearden et al. 2019; Burrow 2021) and identified a crucial step in early chondrichthyan evolution. However, to this date, in-depth patterns of chondrichthyan diversification across the Paleozoic have not been quantified.

The Paleozoic era was a period of major geological, environmental, and biotic changes. Despite the importance of this time interval for the initial early chondrichthyan radiation and diversification on both global and regional scales, diversity analyses of Paleozoic chondrichthyans are either constrained to shorter periods such as the Devonian/Carboniferous boundary and the Carboniferous (Sallan and Coates 2010; Feichtinger et al. 2021; Ginter 2021) or based on direct comparisons between and within selected faunal associations and geographic regions (e.g., Zhao and Zhu 2007; Grogan et al. 2012). The Hangenberg extinction event during the transition from the Devonian to the Carboniferous was recovered as representing a crucial bottleneck in the evolutionary history of vertebrates with subsequent large diversification events of major groups in the early Carboniferous, including chondrichthyans (Sallan and Coates 2010). Conversely, the prominent Kellwasser event (one of the “big five” mass extinctions) at the Frasnian/Famennian stage boundary, previously reported to have caused a loss of 50–60% of marine genera (Raup and Sepkoski 1982; McGhee 1996), was shown in a subsequent study to be of minor significance in vertebrate groups, including chondrichthyans, and more likely to be biased by insufficient sampling (Sallan and Coates 2010). Furthermore, changes in elasmobranch diversity and the environment during the Carboniferous, including the ongoing closure of the Rheic-Tethys Gateway and an unstable period of multiple glaciation phases and high sea-level fluctuations, have been proposed to be closely linked (Feichtinger et al. 2021).

Aside from abiotic influences, uneven sampling of the fossil record has long been established as limiting our ability to estimate true diversity (Raup 1972; Sepkoski et al. 1981; Alroy et al. 2001; Peters and Foote 2001). Several studies have investigated the influence of a variety of biases on observed diversity in different fossil groups, including terrestrial and marine vertebrates, marine invertebrates, insects, and plants (Alroy et al. 2008; Barrett et al. 2009; Butler et al. 2011; Cascales-Miñana et al. 2013; Vilhena and Smith 2013; Clapham et al. 2016; Dunne et al. 2018; Close et al. 2020a, b). Most recently, the fossil record of Paleozoic actinopterygians was found to be heavily skewed by sampling biases, resulting in a lack of taxonomic signal throughout most of the era (Henderson et al. 2022). To estimate diversity with the

incompleteness of the fossil record in mind, statistical methods have been introduced to standardize samples to equal levels of completeness and at least partially mitigate these biases (Alroy 2010; Chao and Jost 2012; Close et al. 2018).

The present work has two aims: First, we present a comprehensive genus- and species-level dataset of Paleozoic chondrichthyans from the Ordovician to the end-Permian to explore patterns in global diversity through time using two measures of sampling standardization (coverage-based sampling standardization and squares extrapolation). Second, we examine the impact of the Kellwasser and Hangenberg extinction events on the major chondrichthyan grades.

Methods

Dataset

We compiled a dataset of 1318 occurrences, representing 443 genera of Paleozoic total-group chondrichthyans, from the Late Ordovician (Darriwilian) to the end of the Permian (Changhsingian) (<https://doi.org/10.5061/dryad.zpc866tfn>). Fossil occurrences were initially gathered from museum visits and augmented with peer-reviewed literature. Taxonomic information from museum catalogs was checked for validity and corrected to the latest accepted taxonomic name and systematic position if applicable. Taxa were included based on both standard and more recent taxonomic literature and reviews (e.g., Denison 1979; Zangerl 1981; Stahl 1999; Ginter et al. 2010; Burrow 2021). The total-group chondrichthyan dataset includes the acanthodian grade as part of the chondrichthyan stem-group as well as putative stem chondrichthyan taxa such as *Kathemacanthus*, *Seretolepis*, and *Doliodus* (e.g., Brazeau 2009; Davis et al. 2012; Coates et al. 2018; Dearden et al. 2019; Frey et al. 2020) and the Ordovician scale-based taxa *Tezakia*, *Canyonlepis*, *Tantalepis*, and *Solinallepis* (Sansom et al. 2001, 2012; Andreev et al. 2015, 2016; see Supplementary Information for a full list of included genera and species; acanthodian data and information obtained from Schnetz et al. [2022]).

Tooth-based taxa whose taxonomic status is debated but has not been officially revised or formally considered as *nomina dubia* were retained in the dataset. Most of the taxonomic uncertainty for fossils identified beyond family level in chondrichthyans occurs at the species level (e.g., in several holocephalan lineages; see Stahl 1999) and will not substantially affect genus-based diversity analyses. Two iniopterygian specimens described as members of the Sibirhynchidae by Pradel (2010) were included as separate operational taxonomic units (OTUs) because they probably represent distinct but currently unnamed taxa (following the approach of Cashmore and Butler (2019) in dealing with OTUs in theropods) and likely increase the diversity of the group in the late Carboniferous. Additionally, two very incomplete acanthodian specimens were included in the analyses as separate OTUs because they extend the acanthodian occurrence range into the middle Permian (Mutter and Richter 2007). Information on lithostratigraphy (e.g., geological formation), geographic locality, and chronostratigraphic age were recorded for each occurrence. Paleoenvironmental information was gathered from published sources where detailed lithostratigraphic descriptions for the occurrences were available. Modern coordinates were obtained for each locality and were translated into paleocoordinates using the function *reconstruct()* (default model option) in the R package *rgplates* (v. 0.3.2; Kocsis et al. 2023).

Subsets and Explanation of Phylogenetic Concepts Used

The dataset was subsampled using multiple parameters to compare the diversity patterns of different subsets. Total-group chondrichthyans examined in this study were subsampled to assess relative diversity patterns of major chondrichthyan groups. First, the data were arbitrarily divided into acanthodian chondrichthyans and non-acanthodian chondrichthyans following the data and divisions used in Schnetz et al. (2022). Following recent phylogenetic analyses by Dearden et al. (2019) and Frey et al. (2020), acanthodians are placed as paraphyletic grade stem-group chondrichthyans. *Pucapampella* and all taxa more closely related to the chondrichthyan crown are excluded from the acanthodian division. *Brochoadmones* and *Lupopsyrus* are retained, even though they fall outside the acanthodian grade (sensu Dearden et al. 2019), as they were traditionally described as acanthodians and possess an acanthodian-like body plan (Hanke and Wilson 2006; Hanke and Davis 2012).

Subsequently, the chondrichthyan crown was subsampled into total-group Holocephali (which includes the symmoriiforms) and total-group Elasmobranchii following the phylogenetic analyses mentioned earlier (and detailed in the Supplementary Data). Clades that were not included within these analyses (petalodontiforms, eugeneodontiforms, etc.) but that are generally included within either Holocephali or Elasmobranchii based on extensive catalogs (see Stahl 1999; Ginter et al. 2010) were also added. Additionally, we grouped together taxa falling on the chondrichthyan stem (such as acanthodians, sinacanthids, mongolepids, elegestolepids, omalodontiforms, antarctilamniiforms, etc.) to contrast their diversity trajectories with the patterns of the crown-group. This is an inclusive approach that has not been adopted before, and we acknowledge that some of these taxa might occupy an *incertae sedis* location on the stem, while others introduce no more than a cluster of unresolved branches within the chondrichthyan tree. Further information is available in the Supplementary Data files.

