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Skeletal and soft tissue completeness of the acanthodian fossil record

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Abstract: Acanthodians are a poorly understood paraphyletic grade of extinct Palaeozoic fishes. They play an increasingly prominent role in our understanding of vertebrate evolution as part of the chondrichthyan stem-group even though their evolutionary history is scarce. The limited preservation of their mostly cartilaginous skeleton largely results in a bias towards isolated remains such as fin spines and scales. Here, we quantify the quality of the acanthodian fossil record by using a variation of the Skeletal Completeness Metric (SCM), an approach that calculates how complete the skeletons of individuals are compared to their theoretical complete skeleton. A novel Soft Tissue Completeness Metric (STCM) is introduced to estimate the percentage of soft body tissue preserved as an alternate measurement of completeness. Completeness scores for >1600 specimens comprising >300 taxa obtained from museum collection visits and literature surveys were assembled into a database. Acanthodian completeness peaks in

the Lower–Middle Devonian, Pennsylvanian, and earliest Permian. There is no correlation between acanthodian taxonomic richness and completeness. Acanthodians show a significantly lower completeness distribution than many tetrapod groups, but a similarly low distribution to bats. Skeletons deposited in freshwater are significantly more complete than in marine environments where sea level significantly negatively correlates with observed completeness. Our assessment reveals only weak spatial biases influencing the acanthodian fossil record while environmental biases are much higher. This quantified evaluation of acanthodians provides a foundation for further assessments of the likely influence of character absences from morphological datasets on estimates of early chondrichthyan and, therefore, early gnathostome evolution.

Key words: acanthodian, completeness, fossil record, fishes, Palaeozoic, sampling bias.

WITHIN the past 15 years, an array of new approaches to examining and estimating the quality of the fossil record based on specimen completeness have emerged. Initially, these assessed the quality of preservation of a fossil skeleton on the basis of four to five broad categories (e.g. one bone, more than one bone, one specimen and more than one specimen) (Benton *et al.* 2004; Fountaine *et al.* 2005; Smith 2007; Benton 2008a). Subsequent expansion included categorizing completeness within different skeletal regions rather than just for the entire skeleton (Beardmore *et al.* 2012a, 2012b). The most widely used approach in recent years follows Mannion & Upchurch (2010) who proposed two completeness metrics to accurately quantify the completeness of individual specimens and species, initially applying these to sauropodomorph dinosaurs. These metrics are the skeletal completeness metric (SCM), which measures absolute proportions

of the preserved skeleton of a given species, and the character completeness metric (CCM), which measures the proportion of potential phylogenetically informative characters preserved. Several studies have subsequently used this methodology to assess completeness based on individual specimen data for the fossil record of different terrestrial (Brocklehurst *et al.* 2012; Walther & Fröbisch 2013; Brocklehurst & Fröbisch 2014; Dean *et al.* 2016; Gardner *et al.* 2016; Verrière *et al.* 2016; Davies *et al.* 2017; Brown *et al.* 2019; Cashmore & Butler 2019; Mannion *et al.* 2019; Cashmore *et al.* 2020) and marine vertebrate groups (Cleary *et al.* 2015; Tutin & Butler 2017; Driscoll *et al.* 2018).

Comparisons of completeness metrics with changes in taxonomic diversity, geography, sampling effort, preservation and environmental deposition have revealed a number of correlations and highlighted different biases.

Environmental factors such as changes in sea level can correlate with changes in completeness, diversity and abundance of a group and reveal underlying ecological mechanisms such as habitat preferences (Mannion & Upchurch 2010; Cleary *et al.* 2015; Tutin & Butler 2017). In some groups, an uneven sampling on both geographical and historical levels has led to a substantial bias in the completeness of their fossil record as more effort is directed towards particular taxa or localities of interest by researchers (see e.g. Cleary *et al.* 2015; Driscoll *et al.* 2018; Cashmore & Butler 2019; Cashmore *et al.* 2020). This is likely to yield a higher number of potentially more complete fossils compared to taxa or localities that are not considered as important, thus resulting in a significant bias within the group. However, these increasingly sophisticated studies of tetrapod record quality have not yet been applied to the fossil record of fishes, especially those with little or no bone and which might therefore be subject to considerable preservation bias.

Acanthodii are a grade of extinct fishes from the Palaeozoic. They first emerged in the early Silurian, diversified in the Devonian, declined in the Carboniferous and departed from the fossil record in the Permian (Moy-Thomas 1971; Nicol 1982; Janvier 1996; Mutter & Richter 2007; Burrow & Rudkin 2014; Dearden *et al.* 2019). Acanthodians were globally distributed in both freshwater and marine habitats and are thought to have been microphagous for the most part (Denison 1979). The most prominent characteristic of acanthodians is the numerous bony fin spines located in front of all paired and midline fins, except the caudal fin (Denison 1979). These fin spines could grow to extreme sizes in certain taxa, and are sometimes the only skeletal part that is preserved. Notably, possession of a pre-anal-fin spine remains the only putative synapomorphy of a monophyletic Acanthodii (Brazeau & Friedman 2014). Acanthodians show little diversity in range of body shape, inferred function and ecomorphology compared to other major groups of fishes (Denison 1979; Blais 2017).

A slew of proposals have considered the monophyletic or paraphyletic status of the acanthodians and their assignment to the chondrichthyans or the osteichthyans as sister group or stem lineage (e.g. Nelson 1969; Miles 1973a, 1973b; Jarvik 1977; Denison 1979; Maisey 1986; Long 1986; Janvier 1996; Hanke & Wilson 2004; Brazeau 2009; Burrow & Turner 2010; Davis *et al.* 2012; Zhu *et al.* 2013; Brazeau & Friedman 2014). Recent phylogenetic analyses have stabilized an increasing proportion of acanthodians as stem-chondrichthyans, rejecting their status as a monophyletic clade, while debates around the position of other stem gnathostomes such as placoderms are ongoing (Brazeau 2009; Davis *et al.* 2012; Zhu *et al.* 2013; Long *et al.* 2015; Brazeau & de Winter 2015; King

et al. 2016; Qiao *et al.* 2016; Zhu *et al.* 2016; Coates *et al.* 2018; Dearden *et al.* 2019; Frey *et al.* 2020; King & Rücklin 2020). Fossil discoveries from the Lower Devonian (Lochkovian) Man On The Hill (MOTH) locality of Canada provided some of the earliest articulated acanthodians, including taxa with both acanthodian-like features and characteristics more usually associated with conventional chondrichthyans, thus blurring the line between grade and clade (e.g. Hanke *et al.* 2001; Hanke & Wilson 2006, 2010; Hanke & Davis 2012). Further instances of this are becoming evident in chondrichthyans from multiple localities in North America, Antarctica, Australia and Asia, but exemplified most notably by the early Devonian chondrichthyan *Doliodus problematicus* from New Brunswick, Canada, demonstrating a widespread distribution of paired fin spines, previously considered to be an acanthodian synapomorphy (Young 1982; Janvier 1996; Zhu *et al.* 1999; Miller *et al.* 2003; Zhu *et al.* 2009).

In general, acanthodian species have been diagnosed by characteristics of the dermal skeleton and/or specific isolated skeletal characters because the rarely preserved endoskeleton (Brazeau 2009; Davis *et al.* 2012; Brazeau & Friedman 2014; Coates *et al.* 2018; Dearden *et al.* 2019) often includes little anatomical detail (Sansom *et al.* 2011; Chevrinais *et al.* 2015) and the micromeric dermal skeleton is commonly disintegrated post mortem. However, ascertaining the potential taphonomic filters in the nature and quality of the fossil record of these predominantly cartilaginous vertebrates has not been attempted to date. Quantifying the completeness of the acanthodian fossil record might therefore yield novel insights into the impact that ecological, geographical and sampling biases may have on it, contributing to our understanding of the macroevolutionary patterns of this group.

In the present study, we quantify the completeness of the acanthodian fossil record for the first time using modified versions of previously developed completeness metrics (Mannion & Upchurch 2010; Beardmore *et al.* 2012a, 2012b). This also provides the first quantitative completeness analyses for a non-tetrapod vertebrate group. We statistically compare the variations in completeness of the acanthodian fossil record through time with taxonomic diversity, geographical distribution and depositional environment. We aim to improve our understanding of the hypotheses concerning origin and early evolution of the acanthodian grade by identifying biases and filters that influence dataset quality. In turn, these results are likely to provide a more informed perspective on the potential biases introduced by missing data (Sansom & Wills 2013) on hypotheses of early chondrichthyan evolution, and the sequential assembly of what are now understood as conventional chondrichthyan conditions (Coates *et al.* 2018).

MATERIAL AND METHOD

Dataset

Despite these recent reconsiderations of acanthodian interrelationships, a detailed and thorough systematic revision of the Acanthodii has yet to be tackled and is beyond the scope of the present study. We therefore adhere to the conventional definition and consider all species formally assigned to the Acanthodii as acanthodians for this study (a more detailed explanation is given in the taxonomic groups section below).

The Paleobiology Database (PBDB; <https://www.paleobiodb.org>) included only 56 total occurrences limited to 26 taxa from 22 geological formations in 36 collections (as of 12 May 2020). These data are evidently unsuitable and would considerably skew any completeness estimates. Therefore, unlike most previous completeness studies that used published literature and the PBDB (Mannion & Upchurch 2010; Brocklehurst *et al.* 2012; Dean *et al.* 2016; Gardner *et al.* 2016; Verrière *et al.* 2016; Davies *et al.* 2017; Tutin & Butler 2017; Brown *et al.* 2019; Cashmore & Butler 2019; Mannion *et al.* 2019; Cashmore *et al.* 2020), primary data were gathered from museum collections. These were then augmented via reference to peer-reviewed literature (illustrations and text). Where applicable, taxonomic information on museum catalogues was checked for validity and corrected to the currently accepted taxonomic name and systematic position. Together with the completeness scores, information on the lithostratigraphy (e.g. geological formation), geographical locality and chronostratigraphic age were recorded for subsequent analyses. Additionally, palaeoenvironmental information was extracted from published sources where detailed lithostratigraphy descriptions for specimen occurrence were available. The final dataset contains an unprecedented survey of over 1600 acanthodian specimens in 300 species and 121 genera, plus two acanthodian specimens in open nomenclature, and is up to date as of June 2021. We additionally generated three subsets excluding isolated scale-based taxa, isolated fin spine-based taxa as well as excluding both isolated scale and fin spine-based taxa from the dataset and ran some of the analyses multiple times using each subset. This allows us to compare and contrast how isolated skeletal remains that are commonly used in acanthodian species identification impact on acanthodian completeness.

Completeness metrics

Background. Several methods have been proposed to quantify the quality of the fossil record, with different

levels of precision (e.g. Benton & Storrs 1994; Fountaine *et al.* 2005; Benton 2008b; Mannion & Upchurch 2010; Beardmore *et al.* 2012a, 2012b). The two most commonly used metrics for estimating the completeness of a fossil vertebrate skeleton are the character completeness metric (CCM) and the skeletal completeness metric (SCM) by Mannion & Upchurch (2010). CCM quantifies the proportion of potential phylogenetic characters preserved from different parts of the skeleton in a given species based on calculating the percentage of characters attributed to each body region from published phylogenies. SCM measures the absolute proportion of the overall skeleton preserved in a given species based on dividing the skeleton into different regions and estimating how much of it is represented. Both of these metrics were established in two variants, CCM1/SCM1, which establishes the completeness of a single most complete specimen for a given species or taxon, and CCM2/SCM2, which estimates completeness using all specimens of a given species or taxon (a composite of all investigated specimens). The latter has been preferred for both CCM and SCM in subsequent studies (Brocklehurst *et al.* 2012; Dean *et al.* 2016; Verrière *et al.* 2016; Cashmore & Butler 2019; Cashmore *et al.* 2020). Another completeness metric (Beardmore *et al.* 2012a, 2012b) estimates preservation of a fossil based upon both disarticulation and completeness. Rather than scoring total numbers of individual bones, this method divides the body into equally weighted skeletal regions and uses an index of 0–4 to score the levels of completeness in each region.