Similarly, we created an additional subset within total-group Holocephali, capturing all taxa with tooth plates, which is perhaps the most distinctive of holocephalan characteristics. The aim here was to assess whether the emergence of this dentition type coincides with major patterns of diversification. This includes no prior assumption that tooth-plated forms constitute a monophyletic group. Tree-based systematics were contrasted with the use of traditional, but not strictly phylogeny-based, taxonomic schemes employed by Ginter et al. (2010) and in part by Stahl (1999). These schemes group chondrichthyans into the two subclasses Elasmobranchii (which includes the symmoriiforms) and Euchondrocephali (which includes the Holocephali as well as orodontiforms, eugeneodontiforms, and petalodontiforms) on generalities of dental morphologies rather than a character-based hierarchy, resulting in a different setup of groupings (see the Supplementary Data). This differential division was undertaken to test how robust subgroup chondrichthyan diversity inferences are through time under conflicting phylogenetic estimates.

Following the subdivisions, we subsampled the data for chondrichthyans iteratively, excluding Holocephali (following the phylogenetic divisions) as well as Euchondrocephali (sensu Ginter et al. 2010) to assess whether they dominated specific time intervals. Finally, possible environmental influences were tested by subsetting the dataset into occurrences from freshwater or marine deposits. Depositional settings of each occurrence were then further divided into benthic assemblage zones (BA) in subsequent

analyses. Benthic assemblage zones are categorized into fresh water (BA0); intertidal above typical wave base (BA1); shallow subtidal and/or lagoon (BA2); deeper subtidal and/or reefs (BA3); middle to outer shelf (BA4 and BA5); and shelf margin toward the bathyal region (BA6) (Boucot and Janis 1983; Boucot and Lawson 1999; Sallan et al. 2018).

Sampling and Diversity

All data manipulation, statistical analyses, and data plotting were conducted in R v. 4.2.0 (R Core Team 2019). Fossil occurrences were binned into single geological stages and used to estimate raw global sampled-in-bin richness curves for chondrichthyans. We also counted the total number of formations and collections for each geological stage to check for sampling biases. Local richness, or alpha diversity, was estimated by counting genera per collection and genera by formation. Collection here is equivalent to an individual fossil locality (e.g., a quarry or road cutting). The fossil record of any given group will have spatial and temporal variations in sampling that must be accounted for when reconstructing diversity patterns through time (e.g., Raup 1972; Benson and Upchurch 2013; Close et al. 2018; Alroy 2020; Dillon et al. 2023). We largely follow the protocols used in recent fossil diversity studies (e.g., Dunne et al. 2018; Allen et al. 2020; Dean et al. 2020) and use shareholder quorum subsampling (SQS) as our method of coverage-based sampling standardization to correct for uneven sampling when estimating changes in global diversity through time (Alroy 2010). Diversity and subsampling analyses were generated using the R packages *divDyn* (v. 0.8.1; Kocsis et al. 2019) and *iNEXT* (v. 3.0.0; Hsieh et al. 2016). *iNEXT* implements coverage-based rarefaction using the equations of Chao and Jost (2012) and is analogous to SQS. We did not conduct the optional three-collections-per-reference protocol proposed by Alroy (2010) for either analysis because Paleozoic chondrichthyans are not subject to overreporting of common taxa (Supplementary Fig. S1). We additionally estimated sample coverage through time using the Good's *u* estimator (Good 1953), calculated via the *binstat()* function in the *divDyn* package (Supplementary Fig. S2).

Subsampled richness estimates were additionally calculated using the squares estimation implemented by Alroy (2018). Squares is a simple extrapolator that was developed to minimize underestimation when abundance distributions are uneven (see Supplementary Fig. S1 for the data used in this study) and is based on the proportion of singletons in a given sample (Alroy 2018). In contrast to coverage-based subsampling, squares is more robust when distributions are highly uneven and samples are small (Alroy 2020). Squares richness estimates were calculated based on the protocol by Allen et al. (2020), which uses Alroy's squares equation (Alroy 2018). In addition to curves of diversity through time, we also calculated coverage-based rarefaction curves for each geological stage to illustrate how sampling coverage of genus richness estimates varies between time intervals. We analyzed evolutionary dynamics of speciation and extinction for Paleozoic chondrichthyans based on speciation and extinction rates using the package *divDyn* and calculated second-for-third extinction rates implemented by Alroy (2015). We used generalized least-squares regressions (GLS) to make time-series comparisons between the changes in diversity of the raw and subsampled curves, calculated using the R package *nlme* (Pinheiro et al. 2018). A first-order autoregressive model (corARMA) was used to reduce temporal autocorrelation of regression lines, and

likelihood ratio-based pseudo- R^2 values were calculated to determine the amount of variance, using the function *r.squaredLR()* in the R package MuMIn (v. 3.1-157; Barton 2018). While our analyses focus on temporal patterns, we additionally quantified geographic sampling in the chondrichthyan fossil record using mean pairwise distance (PD), great-circle distances (GCD), and summed minimum spanning tree length (MST) (Close *et al.* 2017). The spatial metrics were calculated for each continent and time bin using the function *sdSummary()* in the R package *divvy* (v. 0.2.0.9000; Antell 2023).

Results

Raw counts of Paleozoic chondrichthyan global genus richness peak in the Early Devonian and early Carboniferous before dropping steeply over the Carboniferous/Permian boundary with no significant recovery throughout the Permian (Fig. 1). Local richness (alpha diversity) is highest during the Mississippian of the Carboniferous, with two exceptionally well-sampled sites in the Viséan (>50 genera) (Fig. 1). However, most collections (= localities) throughout the Paleozoic contain fewer than 10 genera (Supplementary Fig. S3). Raw genus richness closely tracks patterns of sampling, especially in the number of collections, which is equivalent to the number of fossil localities ($p = 3.3 \times 10^{-15}$, $R^2 = 0.86$). This relationship between raw richness and sampling is also strong for the total number of formations ($p = 7.7 \times 10^{-14}$, $R^2 = 0.83$). Geographic sampling through time varies among continental regions (Supplementary Figs. S10, S11). While data are too limited to quantify MST, GCD, and PD metrics for Africa, South America, and Antarctica, curves are similar for North America, Europe, and Asia (Supplementary Fig. S11). GCD shows little variation through time, while PD fluctuates considerably. MST varies throughout the Silurian and Early Devonian but remains fairly constant throughout the remaining Paleozoic.

Coverage-standardized richness estimates produce similar diversity-through-time curves to those for raw diversity (Fig. 2A, Table 1). The most notable differences can be seen in the Middle and Late Devonian: standardized diversity for chondrichthyans drops in the Eifelian and decreases from the Frasnian to Famennian, which is the reverse of the pattern in the raw richness curve. The relative changes in diversity, specifically the prominent spikes in the Devonian, Carboniferous, and early Permian, are less pronounced at lower quorum levels (0.5 and 0.6) but are still recovered. The investigated intervals of the Paleozoic have varying degrees of completeness as shown by the coverage estimates, but most are higher than 75% (Supplementary Fig. S4). The slopes of the rarefaction curves indicate that sampling is more complete in most stages of the Devonian and Carboniferous and limited in the Silurian. In the Permian, we find stages with both more complete sampling (e.g., Roadian, Wordian, and Capitanian) and limited sampling (e.g., Changhsingian, Sakmarian, and Asselian).

Squares diversity estimates differ from coverage-standardized richness estimates in several instances; higher values are recovered for the Permian after an initial drop across the Carboniferous/Permian boundary, and there are more pronounced diversity estimates in the Roadian and Wuchiapingian (Fig. 2B, Table 1). Second-for-third (= corrected) origination and extinction rates show major origination peaks in the Gorstian, Lochkovian, and Tournaisian, while rates of extinction are highest in the Homerian, Famennian, Gzhelian, and Kungurian (Fig. 2C, Supplementary Table S1).

Coverage-standardized diversity is dominated by acanthodian chondrichthyans in the late Silurian and the Early Devonian, but this group decreases in diversity throughout the Middle and Late Devonian (Fig. 3). Diversity of acanthodians plummets across the Devonian/Carboniferous boundary and steadily decreases throughout the Carboniferous and Permian. By contrast, non-acanthodian chondrichthyan richness rises substantially from the Middle Devonian through to the early Carboniferous (Eifelian–Viséan) and remains at high levels during the remaining stages of the Carboniferous before decreasing substantially across the Carboniferous/Permian boundary (Fig. 3). The Permian is dominated by non-acanthodian chondrichthyans, but diversity remains at generally lower levels than in the Carboniferous.

Total-group Elasmobranchii and Holocephali first appear in the Early Devonian, although holocephalans are first detected slightly later in time (Fig. 4). Holocephali dominate the rise in chondrichthyan diversity throughout the Carboniferous (Supplementary Fig. S7). Upon removal of holocephalans from the dataset, coverage-standardized richness estimates and squares diversity are considerably lower throughout the Carboniferous (Supplementary Fig. S5). When the chondrichthyan stem-group is considered as a whole, the pattern of Early Devonian diversification and Late Devonian fall, as already seen in the acanthodian chondrichthyans, is reinforced and further amplified (Fig. 4). Stem chondrichthyans appear to persist throughout the remainder of the Paleozoic but in lower numbers. Tooth-plated holocephalans emerge in the Middle Devonian and diversify considerably post-Devonian before decreasing heavily at the Carboniferous/Permian boundary, together with all other subgroups (Fig. 4). Raw and subsampled richness estimates recover similar patterns of diversity for total-group elasmobranchs and holocephalans, except for a slight temporal shift in holocephalan peak diversity from the Viséan toward the Serpukhovian in the subsampled curve (Fig. 4A,B). Comparisons with patterns of subclasses as implemented by Ginter *et al.* (2010) reveal highly similar diversity trajectories through time (Supplementary Fig. S6).

Chondrichthyans are recovered solely from marine localities in the Ordovician and early Silurian, with the first freshwater occurrences appearing in the middle Silurian (Supplementary Fig. S8). The Carboniferous shows an increase in marine alpha diversity in the Mississippian, and a peak in marine alpha diversity in the Viséan (Supplementary Fig. S8). Further division into benthic assemblage zones reveals that the initial origination of marine chondrichthyans is restricted to the shallow-marine BA1 and BA2 zones (Supplementary Fig. S9A). Chondrichthyans expand into the deepwater BA5 and BA6 zones in the late Silurian; however, alpha diversity only increases in the Carboniferous, with diverse deepwater localities recovered in the Viséan specifically (Supplementary Fig. S9B).

Discussion

Patterns of Paleozoic Chondrichthyan Diversity

Our results demonstrate how Paleozoic chondrichthyan diversity peaked in the Early Devonian–early Carboniferous before dropping steeply over the Carboniferous/Permian boundary, with no significant recovery throughout the Permian (Fig. 2). Coverage-standardized richness shows a decrease in diversity from the Frasnian to Famennian following the Kellwasser extinction event, albeit less pronounced than the drops in diversity in