Acanthodian ‘problems’ and this study. Previous studies have shown a significant positive correlation of CCM and SCM in different vertebrate clades, thus suggesting that these metrics capture similar signals in fossil record quality (Mannion & Upchurch 2010; Tutin & Butler 2017). CCM is generally scored using an assumption that if one skeletal element is complete, all phylogenetic characters of that element can be assessed. While this correlation may hold true for the three-dimensionally preserved bones of the previously studied tetrapod groups, it is more problematic for acanthodians with fragile cartilaginous skeletons that are prone to fragmentation and erosion, with consequent loss of character information. Acanthodians are often small in size (usually less than 20 cm total length; Denison 1979) and embedded in matrix, hiding potential informative characters from view. Additionally, the composition of the matrix may preclude them from using methods such as acid digestion and lack appropriate resolution for CT scanning. For example, several acanthodian species from the MOTH locality are known from full body specimens but mostly lack detailed skeletal features of neurocranial, jaw or branchial arch elements (e.g.

Hanke 2002; Hanke & Wilson 2006; Hanke & Davis 2008, 2012). Thus, considering the similarity in signal for CCM and SCM observed in other groups (Mannion & Upchurch 2010; Tutin & Butler 2017), the clear connection between SCM and natural taphonomic and environmental processes, and the problem of character loss on cartilaginous skeletons, we follow the protocol by Cashmore & Butler (2019) in assessing fossil record quality using SCM rather than CCM in this study.

Completeness metrics in this study. We calculated acanthodian completeness based on two different metrics. We used the SCM as a base to calculate the completeness of skeletal characters within the fossil record of acanthodians but divide the skeleton into anatomical regions as implemented by Beardmore *et al.* (2012a, b). Contrary to the original application of the SCM,

assessing the relative percentage of the total skeleton made up by any individual bone within fossil fish specimens proved not to be feasible and the total number of elements within a skeletal region in acanthodians (such as the vertebral column or branchial arches) is rarely known. Therefore, following Beardmore's Skeletal Completeness, values between 0 (absent) and 4 (more than 75% complete) were assigned to nine different skeletal regions. Detailed information on the scoring system and descriptions for each individual skeletal region is accessible in Appendix S1. Using this method, an isolated scale would receive a score of 1, while an acanthodian with more than 75% of the body covered in scales is given a score of 4. We divided the acanthodian skeleton into braincase, upper jaw, lower jaw, hyoid and gill arches, pectoral girdle, vertebrae, teeth, fin spines, and scales (Fig. 1).

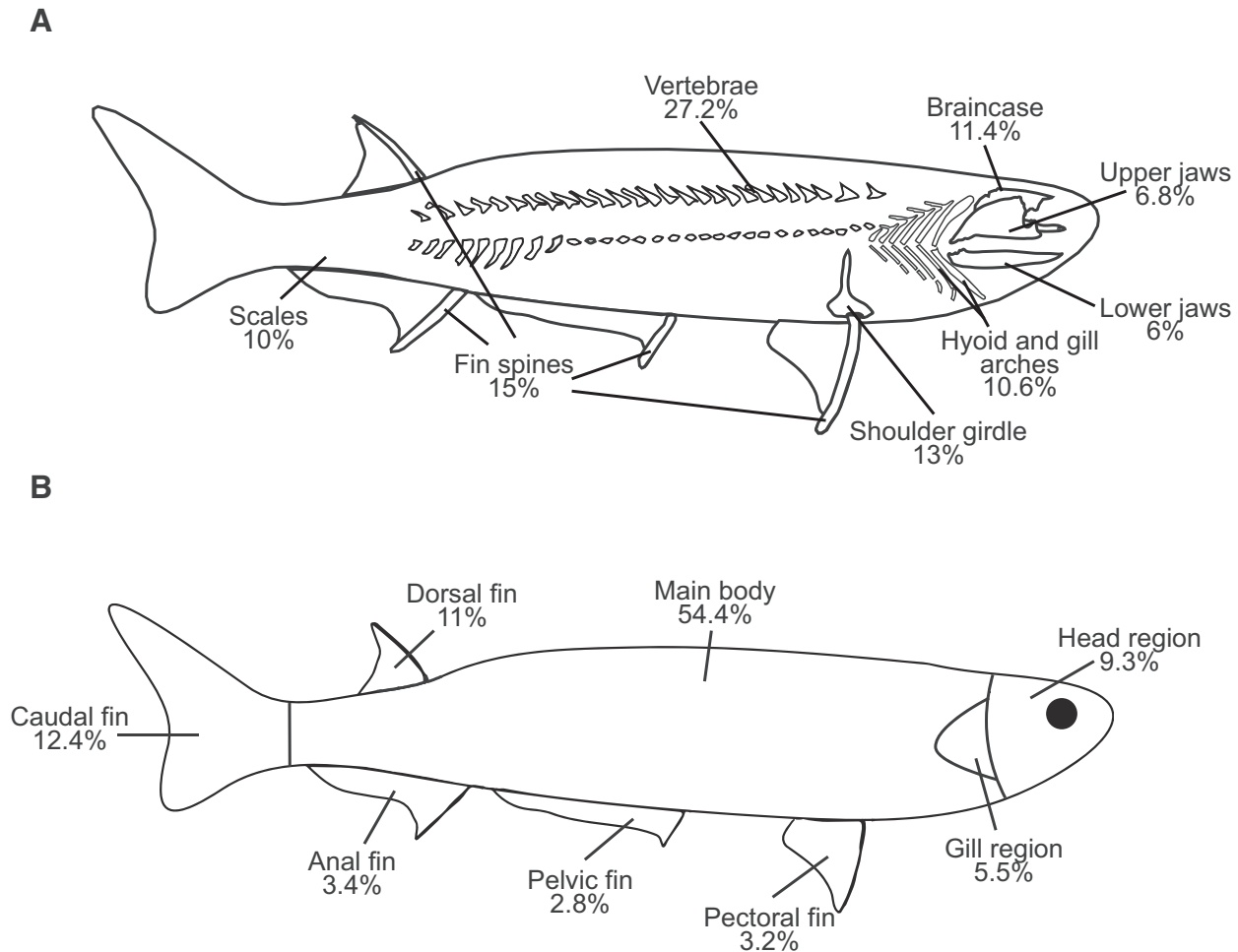


FIG. 1. Skeletal (A) and soft tissue (B) reconstruction of *Acanthodes* based on the vertebral column of *Acanthodes sulcatus* (Miles 1970), the general reconstruction of *Acanthodes lopatini* (Beznosov 2009) and braincase, jaws, hyoid and gill arches of *Acanthodes confusus sensu* Heidtke (2011) (noted as *Acanthodes bronni* in Miles 1973b; Davis *et al.* 2012) to illustrate the relative body proportions of acanthodians. Relative proportions of the different regions were calculated by assessing the surface areas of the reconstructions.

The absence or minimal presence of endoskeletal bone together with the mode of preservation in most acanthodians results in different challenges for assessing the quality of their fossil record compared to the other vertebrate groups that have previously been investigated. To account for this difference in preservation and thus estimating their completeness, we developed a novel completeness metric, the Soft Tissue Completeness Metric (STCM). Its framework is based on Beardmore's non-weighted method. Preservation of muscles, vasculature or nerve fibres in vertebrate fossils can occur under exceptional conditions (Arsenault *et al.* 2004; Trinajstić *et al.* 2007; Conway Morris & Caron 2012). Thus far, reports of acanthodian soft tissues are limited to traces of the internal organs (such as kidney, liver and heart), eyes, and integument outline (Davidson & Trewin 2005; Chevrinais *et al.* 2015). Here, we include the integument outline as a soft tissue component of acanthodians, represented by different head, main body and fin imprints. Soft tissue regions were implemented based on the acanthodian body and preservation potential and divided into head, gill region, main body, dorsal fin, pectoral fin, intermediate fin, pelvic fin, anal fin and caudal fin. Scores of 0–4 were attributed as above. To account for the differences that both skeletal and soft tissue regions contribute to the overall body, we determined relative proportions of the different regions by assessing their surface areas (Fig. 1). For this, 2D reconstructions from literature (see Appendix S1) were used to generate proportion scores for each of the regions using the vector graphics software Inkscape (<https://inkscape.org/>).

Different kinds of acanthodian are known to encompass varying sets or complements of skeletal parts, such as the presence or absence of teeth, or the distribution of fins and parts of fins, including an absence of specific fins and fin spines (see e.g. Denison 1979 for a range of different body exemplars) which may result in biased scores. To account for this, we calculated both skeletal and soft tissue proportions for representatives of eight acanthodian taxa: *Diplacanthus crassissimus* Duff, 1842 (diplacanthid-exemplar), *Acanthodes* Agassiz, 1833 (acanthodid-exemplar A), *Acanthodopsis* Hancock & Atthey, 1868 (*Acanthodopsis*-exemplar), *Traquairichthys pygmaeus* Fritsch, 1895 (acanthodid-exemplar B), *Ischnacanthiformes* Berg, 1940 (ischnacanthid-exemplar), *Mesacanthus mitchelli* Egerton, 1861 (mesacanthid-exemplar), *Climatius reticulatus* Agassiz, 1845 (climatiid-exemplar), *Tetanopsyrus lindoei* Gagnier, Hanke & Wilson, 1999 (*Tetanopsyrus*-exemplar) and an averaged acanthodian-exemplar based on all the measurements (for more details, see Appendix S1). The averaged acanthodian-exemplar exhibits all skeletal and soft tissue body regions defined in this study (including teeth, intermediate fin spines, anal fin, etc.), averaged from the measurements of the representatives of the eight acanthodian taxa. These proportions were then used to correct the initial 0–4 scores for each individual skeletal and soft tissue region before calculating the final

SCM and STCM scores (ranging between 0% and 100%). Body exemplars were attributed to each acanthodian taxon based on best anatomical fit (where possible) and taxonomic similarity. The averaged acanthodian-exemplar is used primarily for taxa that are known exclusively from isolated fragmentary material and could not be assigned to a higher taxonomic level (*Incertae sedis*). Acanthodian body fossils are predominantly preserved in lateral compression. Therefore, we follow Cleary *et al.* (2015), Brown *et al.* (2019) and Cashmore & Butler (2019) and report completeness based on the side visible (assuming a similar preservation of the other side). For other orientations such as dorsoventrally flattened specimens, completeness was calculated based on the skeletal features visible on the respective orientation (either dorsal or ventral) alone. If fossils were split into part and counterpart, both sides were examined to infer completeness. Using the skeletal and soft tissue completeness metrics, we are able to compare completeness of two contrasting modes of preservation and account for the problems of limited preservation of skeletal material resulting from the absence of bone.

Acanthodian completeness data

Time series. Stage-level time bins were used to conduct the temporal analyses and time series starting from the Rhudanian (basal stage of the Silurian) and ending with the Capitanian (Guadalupian, middle Permian). Chronological ages, time bin lengths and stage midpoints were established in accordance with the latest information from the International Commission on Stratigraphy (IUGS) stratigraphic charts (v2020/03; Cohen *et al.* 2013). Stage bin length varies substantially in the Palaeozoic, ranging from 1.8 Ma (Gorstian) to 15.8 Ma (Visean). An epoch-level time bin had to be used for the Pridoli (Silurian) as there are currently no officially recognized stages within this epoch. A finer resolution than stage-level (such as substage) proved impossible for the acanthodian fossil record as the required stratigraphic information is not available for the majority of taxa. We recognize that this might result in a bias towards stretching out single spot occurrences to the lower and upper boundaries of the stage. However, stage-level analyses generally provide the norm for macroevolutionary and macroecological studies of the fossil record through deep time and are suitable for our completeness studies. Mean and median completeness scores for both SCM and STCM were calculated for all species for each time bin. Sampled-in-bin occurrences of specimens were used to determine the temporal range of individual taxa.

Taxonomic groups. In this study, we are following the phylogenetic analysis by Dearden *et al.* (2019), subsequently corroborated by Frey *et al.* (2020), which places

the acanthodians as a paraphyletic grade on the stem-group chondrichthyans. We exclude *Pucapampella* and all taxa more closely related to the chondrichthyan crown except for *Brochoadmones* and *Lupopsyru*s which were traditionally described as acanthodians and have an acanthodian-like body plan (Hanke & Wilson 2006; Hanke & Davis 2012) but fall outside the acanthodian grade *sensu* Dearden *et al.* (2019). See Schnetz *et al.* (2022) for a full list of included genera and species. Two very incomplete acanthodian specimens were included in the analyses because they extend the acanthodian occurrence range into the middle Permian (Mutter & Richter 2007). These specimens were recorded as separate taxa because of their contrasting skeletal composition (isolated scale vs isolated fin spine fragments), but taxonomic information beyond classification as members of the Acanthodii is lacking. This assignment as operational taxonomic units (OTUs) is consistent with procedures used in a previous study (Cashmore & Butler 2019).