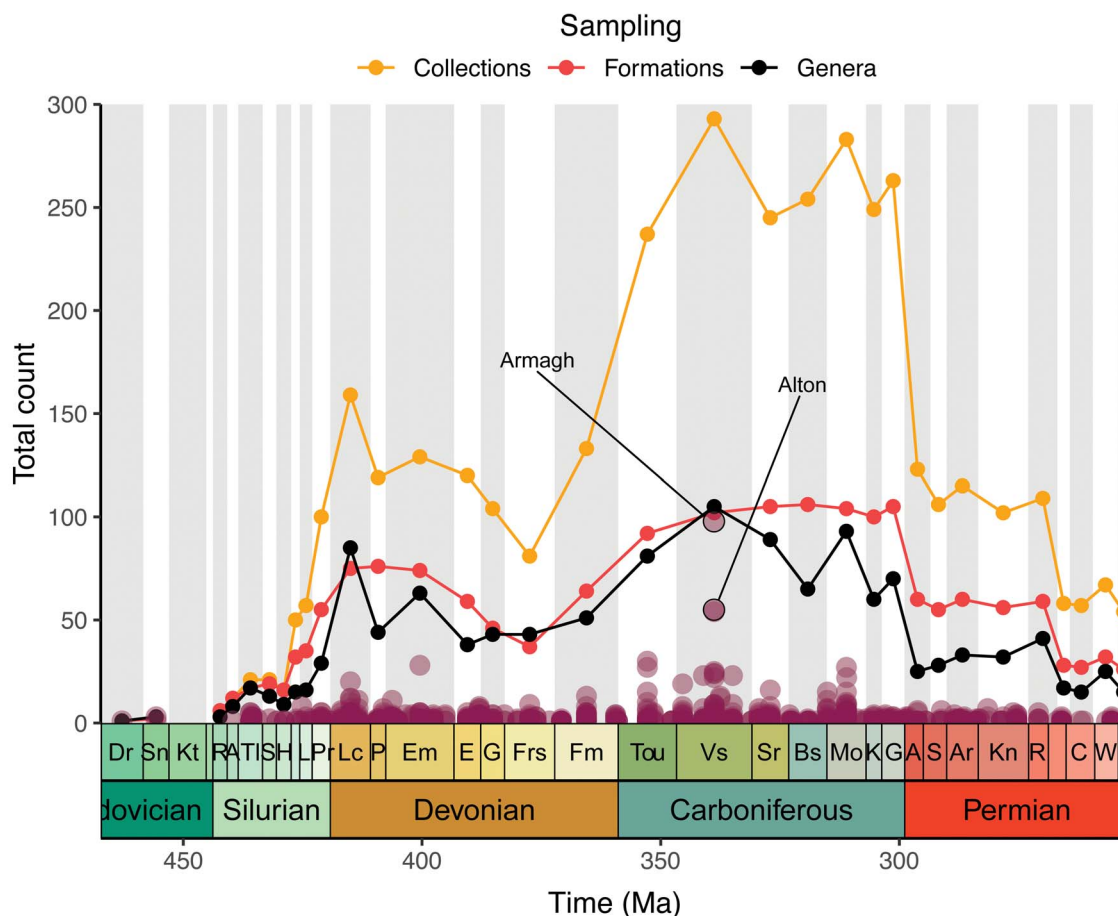


Figure 1. Chondrichthyan raw genus richness, local richness (alpha diversity), and sampling proxies in the Paleozoic. Sampling proxies include counts of total collections and fossiliferous formations containing Paleozoic chondrichthyans for each interval. Alpha diversity here is the number of genera per collection (= locality), depicted as purple density circles. Chronostratigraphic stage abbreviations from left to right: Dr, Darriwilian; Sn, Sandbian; Kt, Katian; R, Rhuddanian; A, Aeronian; Tl, Telychian; S, Sheinwoodian; H, Homerian; L, Ludfordian; Pr, Pridoli; Lc, Lochkovian; P, Pragian; Em, Emsian; E, Eifelian; G, Givetian; Frs, Frasnian; Fm, Famennian; Tou, Tournaisian; Vs, Viséan; Sr, Serpukhovian; Bs, Bashkirian; Mo, Moscovian; K, Kasimovian; G, Gzhelian; A, Asselian; S, Sakmarian; Ar, Artinskian; Kn, Kungurian; R, Roadian; C, Capitanian; W, Wuchiapingian. Empty stage cells from left to right correspond to the Hirnantian, Gorstian, Wordian and Changhsingian.

the Lochkovian–Pragian and Emsian–Eifelian (Fig. 2A). However, raw richness and squares diversity instead show steep increases in diversity during the Kellwasser event (Figs. 1, 2B). A disagreement between SQS estimates and squares estimates has also been reported in previous diversity studies (Brocklehurst 2021; Henderson et al. 2023) and may be a result of the data or the methods themselves. Squares was introduced to estimate diversity more accurately than SQS when abundance distributions are highly uneven (Close et al. 2018; Alroy 2020). However, previous studies have also pointed out that richness extrapolators such as squares may be strongly sample size-dependent when samples are relatively small and incomplete, which is a caveat for most fossil record data (Close et al. 2018). Therefore, focusing on the results from SQS, we find that chondrichthyan diversity increases over the Devonian/Carboniferous boundary following the Hangenberg extinction event at the end of the Famennian stage (Fig. 2A,B). Chondrichthyan alpha diversity showed an increase in deeper-water localities in the Mississippian and again in the Middle Pennsylvanian (see Supplementary Fig. S8). This indicates that Carboniferous chondrichthyans may have refilled the deep-water environments that became available after the Hangenberg extinction. However, this apparent pattern may also be skewed

by sampling biases against available outcrop for marine deepwater sediments compared with the continental shelf in other periods of the Paleozoic (Gregor 1970; Smith et al. 2002).

When total-group chondrichthyans are separated into acanthodian and non-acanthodian chondrichthyans, coverage-based subsampling shows a substantial loss for acanthodians throughout the Middle and Late Devonian while non-acanthodian chondrichthyans gradually increase in diversity through the Late Devonian (Fig. 3). Sallan and Coates (2010) illustrated a similar pattern, albeit with a less severe decrease in acanthodians. As suggested previously, the Kellwasser event might be overreported in severity by insufficient sampling of Famennian localities relative to Frasnian localities (Sallan and Coates 2010; Friedman and Sallan 2012). Our coverage-based rarefaction curves, however, do not show considerable differences between the two stages (Supplementary Fig. S4A), and thus fail to support this qualification. Acanthodians thrived in the Early Devonian but declined from the Middle Devonian onward. The diversity of non-acanthodian chondrichthyans shows a similar pattern in the Early Devonian but, conversely to acanthodians, significantly increases from the latest Devonian onward. Few acanthodian-grade chondrichthyans survived the Hangenberg extinction,

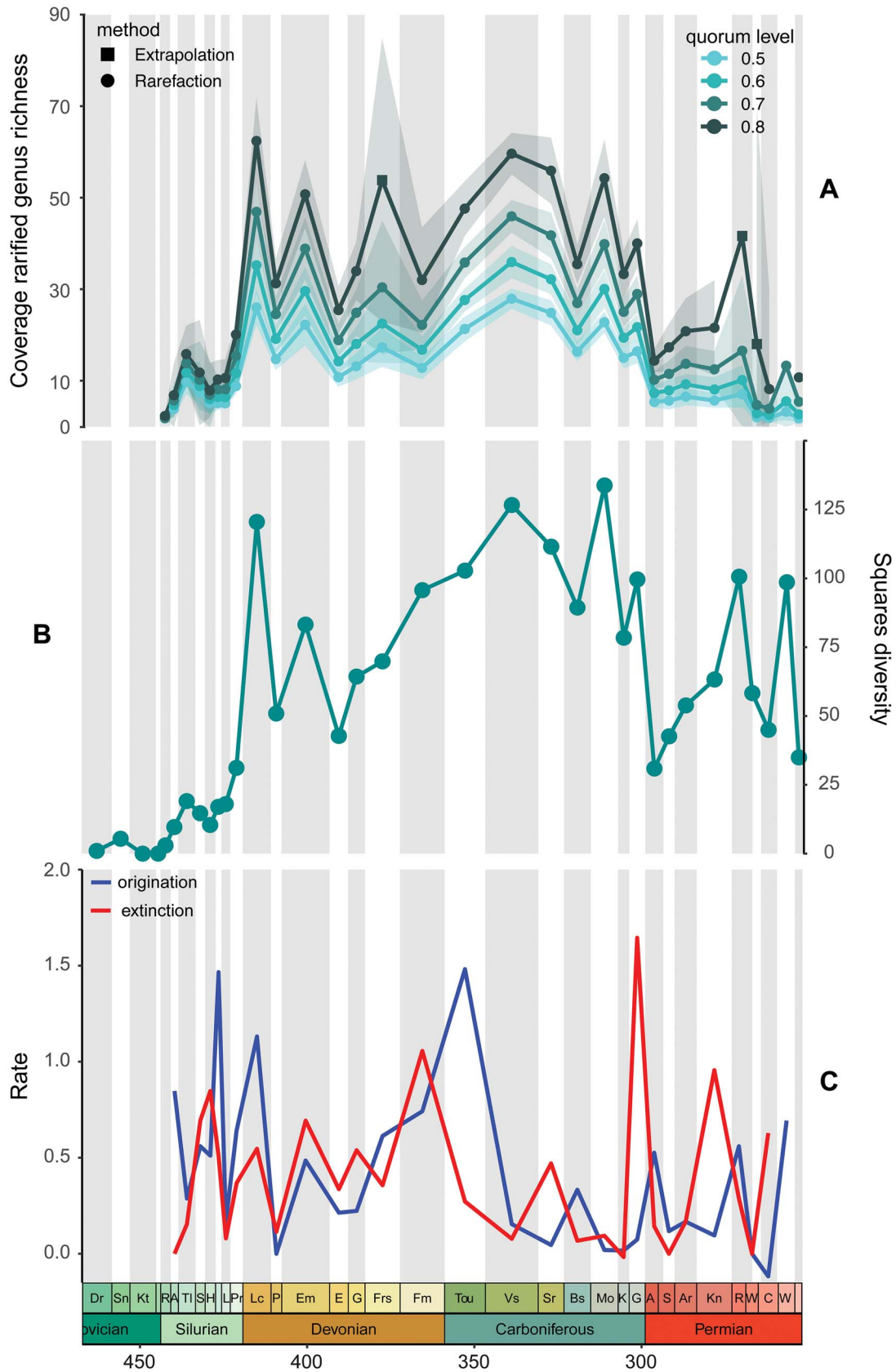


Figure 2. Chondrichthyan subsampled genus diversity and origination/extinction rates in the Paleozoic. A, coverage-standardized diversity at different quorum levels. Quorum levels represent the target sampling (coverage) level. B, Squares diversity. C, Second-for-third origination/extinction rates. See Fig. 1 for stage abbreviations.