The traditional separation of acanthodians into three orders, the Climatiiformes, Ischnacanthiformes and Acanthodiformes, has been rejected (e.g. Gagnier & Wilson 1996; Janvier 1996; Hanke & Wilson 2004; Brazeau 2009; Burrow & Turner 2010). Diplacanthiformes and Tchnacanthida were recovered as distinct orders of acanthodians alongside this traditional tripartite division (Hanke *et al.* 2001; Karatajūtė-Talimaa & Smith 2003; Burrow & Turner 2010; Burrow *et al.* 2016). However, the Climatiiformes/Climatiidae now form a grade capturing a section of the chondrichthyan stem, exclusive of *Pucapampella* and more crownward taxa, and exclusive of the acanthodid stem, which forms a monophyletic sister group (acanthodids + ischnacanthids + diplacanthids) to all other chondrichthyans (Coates *et al.* 2018; Dearden *et al.* 2019). While the position of the diplacanthiforms has been resolved in these most recent analyses, the Tchnacanthida have not been reassigned and formally remain as a distinct order of acanthodians.

To compare SCM and STCM scores between the major subgroups, acanthodians were subdivided into Acanthodiformes, Ischnacanthiformes, Diplacanthiformes, Climatiidae, Tchnacanthida and *Incertae sedis* taxa. As there has not been any formal reassessment of the Climatiidae family to date, we follow the currently accepted taxonomic recognition of this group as a taxon-rich delimitable grade and use them as subgroup for our analysis. The Tchnacanthida are included here as they have been formally erected as a distinct order of acanthodians by Karatajūtė-Talimaa & Smith (2003) but it should be noted that the described material is limited to isolated scales from four sampled horizons of northern Asia. The *Incertae sedis* subgroup is most likely to be polyphyletic as it contains a multitude of taxa that were not assigned to an order or family when assessed taxonomically. We use

the division here to illustrate the status of taxon completeness contained therein and the impact of such incompleteness on taxonomic issues.

Spatial correlations and lagerstätten. To investigate if acanthodian fossil record quality varies on a global scale, completeness scores were grouped by the hemispheres and geographical regions in which they were collected. The geographical localities are based on modern-day regions. Acanthodians have been recovered from all modern-day continents, including taxa from Africa (2), Asia (68), Australia and Oceania (17), Antarctica (5), North America (68), South America (9) and Europe (164). Previous studies have taken the influence of lagerstätten, sites of exceptional fossil preservation, into account when calculating completeness scores (Brocklehurst *et al.* 2012; Dean *et al.* 2016; Brown *et al.* 2019; Cashmore & Butler 2019; Cashmore *et al.* 2020) as they can bias the overall trend of completeness through time. However, we follow completeness studies on other marine vertebrates (Cleary *et al.* 2015; Tutin & Butler 2017) and do not separate taxa derived from concentration or conservation lagerstätten for statistical comparisons as there are no clearly defined lagerstätten for acanthodians.

Environment. To assess whether levels of completeness correlate with their depositional environment, we classified the information on the depositional settings of each specimen into benthic assemblage zones (BA). 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 & Janis 1983; Boucot & Lawson 1999; Sallan *et al.* 2018). While there is some inconsistency about the exact distinction between BA4 and BA5, we here consider BA4 to be right at the limit of subtidal influence before getting into the deepest extremities of the shelf in BA5. Completeness scores were categorized into the benthic assemblage zones in which the specimens were deposited. Additionally, completeness scores were divided into those from species obtained from marine or freshwater settings. The subdivided completeness scores were then compared to understand the impact of environmental taphonomic and preservational influences on the fossil record of acanthodians. Changes in average sea level through time were used as a sampling proxy for the environmental effect on acanthodian completeness. It has previously been proposed that high sea levels lead to the expansion of marine environments and thus potentially increasing diversity and accumulation of fossiliferous sediments as well as habitat preservation (Sepkoski 1976; Peters 2005; Wall *et al.* 2009; Hannisdal & Peters 2011). Average sea level data were derived from

Hannisdal & Peters (2011) who provided a composite Phanerozoic sea level reconstruction based on previous studies. For stages which were not represented in the reconstructions due to time bin resolution, we chose to use NA rather than an average of the sea level of the previous and next stage as sea level could potentially fluctuate quite drastically between time bins.

Statistical analyses

The statistical analyses were performed in R (v3.5.1; R Core Team 2018). We largely follow the protocol of the most recent completeness studies in terms of statistical analyses (e.g. Brown *et al.* 2019; Cashmore & Butler 2019). Trends of completeness through time series were tested using linear regressions. Generalized least-squares regressions (GLS) with a first order autoregressive model (corARMA) were chosen as they reduce the chance of overestimating the statistical significance of the regression lines due to temporal autocorrelation. GLS were calculated using the function `gls()` in the R package `nlme` (Pinheiro *et al.* 2018). The time series and completeness scores were log-transformed prior to analysis, ensuring normality and homoskedasticity of residuals. For time bins with completeness values or taxonomic richness of 0 rather than NA, a value of 1 was added to allow the data series to be logged for subsequent analyses. Given that $\log(1) = 0$ and the focus of these analyses lies on relative changes rather than absolute time bin values, we consider this approach appropriate for these analyses. Likelihood-ratio-based pseudo- R^2 values were calculated to determine the amount of variance explained by our GLS models using the function `r.squaredLR()` of the R package `MuMIn` (Barton 2018). GLS autoregressive models were used to make time series comparisons between completeness metrics through time as well as compare temporal changes in completeness to different combinations of potential explanatory variables (species richness, time bin length as well as stage midpoints and sea level). Similarly, we tested whether species richness through time correlates with any combinations of completeness scores, time bin length and stage midpoints and sea level. Stage midpoints were used to test for a general trend through time and time bin lengths were used to examine any effects of the variable time durations of the different stages. To measure how well the data fits the models while also taking the model's complexity into account, Akaike's information criterion (AICc) and consequently Akaike weights were calculated using the functions `AICc()` of the R package `qpcR` (Spiess 2018) and `aic.w()` of the R package `phytools` (Revell 2012).

Non-temporal pairwise comparisons of completeness values were calculated using non-parametric Mann–Whitney–Wilcoxon tests which assess the differences in

standard deviations and medians of datasets. A variety of comparisons of median and standard deviation of SCM2 values were made between subsets of the original dataset, including the three subsets excluding isolated material, as well as subsets of the major acanthodian subgroups, comparisons with previously published vertebrate SCM2 values and geographical and environmental comparisons. For comparisons of more than two datasets/subsets, Kruskal–Wallis tests were performed which determine dominances of specific variables. The acanthodian completeness values were also compared to the published SCM2 data of other vertebrate groups, including sauropodomorphs (Mannion & Upchurch 2010; updated dataset by Cashmore *et al.* 2020), pelycosaurs (Brocklehurst & Fröbisch 2014), ichthyosaurs (Cleary *et al.* 2015), parareptiles (Verrière *et al.* 2016), plesiosaurs (Tutin & Butler 2017), bats (Brown *et al.* 2019) and theropods (Cashmore & Butler 2019).

Time series plots were generated using the package `ggplot2` (Wickham 2016) and completeness distribution plots (non-temporal) were generated using the package `vioplot` (Adler & Kelly 2020).

RESULTS

Changes in acanthodian completeness through time

Mean skeletal (SCM2) and soft tissue (STCM2) completeness of acanthodians show highly consistent patterns to one another through time, with the STCM2 values (range between 0 and 92.6%) being slightly higher than the SCM2 (range between 3.8% and 60.6%) (Fig. 2A, B). Mean completeness is lowest throughout the Silurian, rises throughout the Devonian and Carboniferous before reaching its maximum peak in the Asselian. There are no values in the Sakmarian and Artinskian but low mean SCM2 values are again recovered in the Kungurian up to the Capitanian where the last occurrences occur. Notable peaks include the Lochkovian (15.6% SCM2, 21% STCM2) and Givetian (19.6% SCM2, 27.2% STCM2) in the Devonian, the Bashkirian–Moscovian (26.9–19.4% SCM2, 48.2–40.1% STCM2) in the Carboniferous, and Asselian (60.6% SCM2, 92.6% STCM2) in the Permian. When taxa based on isolated scales are removed, overall mean SCM2 and STCM2 show slightly higher values throughout the Silurian and Devonian time bins but this difference diminishes in the Famennian. Mean values for the Carboniferous and Permian do not change considerably on exclusion of isolated scale-based taxa. Excluding acanthodian taxa consisting of only isolated fin spines results in higher mean SCM2 and STCM2 values throughout almost all of the Palaeozoic time bins. The highest differences between original SCM2 and the subset

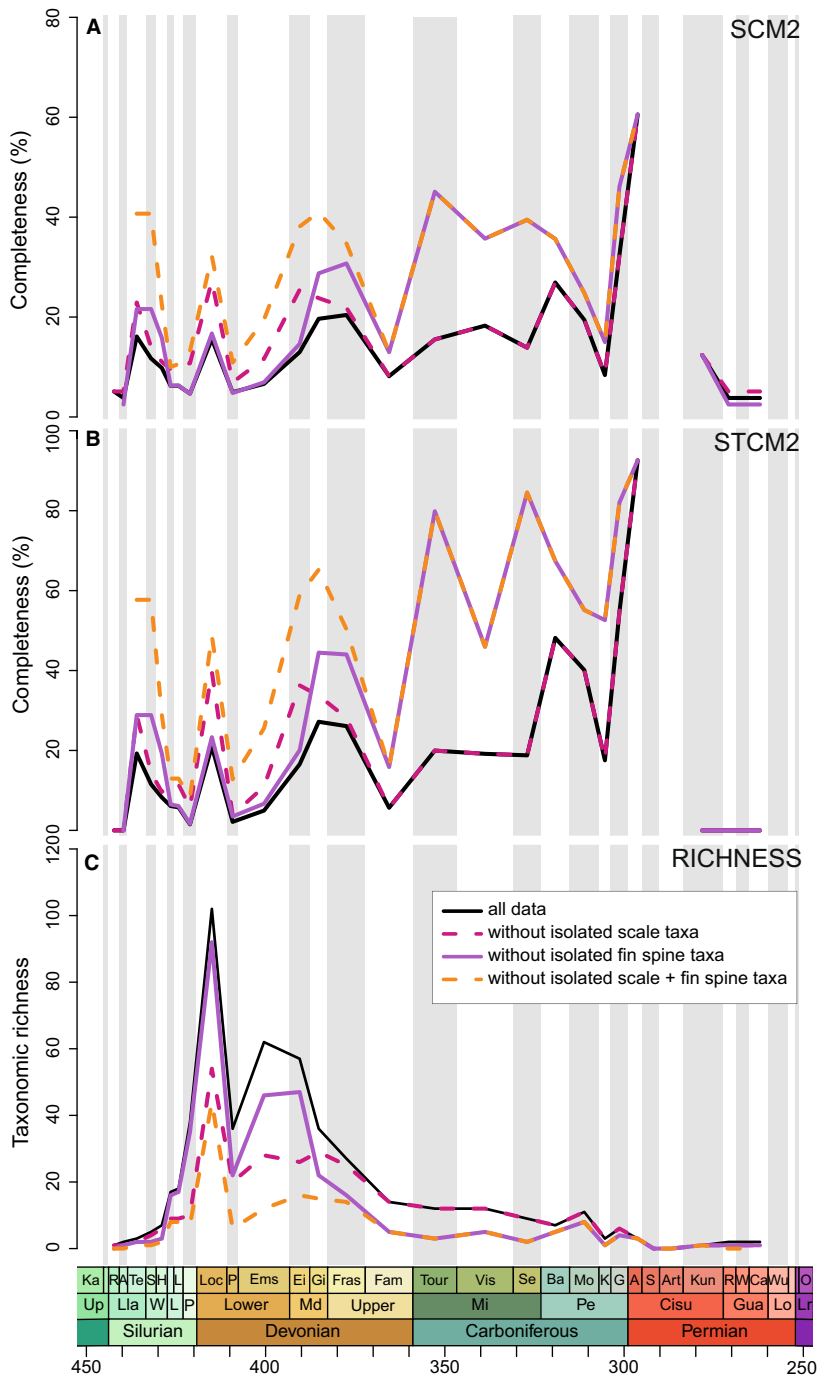


FIG. 2. Changes in acanthodian completeness and raw taxonomic richness through time. A, mean skeletal completeness. B, mean soft tissue completeness. C, raw taxonomic richness.

excluding isolated fin spines can be observed in the Mississippian, specifically the Tournaisian and Viséan, with over 20% increase. STCM2 values show notable peaks in the Telychian–Sheinwoodian (28.9%), Givetian (44.6%), Tournaisian (79.9%), Serpukhovian (84.5%) and Gzhelian–Asselian (82–92.6%). The highest difference between the original dataset and the STCM2 subset without fin spine taxa is in the Tournaisian with about 60% higher values in the subset. Removal of isolated fin spine and isolated

scale-based taxa yields the overall highest mean acanthodian skeletal completeness throughout the Palaeozoic, ranging between around 10% and 60.6%. STCM2 without isolated fin spine and isolated scale-based taxa has the highest values in the Silurian and Devonian, with highest overall peaks in the Telychian–Sheinwoodian (57.7%), Lochkovian (48.7%) and Givetian (65.2%). However, this subset then shows the same pattern during the Carboniferous and early Permian as that excluding isolated fin spines.

When median acanthodian skeletal and soft tissue completeness values are calculated through time, they show similarly consistent patterns but are very different from the mean completeness curves (Fig. S1). Both median SCM2 and STCM2 stay at low levels throughout the Silurian, Devonian and Mississippian of the Carboniferous, with SCM2 values (range between 2.5% and 62.2%) offset to slightly higher values than STCM2 (range between 0% and 91.9%). Median completeness rises in the Bashkirian (20.7% SCM2, 79.7% STCM2) with a peak in the Moscovian (12% SCM2, 32.3% STCM2) before falling again in the Kasimovian and ultimately increasing to highest values in the Gzhelian–Asselian (28.8–62.2% SCM2, 70.9–91.9% STCM2) before dropping to low levels in the middle Permian. STCM2 values are higher than SCM2 values in these time bins. Excluding isolated scale-based taxa does not change the pattern of median SCM2 and STCM2 completeness for acanthodians except for some higher values in the later stages of the Silurian and Lower to Middle Devonian (maximum change from 0% to 26.9% STCM2 in the Lochkovian). When isolated fin spine-based taxa are removed from the dataset, both median SCM2 and STCM2 patterns change drastically. Median SCM2 rises and plateaus early on in the Silurian and then falls back to low levels throughout the Lower Devonian before rising again in the Givetian (33.7%). It dips again in the Famennian (4.8%) but increases throughout the Mississippian stages with values around 40% and the highest peak in the Asselian (62.2%, same as the other median SCM2 datasets). Median STCM2 shows notable peaks in both the Telychian (28.9%) and Sheinwoodian (28.9%), Givetian (64.3%), Tournaisian (82.4%), Bashkirian (80.4%) and Asselian (91.9%), with a maximum change of values of about 82% within a stage compared to the original dataset. Removal of both isolated scale and fin spine-based taxa shows little variation in this scenario in both SCM2 and STCM2 for the later stages of the Palaeozoic. However, both median SCM2 and STCM2 values are higher in both the Silurian and Devonian with notable peaks in the Telychian–Sheinwoodian (40.7% SCM2, 57.7% STCM2), Lochkovian (34.4% SCM2, 51.4% STCM2) and the Eifelian–Givetian–Frasnian (41.6–43–42% SCM2, 75.2–77.2–73.4% STCM2) when both scale and fin spine-based acanthodian taxa are excluded.

Mann–Whitney–Wilcoxon tests show significant differences between both the distributions of original SCM2 and STCM2 values and the different corresponding SCM2 and STCM2 subsets except for total SCM2/STCM2 and SCM2/STCM2 subset 2 excluding isolated fin spine taxa which is non-significant (Table S1). There is a significant correlation of full acanthodian SCM2 with time bin length but the strength of the model is low ($p = 0.0352$; $R^2 = 0.22$) (Table S2). A wider time bin results in higher

levels of SCM2. Total STCM2 of acanthodians significantly correlates with taxonomic richness through time ($p = 0.017$; $R^2 = 0.39$) but also shows a low model fit, however, the richness coefficient is recovered as significant in all of the models within which it is included (Table S3). Higher soft tissue completeness is recovered in time bins with lower taxonomic richness. SCM2 time series are best explained by the GLS models including sea level, time bin length + sea level and stage midpoints + sea level with high model fits but none of the coefficients are significant in any model. Similarly, STCM2 time series are best explained by the GLS models including sea level, richness + sea level, and time bin length + sea level, with high model fits but only the taxonomic richness coefficient is significant in the second model.

Correlations with taxonomic richness

Raw taxonomic richness of acanthodian species is initially low in the first stages of the Silurian and steeply rises from the Pridoli into the Lower Devonian with a maximum peak in the Lochkovian (121 species) (Fig. 2C). Richness then falls in the Pragian but rises to a relative peak again in the Emsian before gradually sinking throughout the Middle and Upper Devonian, staying at a consistently low level throughout most of the Carboniferous, and then slightly decreasing again towards and into the Permian. Removing either isolated scale, isolated fin or both isolated scale and fin spine-based taxa does not substantially change the general pattern of acanthodian richness through the Palaeozoic. Species counts are reduced to lower values, especially when isolated scale-based taxa are excluded but peaks still occur in the Lochkovian and Emsian.

There is a significant trend towards lower values through time in raw taxonomic richness throughout the Palaeozoic when STCM2 is used as the explanatory variable ($p = 0.008$; $R^2 = 0.90$). None of the other explanatory variables have a significant relationship with raw richness (Table S4). The models that best explain the acanthodian taxonomic diversity time series include STCM2 ($R^2 = 0.90$; AIC weight = 0.18), sea level + STCM2 ($R^2 = 0.97$; AIC weight = 0.36) and SCM2 + STCM2 ($R^2 = 0.90$; AIC weight = 0.06) as explanatory variables with only the STCM2 coefficient being significant in all three models.

Differences between skeletal and soft tissue completeness metrics

The SCM values show a slight offset towards higher median values compared to the STCM while STCM has higher individual percentages of completeness than SCM2

(Fig. S2). A time series comparison of both metrics using GLS analyses shows a significant positive correlation ($p < 0.0001$; $R^2 = 0.96$). Non-temporal Mann–Whitney–Wilcoxon tests show that there is a significant difference between the observed acanthodian SCM2 and STCM2 values ($W = 71\,753$; $p < 2.1 \times 10^{-28}$) as well as SCM1 and STCM1 values ($W = 71\,633$; $p < 2.1 \times 10^{-28}$) (Table S5). When comparing both variants of the completeness metrics, neither SCM1/SCM2 nor STCM1/STCM2 are significantly different from each other when Mann–Whitney–Wilcoxon tests are used, confirming results from previous studies.

We additionally calculated the relative percentages of each of the acanthodian body region divisions to quantify how well they are represented in our dataset. Scales and fin spines together make up about 60% of the skeletal regions in the whole dataset while the neurocranium (3.1%), hyoid and gill arch (3.2%), teeth (2.9%) and vertebrae (0.1%) are the least likely to be recovered in the acanthodians investigated (Fig. 3A). If both isolated scales and fin spines are removed, the relative percentages of each skeletal region approximately triple in quantity, with the scapula (38.9%) and Meckel’s cartilage (25.5%) predominantly represented. For the soft tissue regions, the main body is preserved in 33.2% of taxa while the

intermediate fin or fins and the pectoral fins are only present in about 0.3% and 1.3% respectively (Fig. 3B).

Acanthodian subgroups

Acanthodiformes have the widest distribution of SCM2 values with the highest median (42.5%) and interquartile range compared to any of the other subgroups (Fig. 4A). *Incertae sedis* have the next highest SCM2 distribution with 5.1%. The remaining subgroups all have similar bottom-heavy SCM2 distribution and similar medians and interquartile ranges (<5%). Both Kruskal–Wallis and Mann–Whitney–Wilcoxon tests show that there is a significant difference between the subgroups ($H = 47.477$; $p = 4.54 \times 10^{-9}$), with the latter demonstrating that there is a significant difference between SCM2 value distribution of Acanthodiformes and the other subgroups as well as between Diplacanthiformes and Climatidae and *Incertae sedis* and Climatidae (Table S6). Removal of isolated fin spine taxa does not change the distribution of SCM2 values much (Fig. S3C, Table S7). When isolated scales and isolated fin spines are excluded, median SCM2 of diplacanthiform (39.8%), *Incertae sedis* (27.5%) and climatid (29.7%) subgroups are considerably higher than

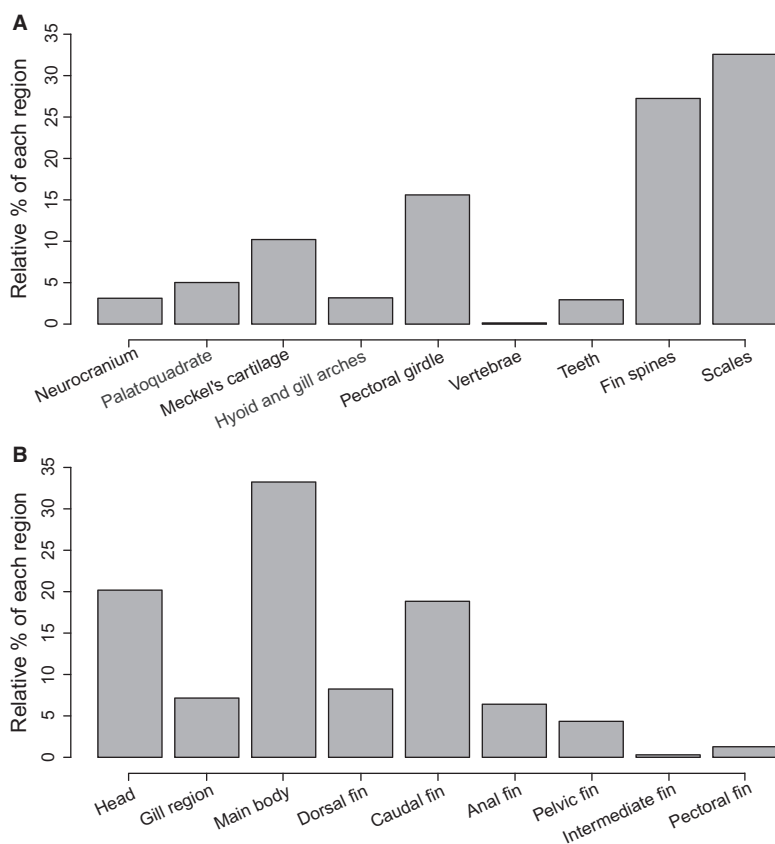
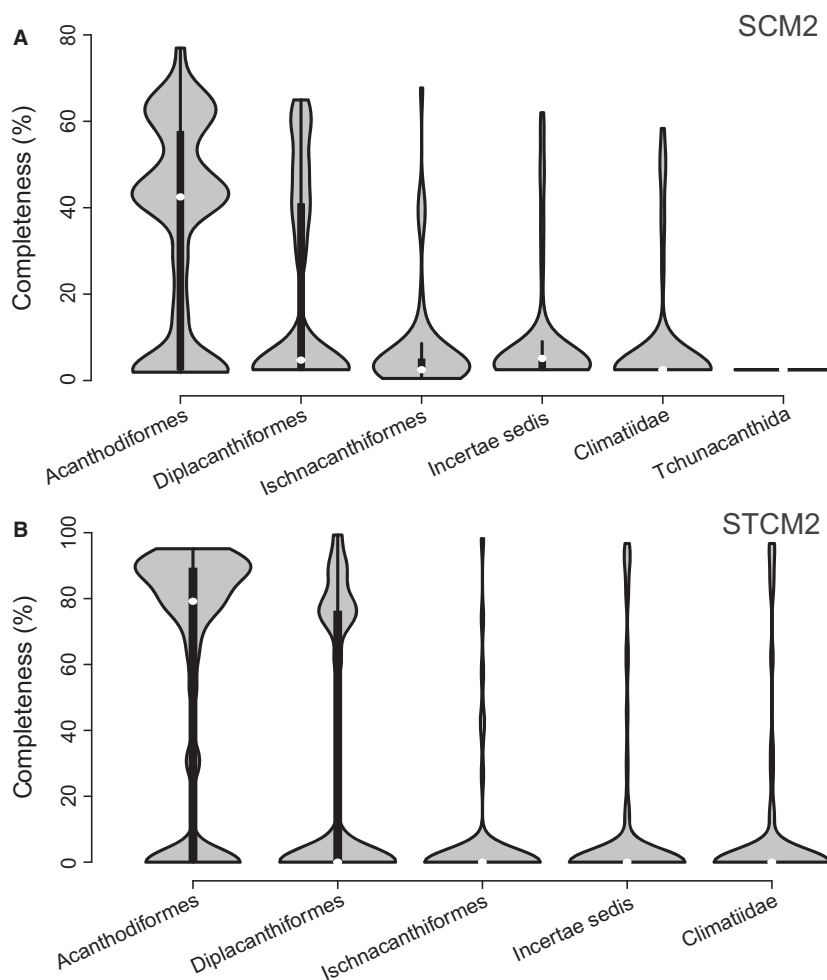


FIG. 3. Relative percentage distributions of the different body regions used in the dataset. A, skeletal regions. B, soft tissue regions.