Table 1. Results of pairwise comparisons of different diversity estimates using generalized least-squares regressions (GLS).

Comparison ^a	Slope	t-value	p-value ^b	R ²
Raw richness ~ squares diversity	0.54	11.67	>0.00001	0.915
Raw richness ~ SQS diversity (0.5)	3.22	15.36	>0.00001	0.945
Raw richness ~ SQS diversity (0.6)	2.41	16.54	>0.0001	0.952
Raw richness ~ SQS diversity (0.7)	1.79	16.71	>0.00001	0.952
Raw richness ~ SQS diversity (0.8)	1.20	10.75	>0.00001	0.925
Squares diversity ~ SQS diversity (0.5)	4.47	7.30	>0.00001	0.744
Squares diversity ~ SQS diversity (0.6)	3.44	7.99	>0.00001	0.772
Squares diversity ~ SQS diversity (0.7)	2.70	9.72	>0.00001	0.828
Squares diversity ~ SQS diversity (0.8)	1.83	10.65	>0.00001	0.905

^aSQS, shareholder quorum subsampling

^bStatistically significant results indicated in bold.

and they failed to diversify substantially in the post-Devonian. They appear to have been outcompeted and niche-restricted “Dead Grade Swimming” (adapted from “Dead Clade Walking” of Jablonski 2001; Sallan and Coates 2010). The earliest acanthodians inhabited the shallow seas of the early Silurian (Andreev et al. 2022b; Zhu et al. 2022) but quickly expanded into freshwater habitats during the late Silurian and Early Devonian (Supplementary Fig. S8), a pattern consistent with previously published hypothesis of early vertebrate diversification (Sallan et al. 2018). This transition may have allowed them to mitigate competition and predation pressure, particularly from the dominant Silurian macropredatory eurypterids (Lamsdell and Braddy 2010). By the end of the Devonian, diverse assemblages of jawed vertebrates, including chondrichthyans, osteichthyans, placoderms, and tetrapods, are found in the increasingly productive and complex estuarine and freshwater ecosystems, linked to the expansion of terrestrial vascular plants during the Middle and Late Devonian (Beerbower 1985; Davies and Gibling 2010). However, acanthodians started to decline during this time interval, and post-Devonian acanthodians primarily consist of only two highly specialized genera, *Gyracanthus* and *Acanthodes*.

While acanthodians struggled, non-acanthodian chondrichthyan diversity increased from the Early Devonian on, albeit dipping in the Middle Devonian, and peaked throughout the Carboniferous following the Hangenberg extinction (Fig. 3). The great post-Hangenberg diversification of chondrichthyans is predominantly driven by the rise of the Holocephali (or Euchondrocephali sensu Ginter et al. 2010), a division of crown-group chondrichthyans of which the chimaeras still exist in today’s deeper-water environments (Lund and Grogan 1997, 2004; Grogan and Lund 2000). They first appeared in the Devonian, but their fossil record is scarce and fragmentary at best until the latest Devonian (see Supplementary Information). Following the Hangenberg extinction, holocephalans greatly diversified and drove total chondrichthyan diversity throughout the Carboniferous before losing diversity across the Carboniferous/Permian boundary (Fig. 4, Supplementary Fig. S7). This diversification follows major changes in the jawed vertebrate biota over the Late Devonian and early Carboniferous, most notably the extinction of placoderms and severe decreases in diversity of aquatic sarcopterygians (Sallan and Coates 2010). It is possible that this faunal transformation

is the subject of gradual and/or competitive displacement (Jablonski 2005; Zhao and Zhu 2007) as well as the refilling of niche space following a large-scale mass extinction (Sallan et al. 2011). As suggested by Janvier (1996) and Blieck (2011), holocephalans may have experienced a lowered predation pressure and competition for available niches, allowing them to thrive and establish themselves in the postextinction conditions of the early Carboniferous. There is further evidence for this in the response of crinoid diversity to predator–prey interactions around the timing of the Hangenberg event, showing a shift from reduced pressure after the extinction (removal of major vertebrate predators) to increased pressure in the later Mississippian (introduction of “new” durophagous fishes such as holocephalans) (Sallan et al. 2011). Tooth-plated forms greatly diversify only after the Hangenberg extinction event (Fig. 4). Interestingly, Carboniferous holocephalans predominantly dispersed into both shallow and deeper waters, a pattern similar to the mid-Paleozoic diversification of micromeric stem-group gnathostomes such as the thelodonts (Sallan et al. 2018).

Direct comparisons of our standardized diversity estimates to previous studies are mostly limited to the Late Devonian and Carboniferous (Sallan and Coates 2010; Feichtinger et al. 2021), specifically the Frasnian–Famennian Kellwasser crisis (McGhee 1996), the end-Devonian Hangenberg extinction event that directly precedes the Devonian/Carboniferous boundary (Caplan and Bustin 1999; Marshall et al. 2020), and the end-Permian mass extinction (Raup and Sepkoski 1982). Sallan and Coates (2010) reported no major diversity losses for most jawed vertebrates, including chondrichthyans, through the Kellwasser event. Our SQS analyses recover a decrease in chondrichthyan diversity, albeit very gentle (Fig. 5B,D). In contrast, the increase in chondrichthyan diversity after the Hangenberg extinction reported here is comparable to that seen in the diversity curve of Sallan and Coates (2010) but differs from the diversity curve from Feichtinger et al. (2021), which was based solely on elasmobranchs (Fig. 5). Chondrichthyan diversity steadily increased from the Givetian to the Viséan and dropped in the Serpukhovian, as reported by Sallan and Coates (2010). This pattern is mostly congruent with our estimates of richness, except for a peak in the Frasnian in our coverage-standardized richness estimates that is not shown in Sallan and Coates (2010) (Figs. 2A,5). Feichtinger et al. (2021) reported an increase in diversity through the Mississippian, with highest numbers in the Serpukhovian