FIG. 4. Distribution of completeness between different acanthodian subgroups. A, skeletal completeness. B, soft tissue completeness.



the original dataset (Fig. S3E). While a Kruskal–Wallis test still confirms a significant difference between the distribution of SCM2 values ($H = 38.251$; $p = 9.95 \times 10^{-8}$), Mann–Whitney–Wilcoxon tests do not recover a significant difference in SCM2 values between acanthodiforms and diplacanthiforms when taxa based on isolated scales and fin spines are excluded (Table S8). Exclusion of only isolated-scale-based taxa shows a similar pattern except for the *Incertae sedis* subgroup which is considerably lower (5.1%) and identical to the original dataset values (Fig. S3A, Table S9).

STCM2 distributions of acanthodian subgroups show a similar completeness pattern to the SCM2 (Fig. 4B). Acanthodiforms have the highest median STCM2 (79.2%) and interquartile range, whereas all other subgroups have similar low ranges (median of 0%). A Kruskal–Wallis test suggests a significant difference between the subgroups ($H = 90.024$; $p < 2.2 \times 10^{-16}$). Pairwise Mann–Whitney–Wilcoxon tests of the distribution of STCM2 values show a significant difference between acanthodiforms and the

other subgroups just as with SCM2 (Table S10). Diplacanthiform STCM2 is significantly different from Ischnacanthiformes, *Incertae sedis* and climatiids. Tchnacanthisda do not show any soft tissue completeness in their fossil record. Upon removal of isolated fin spine and scale-based taxa, distribution of STCM2 values changes considerably for diplacanthiform (75.9%), *Incertae sedis* (45%) and climatiid (31%) subgroups while ischnacanthiforms (0%) are not affected (Fig. S3F). While Kruskal–Wallis tests are still significant ($H = 44.09$; $p = 6.15 \times 10^{-9}$), Mann–Whitney–Wilcoxon tests no longer detect a significant difference between acanthodiform and diplacanthiform STCM2 (Table S11). Acanthodiforms are still significantly different from ischnacanthiforms, *Incertae sedis* and climatiids, as diplacanthiforms are from ischnacanthiforms. Ischnacanthiform STCM2 values are also significantly differentiable from *Incertae sedis* and climatiid subgroups. When only isolated scale-based taxa are removed, a similar pattern to the dataset without fin spines and scales is recovered (Fig. S3B, Table S12). As with

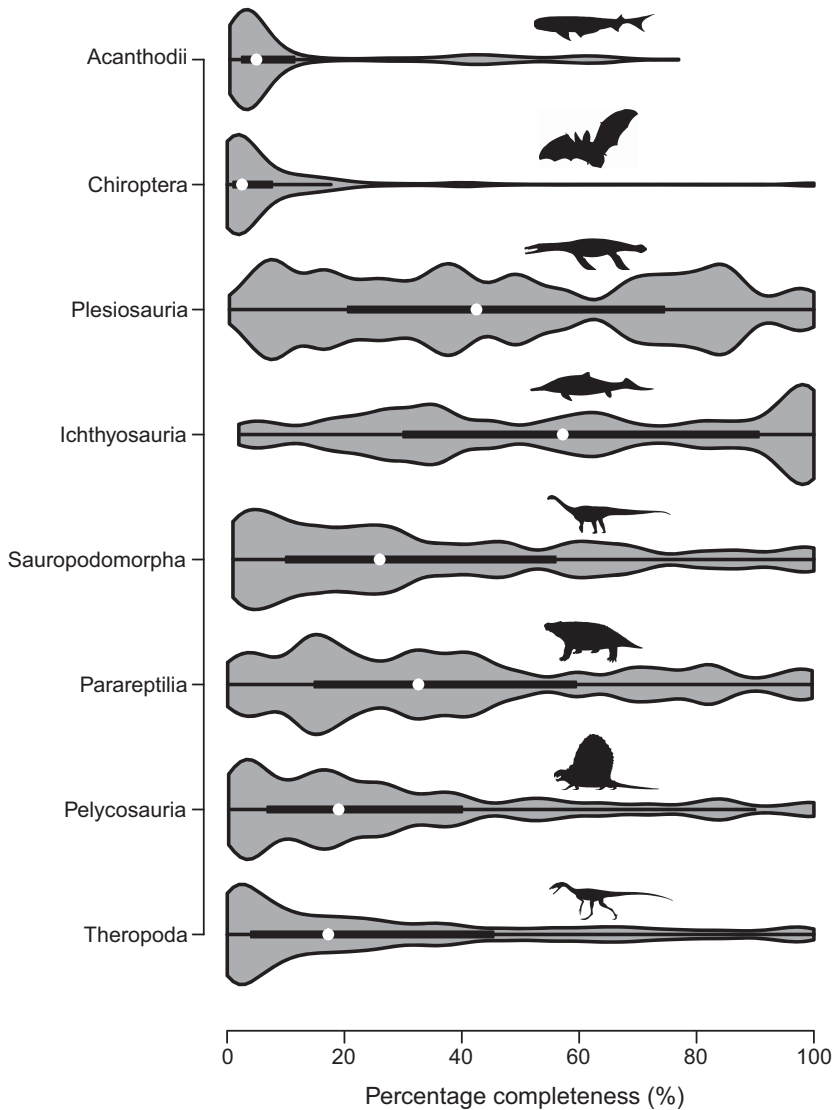


FIG. 5. Distribution of acanthodian SCM2 values compared to other vertebrate groups. Comparative values from bats (Brown *et al.* 2019), plesiosaurs (Tutin & Butler 2017), ichthyosaurs (Cleary *et al.* 2015), sauropodomorphs (Mannion & Upchurch 2010; Cashmore *et al.* 2020), parareptiles (Verrière *et al.* 2016), pelycosaurs (Brocklehurst & Fröbisch 2014) and theropods (Cashmore & Butler 2019). Silhouettes from <http://phylopic.org/> and include work by N. Tamura (acanthodian), G. Monger (ichthyosaur), S. Hartman (plesiosaur), all CC BY 3.0; Smokeybjb (sauropodomorph), Karkemish (vectorized by T.M. Keesey) (parareptile) and D. Bogdanov (pelycosaur), all CC BY-SA 3.0; and S. Hartman (theropod) and Y. Wong (chiropteran), both CC0 1.0.

SCM2, exclusion of isolated fin spine-based taxa does not considerably change the distribution of STCM2 values (Fig. S3D, Table S13).

Comparison to other vertebrate groups

Distribution of acanthodian median SCM2 scores in comparison to other vertebrate groups is considerably lower, with the exception of bats (Fig. 5). SCM2 values for both acanthodians and bats show a very bottom-heavy distribution with more extreme distributions than any other vertebrate groups examined. A comparison using Mann–Whitney–Wilcoxon tests however still show a highly significant difference between acanthodian and bat SCM2 values (Table S14). Even though total STCM2 values of

acanthodians are considerably higher than their SCM2 values, STCM2 values are still significantly lower than the other vertebrate groups including bats (Fig. S4A, Table S15). Violin plots show that median scores for acanthodian SCM2 (5%) are much lower than the scores for plesiosaurs (42.5%), ichthyosaurs (57.2%), sauropodomorphs (21.5%), theropods (17.2%), parareptiles (32.6%) and pelycosaurs (19%) but show a similar score distribution to bats (2.5%). The interquartile range of acanthodians is also narrower than in these groups and comparable to bat SCM2. If isolated scales and fin spines are excluded from the dataset, acanthodian SCM2 scores are more evenly distributed throughout and median values as well as interquartile range are comparable to sauropodomorph, parareptiles and pelycosaurs (Fig. S4D, Table S16).

Geographical comparisons

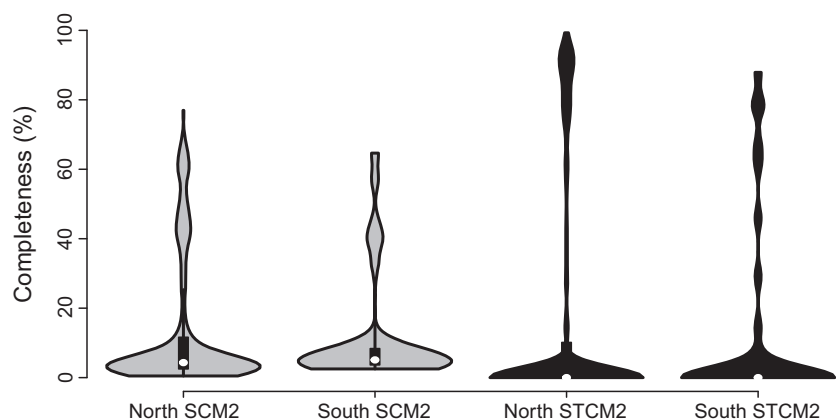
Taxon distribution is highly uneven between the different continents, with highest numbers in Europe (164), North America (68) and Asia (68), intermediate to low in Australia and Oceania (17) and South America (9), and lowest in both Antarctica (5) and Africa (2). For geographical completeness, acanthodian species from northern hemisphere localities were compared to southern hemisphere localities, with non-significant Mann–Whitney–Wilcoxon results for both SCM2 ($W = 4170$; $p = 0.12$) and STCM2 ($W = 4958$; $p = 0.95$) and very similar distribution patterns (Fig. 6). When SCM2 and STCM2 are categorized into continents, the range of values do not vary substantially between most of the continents. Kruskal–Wallis tests however indicate a strong domination of variance of completeness distribution by at least one of the continents for both SCM2 ($H = 29.3$; $p = 5.34 \times 10^{-5}$) and STCM2 ($H = 18.495$; $p = 0.005$). Europe and North America have the highest SCM2 (max. values of 77% vs 68.3%) and STCM2 (max. values of 98.2% vs 99.3%) ranges whereas Africa has the highest overall median SCM2 (24.6%) and Antarctica the highest overall median STCM2 (5.4%) (Fig. 7). Taxa from South America have the least complete record with the lowest range for both SCM2 and STCM2 but the median values are similar to the other continents (5.1% SCM2, 0 STCM2). SCM2 values vary significantly between Europe and North America, North America and Asia and weakly (no adjusted p -values) between South America and Africa, South America and Asia, and Africa and Asia (Table S17). STCM2 values show a somewhat different pattern, with strongly significant differences between North America and Asia only and weakly significant values (no adjusted p -values) between Europe and North America, North America and South America, South America and Antarctica, and Asia and Antarctica (Table S18).

Depositional and environmental comparisons

SCM2 and STCM2 values are statistically different between acanthodian taxa from either freshwater or marine environmental settings (Table S19). There is no difference between marine SCM2 and STCM2; however, there is a significant difference between freshwater SCM2 and STCM2. Specimens from freshwater deposits have both a higher median SCM2 and interquartile range than marine deposits while freshwater STCM2 values only show a higher interquartile range (Fig. S5). Mean temporal SCM2 and STCM2 based on taxa from freshwater deposits is initially higher throughout the Silurian and Lower to Middle Devonian compared to taxa from marine deposits (Fig. 8). This pattern is then reversed in the Givetian–Frasnian and persists throughout most of the Carboniferous, with higher SCM2 and STCM2 values from marine sediments. It then reverts back to higher freshwater completeness in the Gzhelian and Asselian while the last occurrences in the upper Cisuralian and Guadalupian come from marine deposits but only have very low completeness percentages.

For individual benthic assemblage zones (BA), Mann–Whitney–Wilcoxon tests indicate a significant difference for SCM2 of taxa from BA0 compared to any of the other BA1–6 but only a weak signal between BA0 and BA2 (Table S20). BA1 SCM2 is also significantly different from all of BA3, BA4 and BA6 and weakly BA5. The signal for STCM2 is similar but not as clear as there are no significant differences between BA0 and BA1 and only a weak signal between BA0 and BA6 (Table S21). There is, however, a significant difference between BA2 and BA4 and weakly BA2 and BA3 as well as BA2 and BA5. Subsequent Kruskal–Wallis tests further suggest that there are significant differences in SCM2 ($H = 29.167$; $p = 5.66 \times 10^{-5}$) and STCM2 ($H = 28.046$; $p = 9.21 \times 10^{-5}$) completeness distributions between the different BAs, with one or more dominating. GLS pairwise comparisons further show

FIG. 6. Distribution of acanthodian SCM2 (grey) and STCM2 (black) scores between the northern and southern hemispheres.



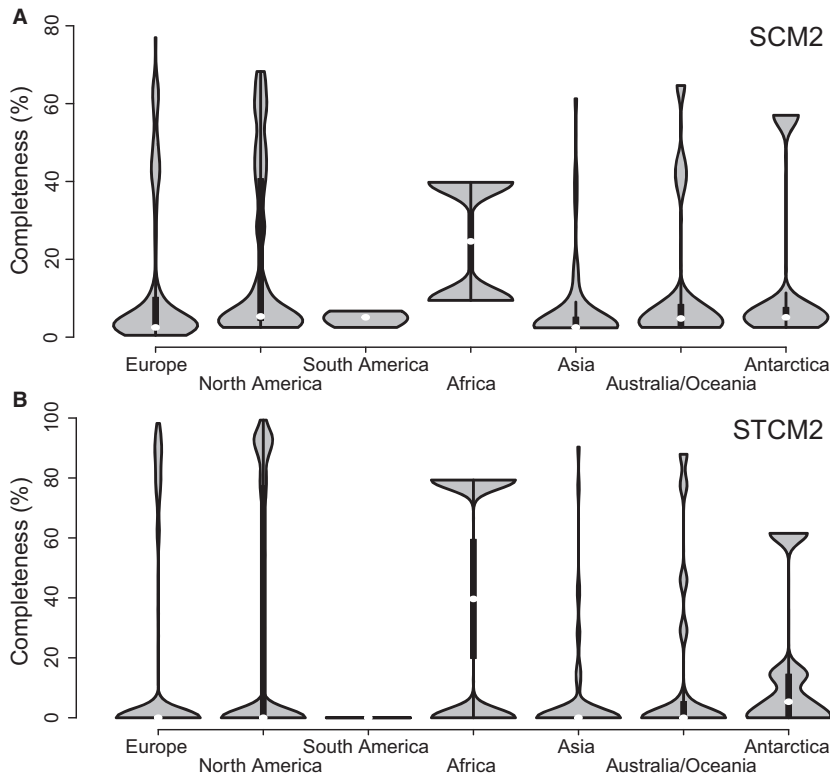


FIG. 7. Distribution of acanthodian completeness between different continents. A, skeletal completeness. B, soft tissue completeness.

significant relationships between each BA0–4 SCM2 and total SCM2 as well as each BA0–BA4 STCM2 and total STCM2 through time (Tables 1, 2). The range of skeletal completeness of acanthodians is lowest in BA6 and the range of soft tissue completeness is lowest in both BA5 and BA6 environments (Fig. S6). Violin plots of both SCM2 and STCM2 show bottom heavy distributions for all BAs, with only a slightly wider top distribution in BA0.

Mean SCM2 and STCM2 by BA through time shows the low completeness of BA6 being restricted to the upper Silurian and Devonian (Fig. 9). Interestingly, there is a peak of 46% in STCM2 of acanthodians from BA6 in the Gorstian–Ludfordian. A similar low pattern to BA6 is observed for BA5. Acanthodian completeness in BA3 and BA4 zones is initially low throughout the Silurian and Devonian but heavily increases at the Devonian–Carboniferous boundary and plateaus at *c.* 60% SCM2 and *c.* 90% STCM2 throughout the Mississippian and into the lower Pennsylvanian. Time series of mean SCM2 and STCM2 of taxa deposited in BA1 closely resemble the patterns observed in BA2 throughout the Palaeozoic. The biggest differences (maximum of 20%) between BA1 and BA2 are found in the Serpukhovian–Bashkirian for SCM2 and STCM2. A low record for BA1 is recovered again from the lower Permian Kungurian stage alone and for BA3–4 from the Roadian to the Capitanian.

Sea level correlations

Average sea level throughout the Palaeozoic does not significantly correlate with any of the completeness metrics or raw taxonomic richness, even when the completeness scores from marine and freshwater deposits are separated (Table S22, Fig. 8). However, on removal of the two fragmentary specimens from the Kungurian and the two fragmentary specimens from the Guadalupian, average sea level significantly correlates with total SCM2 and STCM2, as well as raw taxonomic richness (Table 3). When the data is divided into marine and freshwater completeness, marine SCM2 and STCM2 both recover significant relationships with sea level through time whereas freshwater SCM2 and STCM2 show non-significant correlations. All significant correlations between acanthodian completeness and sea level are negative, showing that acanthodian total SCM2 and STCM2, marine SCM2 and marine STCM2 are higher during lower sea level through time and decrease when sea level rises.

DISCUSSION

The earliest unambiguous acanthodians are recovered from sediments of early Silurian age (lower to middle Llandovery) but consist of exclusively isolated scales and

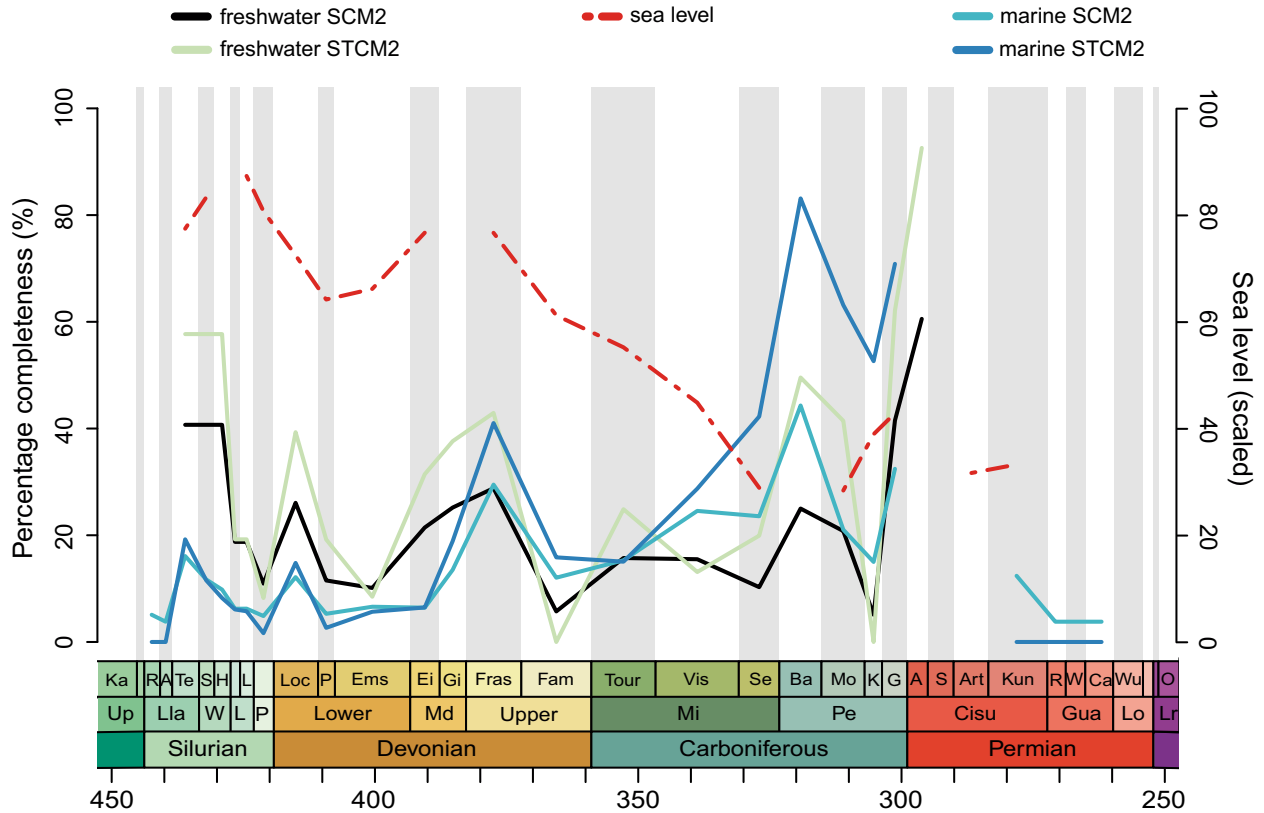


FIG. 8. Changes in acanthodian completeness through time based on freshwater vs marine occurrences together with sea level changes. Sea level values represent arbitrary values taken from Hannisdal & Peters (2011).

TABLE 1. Results of pairwise comparisons between benthic assemblage zone and total acanthodian SCM2 using GLS.

Comparison	Slope	t-value	p-value	R ²
BA0 SCM2 ~ total SCM2	1.1364394	9.45256	<0.0001	0.8615699
BA1 SCM2 ~ total SCM2	0.6510992	4.502837	0.0002	0.7196603
BA2 SCM2 ~ total SCM2	1.1016979	5.187407	0.0001	0.7556846
BA3 SCM2 ~ total SCM2	0.9446167	4.190313	0.0005	0.6516339
BA4 SCM2 ~ total SCM2	0.8740366	3.0107960	0.0083	0.5490754
BA5 SCM2 ~ total SCM2	0.1945695	0.7137465	0.4985	0.1238444
BA6 SCM2 ~ total SCM2	-0.1802193	-1.809638	0.1301	0.6087064

Statistically significant results indicated in **bold**.

fin spines (Karatajūtė-Talimaa & Smith 2003; Valiukevičius & Burrow 2005; Burrow 2011). Throughout the Silurian, the acanthodian fossil record remains fragmentary with the exception of partially articulated

individuals of one ischnacanthiform species, *Nerepisacanthus denisoni* (Burrow 2011). From the Lower Devonian Lochkovian onwards, the record expands significantly with several articulated acanthodian species found from localities in North America, Europe and Asia, next to the abundance of taxa known from isolated remains. This pattern continues throughout the Devonian and most of the Carboniferous. Towards the end of the Carboniferous and lower Permian, several of the last known species in the acanthodian record are preserved as partly articulated and exceptionally complete skeletons; all are referred to the genus *Acanthodes*. The overall record of acanthodians, however, is reflected in their overall low completeness distribution here, with the bulk of taxa ranging between 2.5% and 10% skeletal completeness and 0 and 5% soft tissue completeness (Fig. S2).

Completeness metrics comparisons

The quality of the acanthodian fossil record can be assessed differently depending on whether the skeletal or soft tissue completeness metrics is used. There is a significant difference between the distributions of skeletal

TABLE 2. Results of pairwise comparisons between benthic assemblage zone and total acanthodian STCM2 using GLS.