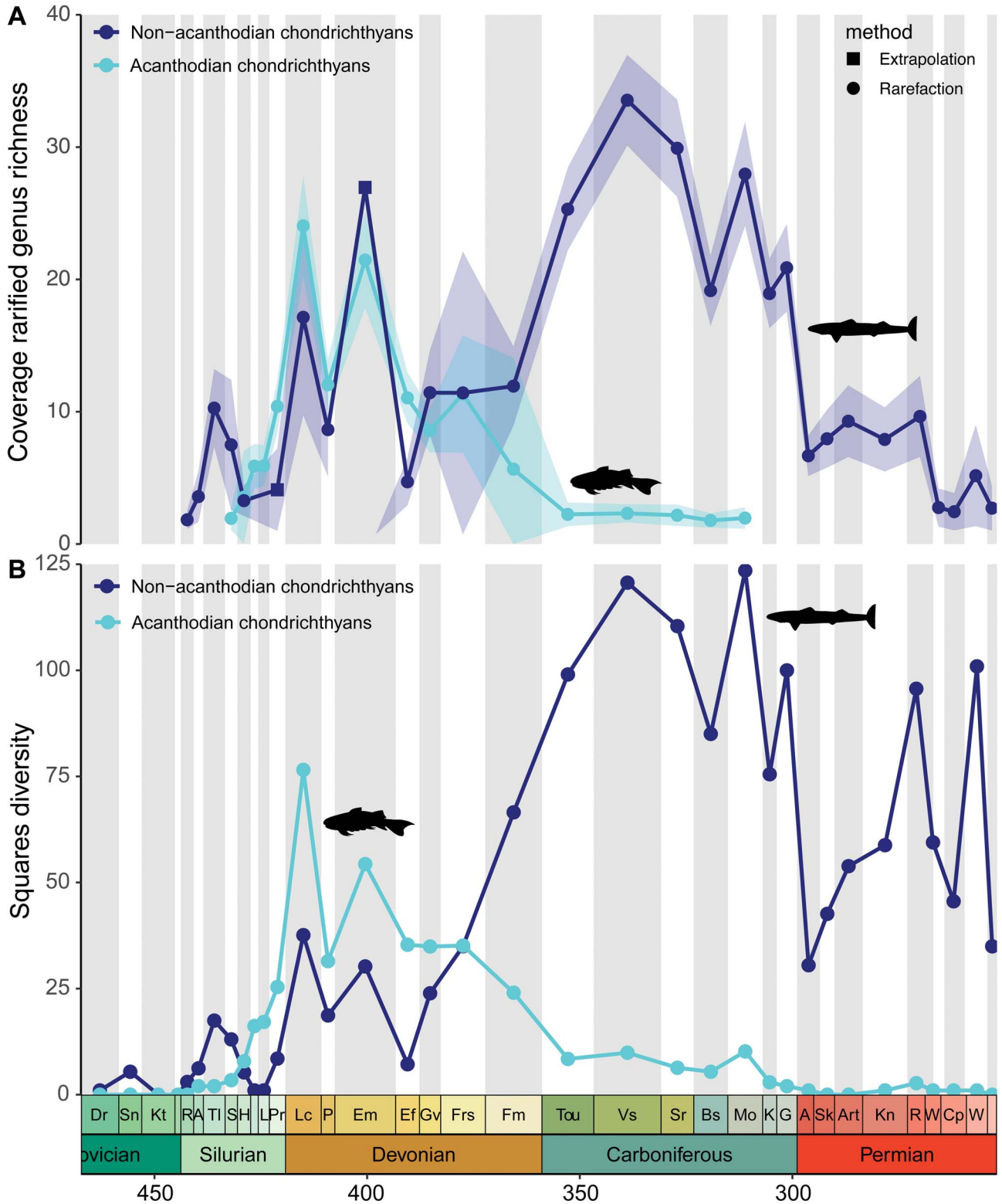


Figure 3. Coverage-standardized diversity (A) and squares diversity (B) for acanthodian and non-acanthodian chondrichthyans through the Paleozoic. Coverage-standardized diversity was computed at quorum level 0.6. Silhouettes taken from <http://phylopic.org>. Chronostratigraphic stage abbreviations from left to right: Dr, Darrivilian; Sn, Sandbian; Kt, Katian; R, Rhuddanian; A, Aeronian; TI, Telychian; S, Sheinwoodian; H, Homerian; L, Ludfordian; Pr, Pridoli; Lc, Lochkovian; P, Pragian; Em, Emsian; Ef, Eifelian; Gv, Givetian; Frs, Frasnian; Fm, Famennian; Tou, Tournaisian; Vs, Visean; Sr, Serpukhovian; Bs, Bashkirian; Mo, Moscovian; K, Kasimovian; G, Gzhelian; A, Asselian; Sk, Sakmarian; Art, Artinskian; Kn, Kungurian; R, Roadian; W, Wordian; Cp, Capitanian; W, Wuchiapingian. Empty stage cells from left to right correspond to the Hirnantian, Gorstian and Changhsingian