Comparison	Slope	t-value	p-value	R ²
BA0 STCM2 ~ total STCM2	0.643705	2.642464	0.0161	0.2441898
BA1 STCM2 ~ total STCM2	0.8663832	7.631916	<0.0001	0.8038241
BA2 STCM2 ~ total STCM2	1.1159227	5.828419	<0.0001	0.7215758
BA3 STCM2 ~ total STCM2	0.8835493	4.676307	0.0001	0.6455123
BA4 STCM2 ~ total STCM2	0.7195042	2.9334506	0.0097	0.5171618
BA5 STCM2 ~ total STCM2	0.1891935	0.5747831	0.5834	0.1763441
BA6 STCM2 ~ total STCM2	-0.5492497	-1.006455	0.3604	0.4097996

Statistically significant results indicated in **bold**.

TABLE 3. Results of pairwise comparisons for sea level trends in different time series using GLS excluding the Permian outliers.

Comparison	Slope	t-value	p-value	R ²
Total SCM2 ~ sea level	-0.651186	-2.327641	0.0343	0.8013668
Total STCM2 ~ sea level	-0.39396	-3.824589	0.0083	0.8305507
Marine SCM2 ~ sea level	-1.070002	-3.087337	0.0075	0.7537432
Marine STCM2 ~ sea level	-0.86458	-3.650602	0.0015	0.817932
Freshwater SCM2 ~ sea level	0.5235253	1.6565592	0.1198	0.623399
Freshwater STCM2 ~ sea level	0.160845	0.7386898	0.4723	0.9605055

Statistically significant results indicated in **bold**.

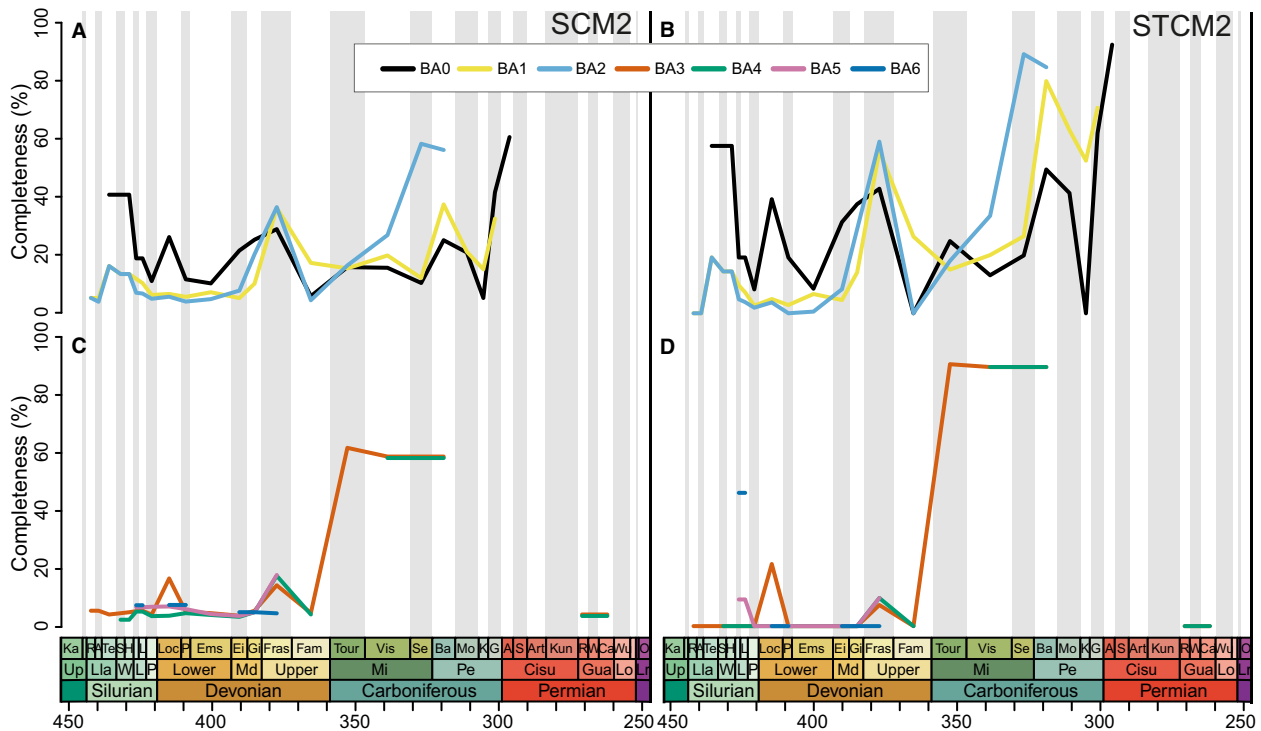


FIG. 9. Changes in acanthodian completeness through time based on benthic assemblage (BA) zones. A–B, BA0 to BA2: A, skeletal completeness (SCM2); B, soft tissue completeness (STCM2). C–D, BA3 to BA6: C, skeletal completeness (SCM2); D, soft tissue completeness (STCM2).

completeness metric values and soft tissue completeness metric values for acanthodians. The STCM2 values have an increased interquartile range and distribution of acanthodian completeness scores compared to the SCM2 values, indicating that there is more variation of completeness in the soft tissue regions than the skeletal regions (Fig. S2). SCM2 has a higher overall median value compared to STCM2. In the time series, mean and median soft tissue completeness is slightly higher than skeletal completeness. The observed differences between the two metrics might be explained by a wide lack of preservation of specific skeletal regions in acanthodians, namely the vertebrae, neurocranium and branchial arches (Fig. 3). As expected, soft tissue imprints of the head, main body and caudal fin were more commonly found in both partially articulated and articulated acanthodian specimens while imprints of the pectoral, pelvic and intermediate fins were regularly absent. However, the skeletal and soft tissue completeness metrics also positively correlate with each other through time, indicating that either one of these two could be used to accurately score completeness patterns of acanthodians. Thus, incorporating soft tissue completeness instead of or complementary to skeletal completeness may broaden the applicability of the completeness methods to the fossil record of other groups, both vertebrate and invertebrate. Nevertheless, preservation of soft tissue components is unevenly spaced in the fossil record (Allison & Briggs 1993) and soft tissue completeness might be restricted to specific groups with a wide range of soft tissue preservation to allow quantitative analyses through time.

In comparison to total SCM2 and STCM2, the three subsets excluding isolated skeletal material (scales and/or fin spines) yield an overall higher mean completeness through time while the general patterns and peaks are retained (Fig. 2). While the overall spikes and drops in completeness are recovered in all of the subsets, mean completeness is considerably lowered by the inclusion of the isolated parts. STCM2 seems to be more heavily affected by limited material than SCM2, with subsets without isolated fin spines and scales leading to differences of up to 60% in mean completeness in specific stages through time, specifically the Tournaisian and Serpukhovian. This is not surprising as these isolated remains of skeletal origin result in a scoring of 0 in terms of soft tissue completeness and therefore may strongly decrease mean completeness through time. Identical curves of total SCM2 and the subset without isolated scale-based taxa as well as the subset without isolated fin spine-based taxa and the subset without both isolated scale and fin spine-based taxa in the Carboniferous can be explained by a lack of isolated scale-based taxa and a high number of isolated fin spine-based taxa during that time period.

Our results show how isolated remains such as scales and fin spines influence our interpretation of the acanthodian fossil record and potentially bias the completeness patterns we observe. While it has been argued that the inclusion of isolated elements could still contain important information on the taphonomic drivers of preservation (Driscoll *et al.* 2018), there are other potential drivers that have to be taken into account. Acanthodian species are predominantly named and assigned to higher level taxa on the basis of isolated scales and fin spines, potentially resulting in taxonomic ‘over-splitting’ at species and genus levels (42.81% isolated scale-based, 18.73% isolated fin spine-based species in our dataset) while a consistent application of a genus and species-level concept is yet to be established. One prominent example is the histological type genus *Nostolepis*, which was characterized based on histological structure rather than morphology of the scales (Gross 1947), and is known from isolated scales recovered from localities worldwide. Specimens of that genus were frequently erected into new species throughout the twentieth century and subsequently transferred into different genera by Valiukevičius & Burrow (2005). The number of species, however, was not significantly reduced and their validity is pending future investigations. Similarly, the genus *Gyracanthus* was originally erected based on ornamented isolated fin spines (Agassiz 1837). These spines range from the Lower Devonian to Upper Carboniferous and contain a multitude of species, some of which may well be synonymous (Denison 1979; Snyder *et al.* 2017). The Palaeozoic shark genus *Ctenacanthus* was also described based on isolated fin spines, specifically their ornament patterns along the fin spine ridge, and synonymy renders the validity of the genus doubtful (Maisey 1981, 1984; Ginter *et al.* 2010). This synonymy reduces the utility of a clade record, as has been recognized for pelycosaur (Brocklehurst & Fröbisch 2014), among many other instances. As our subset comparisons show, datasets excluding such skeletally limited material strongly increase estimates of acanthodian fossil record quality. The causes for this are probably a combination of biases rather than a single factor but ‘over-splitting’ is likely to play an important role in the observed trend.

Taxonomic group comparisons

We found significant differences between the skeletal and soft tissue completeness distributions of Acanthodiformes and all other subgroups (Fig. 4). We excluded the Tchnacanthida for the statistical analyses between the subgroups as the limited distribution of only isolated scales within two single species resulted in analysis errors. Acanthodiformes have a significantly higher median skeletal and soft tissue completeness value as well interquartile

range and show a visually different distribution to all other subgroups. All other subgroups exhibit a bottom heavy skeletal and soft tissue completeness distribution with few highly complete taxa. Interestingly, the *Incertae sedis* subgroup shows a similar total SCM2 and STCM2 distribution to the well-defined acanthodian subgroups such as Ischnacanthiformes or Diplacanthiformes. This suggests that levels of completeness cannot be solely argued to be a limiting factor for resolving the taxonomic issues of the taxa within this group as other acanthodian groups show similar distributions of completeness while being taxonomically well resolved.

Acanthodiformes have been prominently featured in previous anatomical and phylogenetic assessments of skeletal characters, some of which are rarely found in other acanthodian subgroups (e.g. detailed neurocranial structures, remains of vertebrae and unusually complete hyoid arch and gill skeletons) as well as having more extensively perichondrally ossified endoskeletons compared to other acanthodian groups (Miles 1970, 1973a; Beznosov 2009). Thus, their high levels of completeness are not surprising. Some of the most complete acanthodiform taxa, notably the completely articulated skeletons of *Acanthodes confusus*, *A. gracilis* and *A. bronni* (Heidtke 2011), have been found in the upper Carboniferous and lower Permian shortly before the group's extinction, indicating a potential sampling bias where younger sediments have had less time to be destroyed by geological processes (see e.g. Raup 1972; Jablonski *et al.* 2003; Sahney & Benton 2017).

Removal of isolated scale-based taxa does significantly increase the overall completeness of diplacanthiform acanthodians with a high number of taxa in the 40–60% skeletal completeness as well as 60–95% soft tissue completeness ranges. This highlights a potential discrepancy in the fossil record of this subgroup with species being erected on the basis of either very limited material or almost complete skeletons. The lack of a well-sampled fossil record and an abundance of highly complete skeletons for any of the other subgroups has implications for understanding the evolutionary development of acanthodians as a clade in general and their morphology and ecology in particular.

Vertebrate group comparisons

Comparisons of completeness between acanthodians and other marine vertebrate groups such as Mesozoic plesiosaurs and ichthyosaurs illustrate a large discrepancy between clades living in similar environments. Plesiosaur and ichthyosaur skeletal completeness records exhibit the highest overall and median skeletal completeness scores of all tetrapods published to date. These results are probably a consequence of similarities in preservation and

coexistence in respective habitats (Cleary *et al.* 2015; Tutin & Butler 2017). Acanthodians, however, while also living in aquatic environments, show very low overall and median scores but are also considerably older than any of the other published vertebrate groups. This study represents the first thorough account of quantitative completeness analyses in Palaeozoic vertebrates. As there is currently no published data on the distribution of skeletal completeness of any other fish group, Palaeozoic or otherwise, it is difficult to compare groups from truly similar ecological niches and assess whether the low completeness scores are reflected in those groups as well. Fish groups such as Palaeozoic actinopterygians might provide a worthwhile, but rather large and challenging, dataset for comparison.