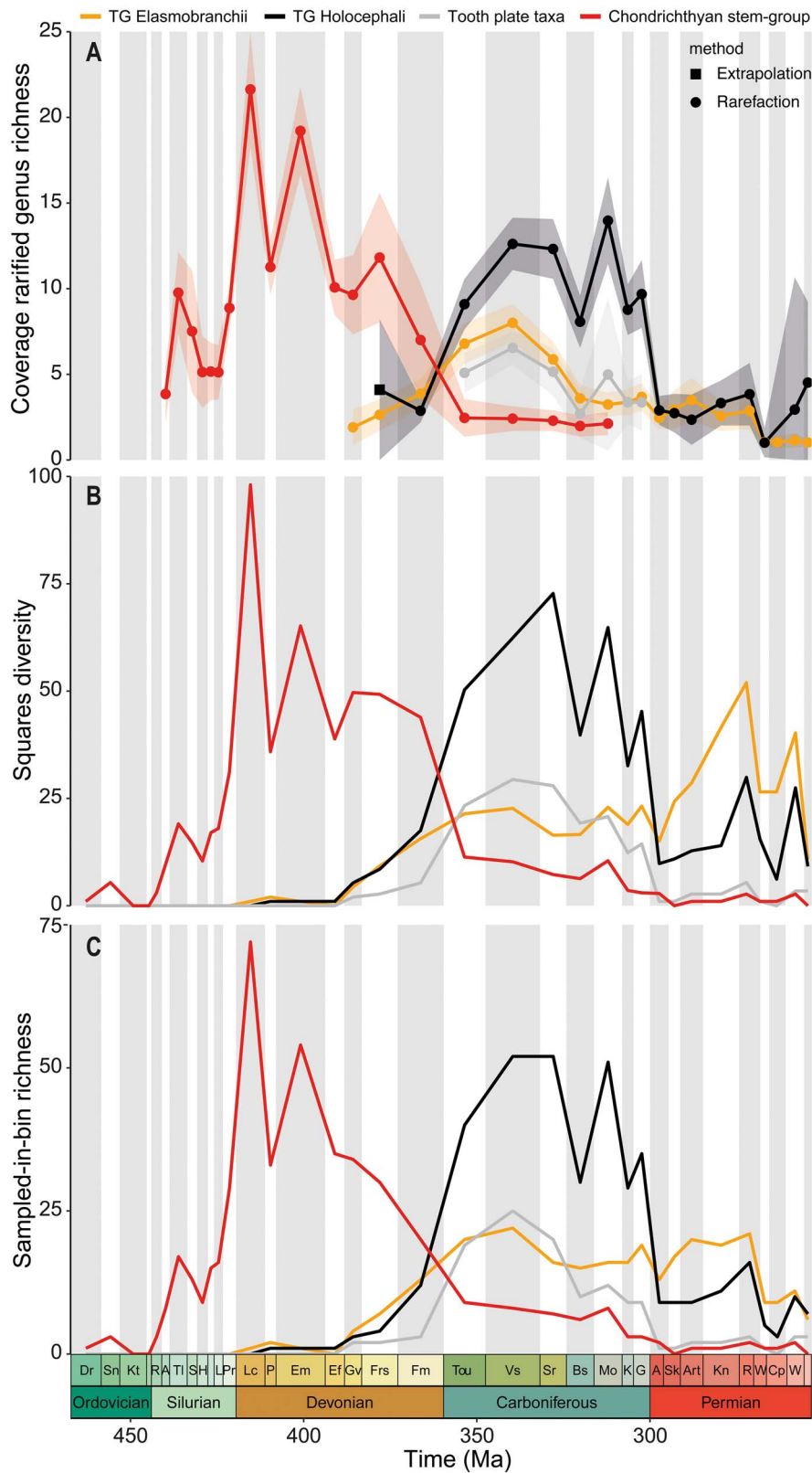


Figure 4. Subsampled and raw richness estimates of chondrichthyan subgroups. Subgroupings are based on the recent phylogenies from Coates et al. (2018), Dearden et al. (2019), and Frey et al. (2020). A, Coverage-standardized diversity. B, Squares diversity. C, Raw sampled-in-bin richness. TG, total group. Tooth plate taxa here are a subset of the total group Holocephali. Coverage-standardized diversity was computed at quorum level 0.5. See Fig. 3 for stage abbreviations.

rather than the Visean. However, they only analyzed non-euchondrocephalian chondrichthyans, and their observations are therefore likely to differ to some degree from our analyses of total-chondrichthyan diversity. Chondrichthyan diversity

follows a similar trend in both our analyses and those of Feichtinger et al. (2021) in the Early and Middle Pennsylvanian, with an initial fall in the Bashkirian, a subsequent peak in the Moscovian, and a second decrease in the Kasimovian. The curves

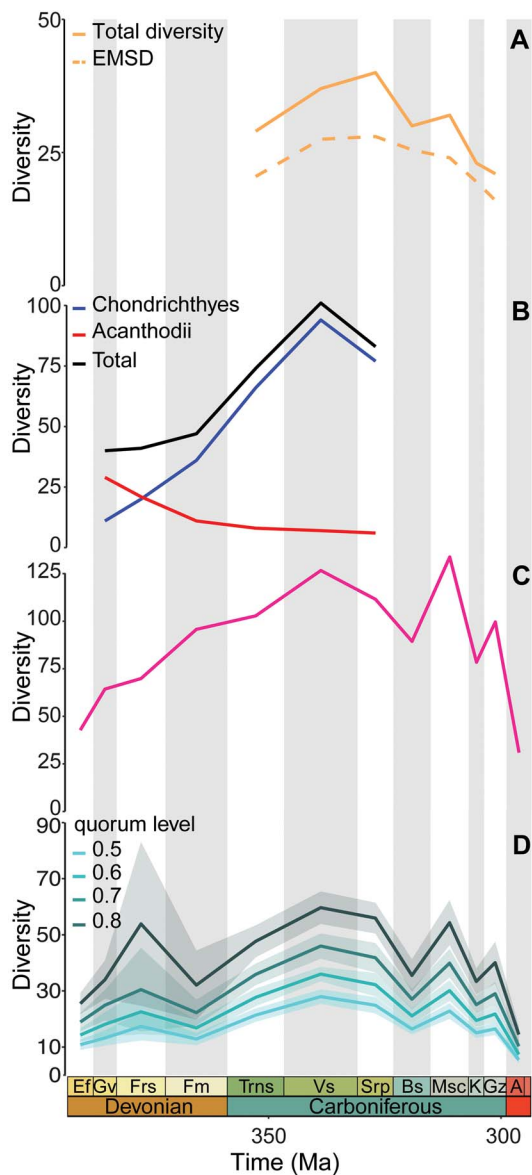


Figure 5. Comparisons of chondrichthyan diversity curves in the Devonian and Carboniferous. A, Total diversity and estimated mean standing diversity (EMSD) of Carboniferous elasmobranch genera by Feichtinger *et al.* (2021). B, Raw chondrichthyan and acanthodian diversity as documented by Sallan and Coates (2010). The divisions Acanthodii and Chondrichthyes refer to the divisions used in that study. C, Squares diversity of chondrichthyans investigated in this study. D, Chondrichthyan coverage standardized richness estimates calculated in this study. Chronostratigraphic stage abbreviations from left to right: Ef, Eifelian; Gv, Givetian; Frs, Frasnian; Fm, Famennian; Trns, Tournaisian; Vs, Visean; Srp, Serpukhovian; Bs, Bashkirian; Msc, Moscovian; K, Kasimovian; G, Gzhelian; A, Asselian.

differ in the Gzhelian, in that diversity continues to drop in the analysis of Feichtinger *et al.* (2021) but rises slightly in our study.

The Impact of Biases and Environmental Influences on Paleozoic Chondrichthyan Diversity

Raw global chondrichthyan richness estimates are subject to similar temporal and spatial sampling biases (Fig. 1) to those observed in Paleozoic actinopterygians (Henderson *et al.* 2022). This correlation is especially evident in the close match between

peaks in raw richness and collection counts. Surprisingly, coverage-standardized richness estimates of diversity and squares diversity estimates both capture patterns resembling raw richness estimates, a result that stands in stark contrast with the biases observed in early actinopterygian diversity (Henderson *et al.* 2022). This might reflect fundamental differences in fossil record quality of chondrichthyans and actinopterygians, but more likely stems from differences in historical sampling techniques. Osteichthyan groups are known to suffer from high-frequency and long-recognized problematic genera (“waste-basket” genera) (e.g., Gardiner and Schaeffer 1989; Gardner *et al.* 2019; Henderson *et al.* 2022, 2023). Chondrichthyan taxa, however, are far more likely to show tendencies of “over-splitting” (Schmetz *et al.* 2022), especially tooth- and scale-based taxa, albeit this is more prevalent on a species level.

Recent studies have illustrated the impact of spatial sampling biases on global diversity curves and advocated toward a shift away from studies of diversity through time alone (Close *et al.* 2020a,b; Benson *et al.* 2021). However, robust quantitative analyses of Paleozoic chondrichthyan diversity are currently missing on both a global and regional level. Our prefatory analyses show that spatial sampling varies among continental regions (Supplementary Figs. S10, S11); in particular, the chondrichthyan fossil record from Africa, South America, and Antarctica is very limited. However, variation in geographic sampling as shown by summed MST and GCD remain fairly constant through time for North America, Europe, and Asia. While the focus of this study was to examine temporal patterns and biases, further work establishing (paleo-)geographic trends and spatial biases will be critical to understanding the macroevolutionary patterns of Paleozoic chondrichthyans.

Sampling is limited in some of the Silurian and in most of the Permian stages; thus, distinguishing between true low diversity and poor sampling is difficult and must be done with caution (Supplementary Fig. S4). Conversely, most of the Devonian (except for the Givetian, Pragian, and Eifelian) and the Carboniferous stages are rather well sampled, suggesting that a more accurate and biologically meaningful signal of chondrichthyan diversity is obtainable during this time. Intense sampling of certain levels within the Carboniferous (see Fig. 1, Supplementary Fig. S4) coincides with strata of long-term historical and geographically widespread economic importance (“Coal Measures”) (Torsvik and Cocks 2016) and/or outcrop availability (“Carboniferous Limestone”) (Smith and McGowan 2007), leading to a series of field biases (for examples of these, see Whitaker and Kimmig 2020). Further sampling and new discoveries from the Ordovician, Silurian, and Permian are needed to better resolve the observed distributions of diversity in the earliest chondrichthyans and during the Permian, especially in the context of the lead up to the end-Permian mass extinction.

Some of the most prominent changes in chondrichthyan diversity occur over time system boundaries, that is, Silurian/Devonian, Devonian/Carboniferous, and Carboniferous/Permian. The Silurian/Devonian and Devonian/Carboniferous boundaries mark steep increases in diversity, while the Carboniferous/Permian boundary leads to a major drop in diversity. The pattern is not surprising for the Devonian/Carboniferous boundary, given that this coincides with the Hangenberg extinction, but the pattern is more difficult to explain for the Silurian/Devonian and Carboniferous/Permian boundaries. Coverage levels and rarefaction curves for the Silurian stages are similar to the Devonian stages, but diversity is considerably

lower (Supplementary Fig. S4). The late Carboniferous to early Permian is marked by irregularly increasing climatic aridity and glaciation and deglaciation sequences, and faunas are mostly represented by lacustrine assemblages (Isbell et al. 2003; Opluštil et al. 2013; Rosa and Isbell 2021). Additionally, tropical rainforests were replaced by dryland vegetation in large parts of the terrestrial settings during the late Carboniferous through to the early Permian (the Carboniferous “rainforest collapse”) and were shown to at least impact on terrestrial faunas (Cleal et al. 2009, 2012; Dunne et al. 2018). How and if these environmental and climatic conditions might have negatively influenced chondrichthyan diversity, resulting in increased extinction rates, has yet to be determined.

Our analyses suggest two initial increases in diversification rates in Paleozoic chondrichthyan diversity in the earliest Devonian and earliest Carboniferous (Fig. 2), which corroborates the two-burst radiation model proposed by Coates et al. (2018). Another origination rate peak appears in the middle Silurian but should be interpreted with caution due to the very limited sampling throughout most of this system. Origination and extinction rates of chondrichthyan genera are high in the Famennian stage of the Late Devonian. This may be an effect of the Kellwasser crisis at the end of the Frasnian stage, thus showing more support for a decrease in chondrichthyan diversity (as also shown by the coverage-based rarefaction estimates) (Sallan and Coates 2010). Extinction rates of chondrichthyan genera are also heightened in the Kungurian stage of the Permian and are only surpassed by the extinction rate peak in the Gzhelian just before the Carboniferous/Permian boundary. The extinction peak in the Kungurian is influenced by lower sampling coverage but may be at least partially influenced by the complex climate dynamics during the large-scale icehouse–greenhouse transition in the late Paleozoic (Nakazawa et al. 2015; Liu et al. 2017b). Widespread ocean stagnation and oxygen-deficient conditions (Liu et al. 2017a) may have contributed to a heightened extinction of chondrichthyan genera in the interval.

Comparisons with Invertebrate Diversity Trends

Comparisons with global Paleozoic diversity trends in marine invertebrate lineages reveal further patterns regarding the initial diversification of chondrichthyans. The radiation of marine diversity in the Early Devonian, both in invertebrates and chondrichthyans, coincides with the “Devonian nekton revolution,” wherein macroecological changes may have led to an expansion in benthic and demersal zones, culminating in a trophic-level shift toward nektonic groups (Klug et al. 2010; Servais et al. 2016). This would suggest an initially high diversity of life accumulating in benthic habitats that became saturated in the Devonian and subsequently promoted dispersal of organisms from the benthos into the water column (Klug et al. 2010). Whether the rise in chondrichthyan diversity over the Silurian/Devonian boundary can be attributed to such a key ecological event or is masked by undersampling remains uncertain for now.

Genus-level diversity of global marine invertebrates shows a similar pattern to our chondrichthyan analysis throughout the Devonian, with higher initial diversity in the early stages and a subsequent fall in the Middle–Late Devonian (Sepkoski 1996; Alroy et al. 2008). Major metazoan reef builders, including corals and stromatoporoids, also increased in diversity in the Early Devonian before declining in the Frasnian and subsequently collapsing in the Famennian (McGhee 1996; Copper 2002). This

general decline in diversity indicates severe changes in conditions that affected multiple trophic levels and may not be solely explained by the Frasnian–Famennian Kellwasser extinction event. The evolutionary role of reefs in harboring and proliferating marine diversity, at least in part through generation of habitat complexity, was highlighted by Kiessling et al. (2010). Specifically, coral and fish diversity share a close relationship and may even depend on each other in some circumstances.

Moreover, comparative analyses of habitat-mediated diversification in modern sharks have indicated a strong influence of coral reef-associated habitats on the diversification of carcharhinid sharks (Sorenson et al. 2014). Carcharhinids (Carcharhiniformes) are predominantly known to be reef-associated species and, together with the Squaliformes, comprise the two most diverse lineages of extant sharks (Sorenson et al. 2014). Thus, reef-associated habitats seemingly have an accelerating effect on lineage diversification in modern sharks. A similar pattern is also found in the rapid synchronous diversification of both teleost and coral lineages in the Oligocene–Miocene, concurrent with increasing reef area and habitat complexity (Bellwood et al. 2015, 2017). By contrast, the middle Paleozoic origins of all major non-tetrapod vertebrate clades, including chondrichthyans, were found in inter- and subtidal zones rather than reef habitats (Sallan et al. 2018). This highlights the need for further investigations into the role of invertebrate diversity and turnover, specifically reef builders, on chondrichthyan diversity. In particular, causes of the Middle–Late Devonian decline deserve investigation to understand the large ecological changes in Devonian ecosystems.

Conclusions

Using a newly genus- and species-level dataset and a range of quantitative approaches to estimate diversity, our results show that Paleozoic chondrichthyans first diversified in the Early Devonian and peaked in the early Carboniferous, before heavily decreasing across the Carboniferous/Permian boundary and remaining at low levels throughout the Permian. The Paleozoic era was a highly complex time period with major geological, environmental, and biotic changes that shaped chondrichthyan diversity. The early diversification in the Devonian was led by acanthodian chondrichthyans, which subsequently diminished toward the end-Devonian. The Carboniferous peak in diversity likely followed a faunal turnover caused by the Hangenberg extinction and major environmental changes. This diversity increase was led by non-acanthodian chondrichthyans and dominated by evolutionary radiations of the holocephalans in both shallow and deep waters. The subsequent plummet in chondrichthyan diversity in the early Permian might be a response to the unstable conditions during that time, most prominently the temperature rise and reduction in marine habitats following the reconfiguration of landmasses. An initial survey reveals, unsurprisingly, the overwhelming influence of North American and European material (Supplementary Figs. S10, S11) throughout the Paleozoic chondrichthyan record. Future examinations should focus on exploring such paleogeographic trends and the extent to which spatial biases influence current estimates of early trends in shark (*sensu lato*) diversity.

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