Acanthodians show a significantly lower skeletal completeness distribution than most of the tetrapod groups previously studied, but show a similar bottom-heavy distribution relative to bats (Fig. 5). Comparisons between acanthodians and bats reveal a significant difference between the two groups, with bats showing a slightly lower median completeness than acanthodians when total SCM2 is used. This is reversed when the subset without isolated scales and fin spines is used (Fig. S4D). Both groups show an abundance of isolated skeletal remains compared to partially articulated or articulated specimens which contributes to their poor skeletal completeness records (Brown *et al.* 2019).

Geographical impacts

Acanthodian fossils are recovered from all continents (Fig. 7). We did not recognize significant differences or strong spatial biases between acanthodian completeness from the northern and southern hemisphere or the different continents (Fig. 6). Surprisingly, Africa has the highest median SCM2 record and Antarctica the highest median STCM2 record even though the number of recovered taxa is low for both continents (Fig. 7). This means that the relatively small number of taxa obtained from those continents yield comparatively high skeletal or soft tissue information. The Waterloo Farm locality in the Witpoort Formation (South Africa) most notably yields fossils with exceptional preservation of soft tissue outlines in fine-grained anoxic sediments (Gess & Whitfield 2020), which can explain the high STCM2 scores. However, given the small sample sizes, this may be the result of sampling bias rather than an environmental or ecological bias and is difficult to establish for now.

There is a considerable difference in the number of taxa distributed between the different continents, with ten times more taxa from the northern compared to the southern hemisphere, which is most likely to be related to

a higher historical collection effort and interest. While collection effort has yielded a considerably higher number of taxa from the northern hemisphere, the completeness records of both hemispheres are very similar, meaning that a comparatively smaller number of taxa from the southern hemisphere contain similar levels of completeness to the taxonomically richer records from the northern hemisphere. Thus, the presence of localities with rich acanthodian records such as MOTH (Canada) (Hanke & Wilson 2004), the 'Old Red Sandstone' (UK) (Miles 1973a; Brazeau 2009) or the Meisenheim Formation (Germany) (Heidtke 2011) in the northern hemisphere do not result in considerably higher SCM2 or STCM2 distribution, as might have been expected. However, given the low number of taxa discovered in the southern compared to the northern hemisphere, it is likely that there is a considerable amount of undiscovered information on the acanthodian fossil record that could play an important role in widening our understanding on both acanthodian completeness and macroevolution.

The significant difference in SCM2 values between Europe and North America (Fig. 7) is interesting given the heightened historical collection effort and interest within and between both continents that has been documented from other taxonomic groups (see e.g. Bernard *et al.* 2010; Brocklehurst *et al.* 2012; Cleary *et al.* 2015; Brown *et al.* 2019; Cashmore & Butler 2019, Cashmore *et al.* 2020). While there has been a high number of isolated scale-based taxa published from European localities and especially the Baltics (e.g. Gross 1973; Valiukevičius & Karatajūtė-Talimaa 1986; Valiukevičius 2003, Pinakhina & Märss 2018) which might partially explain the lower median values for Europe, the causes for this are unknown. South America has the lowest acanthodian record of any of the continents which is in accordance with previous investigations highlighting the scarcity and discontinuity of the continent's Devonian vertebrate record (Gagnier *et al.* 1988; Maisey *et al.* 2002; Janvier & Maisey 2010). South America also currently provides very limited fossil evidence in terms of acanthodian diversity and skeletons beyond disarticulated spines and scales which provides something of a conundrum given that much of South America's fauna was suggested to be dominated by chondrichthyans and acanthodians during Devonian times (Janvier & Maisey 2010).

Environmental and ecological biases

Skeletal and soft tissue completeness of acanthodian species was highest in freshwater deposits (Fig. S5; Table S19), suggesting that the best-preserved fossils are found in these types of environments. Some of the high completeness scores for freshwater acanthodian taxa

probably derive from lake deposits such as the Old Red Sandstone of Scotland where the anoxic conditions within the deeper, stratified parts of Lake Orcadie protected material from scavenging, weathering and decay (e.g. Donovan 1975; Burrow 1996; Dineley & Metcalf 1999). These lacustrine environments are generally characterized by low energy conditions (Rust 1982) where a lack of transport and physical disturbance may prevent disarticulation of skeletons. Conversely, fluvial depositional settings are generally associated with higher energy levels of transportation before burial (Behrensmeier 1988; Evans 2016) which can impact the completeness of specimens preserved in these sediments. Our results, however, also suggest a high completeness of acanthodians from fluvio-lacustrine settings, specifically towards the end of the Carboniferous and early Permian. These are predominantly associated with deposits from the intermontane Saar–Nahe Basin in Germany where volcanic ash fallout deposition together with fluvio-lacustrine dominated settings (Königer & Stollhofen 2001) may have led to a higher preservation potential of acanthodian skeletons.

Median acanthodian skeletal completeness is significantly lower for specimens from marine sediments compared to freshwater environments (Fig. S5; Table S19). One possible explanation for the observed lower completeness in marine deposits may be the strong influence of physical processes acanthodian skeletons are subjected to in these environments, resulting in taphonomic modification through mechanical damage as well as a preservational bias against small and fragile elements (Boessenecker *et al.* 2014). However, while there have been attempts to determine if taphonomic processes are equivalent in different aquatic environments, including freshwater vs marine (Kidwell 1986; Cummins 1994), currently this question remains uncertain.

Environmental and lithological information was used to assign acanthodian fossils to benthic assemblage zones to infer how specific environments impact the acanthodian fossil record rather than only looking at completeness of acanthodians from freshwater and marine sediments. We showed above that acanthodians from non-marine deposits exhibit the highest level of overall completeness (Fig. S6). Within the marine realm, BA1 and BA2 exhibited the most consistent patterns throughout the Palaeozoic, ranging through all stratigraphic stages, and closely track each other (Fig. 9). This is perhaps not surprising as these juxtaposed intertidal and shallow subtidal environments are often coupled in interpretations of lithostratigraphic units and our results may derive from limitations in resolution between the two environments. Skeletal and soft tissue completeness of acanthodians throughout the Palaeozoic is comparatively higher in BA1 and BA2 environments than BA3–6 (Fig. 9) suggesting that tidal flats, strandlines and subtidal

lagoons yield higher levels of preservation and articulation than the deeper marine environments. Notably, highest completeness was found in acanthodians from the Glencarholm Volcanic Member and the Mazon Creek locality where conditions of quick burial, low oxygen and low pH in nearshore, shallow bay type environments, in part representing death assemblages, allowed the fish bodies to remain intact after death (Baird 1979; Schram 1983; Dineley & Metcalf 1999; Clements *et al.* 2019). Fossils of the Glencarholm and Mazon Creek biotas have indeed been previously compared to show similar modes and details of preservation (Schram 1983; Briggs & Gall 1990). In shallow lagoon settings such as shelf lagoons, barriers commonly provide protection from the open sea (Fürsich *et al.* 2016) and can potentially prevent disarticulation by wave action or currents. Furthermore, environmental stress arising from elevated or fluctuating salinity values and decreased oxygen concentrations (Fürsich *et al.* 2016) could play a role in protecting carcasses from scavenging, weathering and decay. However, tidal flats can also be disrupted by physical constraints such as cyclic deposition of alternating sand and mud or the extremes of intertidal zones translating into poor preservation (Gao 2009; Davis 2012). However, the high levels of acanthodian completeness from BA1 and BA2 throughout the Palaeozoic suggest that these physical constraints may have played only a minor role during deposition.

Acanthodians from zones BA3 and BA4 (middle to outer shelf, reef settings as well as subtidal dynamic environments) show generally low completeness scores throughout the Silurian and Devonian but increase heavily in the Mississippian and early Pennsylvanian (Fig. 9). This spike is surprising but can possibly be explained by a combination of environmental deposition and sampling bias. Only two species of acanthodians are present in the Carboniferous BA3 and BA4 and both belong to the genus *Acanthodes*, which is known to be one of the most complete acanthodian taxa to date (Nelson 1969; Miles 1973b; Heidtke 2011; Davis *et al.* 2012). Additionally, the records for the Mississippian and lower Pennsylvanian BA3 and BA4 derive from two lithostratigraphic intervals, the Russian Lower Os'kin Subformation and the North American Heath Formation lagerstätte, where individuals were rapidly buried in wide shallow-water elevated salinity environments as such warm water settings would have otherwise led to rapid decay and disarticulation (Lund *et al.* 1993; Hagadorn 2002; Beznosov 2009).

The correlations between benthic assemblage zones BA0–4 SCM2/STCM2 and total SCM2/STCM2 suggest that they all play a significant role in the completeness of acanthodians and consequently our understanding of their fossil record (Tables 1, 2). Zones BA5 and BA6 do not significantly contribute to total SCM2 or STCM2, and completeness of specimens from these environments

is very low. This is congruent with a general lack of acanthodians from deeper water settings shown in our dataset. Acanthodian occurrence in the deeper water BA5–6 settings is restricted to the upper Silurian up until the Upper Devonian and is characterized by low specimen numbers and completeness values. Whether this absence from deeper water environments represents a true ecological signal, a preservational bias or a sampling bias due to limited rock outcrop availability remains unresolved for now.

Marine acanthodian completeness negatively correlates with average sea level, with higher completeness percentages at intervals when sea level is lower (Fig. 8; Table 3). This negative slope is recovered when using the entire dataset but *p*-values are not significant for any of the correlations. On removal of the four fragmentary specimens of the upper lower and middle Permian, all of the relationships between total SCM2/STCM2 as well as marine SCM2/STCM2 and sea level are quantified as significant with the negative correlation remaining as observed before. We argue that these late occurrences thus represent outliers in the dataset and together with the absence of other occurrences in the majority of the Permian heavily skew the correlations; they were thus removed for a subsequent analysis on the overall influence of sea level on acanthodian completeness. Furthermore, two of the four fragmentary specimens could not be taxonomically assigned beyond *Acanthodii* (Mutter & Richter 2007) but had to be included as separate taxa as we cannot ascertain if they represent distinct taxa and may be of great value to the acanthodian fossil record similar to OTUs in some nonavian theropod analyses (Cashmore & Butler 2019). This inclusion, however, may have also introduced a bias with regards to the sea level comparisons.

A negative relationship with sea level has also been reported for ichthyosaurs (Cleary *et al.* 2015), plesiosaurs (Tutin & Butler 2017) and even sauropodomorphs (Mannion & Upchurch 2010; Cashmore *et al.* 2020) but was absent in mosasaurs (Driscoll *et al.* 2018). Ostracoderms, osteostracans and non-psammosteid heterostracans have also been found to show an inverse proportional relationship between recovery potential of fossils and sea level (Sansom *et al.* 2015). This might be unexpected as deeper water environments are thought to favour better conditions for preservation than shallow waters due to less high-energy deposition, different physical constraints and less potential for scavenging and weathering (Allison *et al.* 1991; Driscoll *et al.* 2018). Additionally, sea level rise can lead to bottom waters and basins in deep shelf areas being placed below physical barriers leading to anoxic conditions (Leggett 1980; Sarmiento *et al.* 1988) that usually favour completeness of skeletons. However, this is not the case for acanthodians as completeness is significantly inversely proportional to sea level. The causes for this inverse

relationship are difficult to ascertain and previous hypotheses on this relationship in ichthyosaurs are limited to likely habitat preferences and death locations (Cleary *et al.* 2015). As for acanthodians, a combination of habitat availability (potential ecological biases) and lack of available rock volume (sampling biases) might explain at least some of the observed relationships. Information on acanthodian ecology and habitat preference is scarce and limited to the general environment of the deposits they were recovered from such as freshwater, marine, deltas, tidal flats, estuaries and lagoons (Denison 1979; Blais 2017). However, as our results indicate, a significant proportion of more complete acanthodian specimens are obtained from benthic assemblage zones in shallow waters which suggests, tentatively, a habit preference. In times of high sea level, the availability of these shallow water environments could be minimized as deeper water facies shift onto the inner shelf during transgression (Smith *et al.* 2002; Armstrong & Harper 2014). Additionally, there is a bias against available outcrop for marine deep-water sediments compared to the continental shelf (Gregor 1970; Smith *et al.* 2002), which may result in fewer acanthodian skeletons being sampled from deep water environments compared to shallow waters. This in turn may influence the observed negative correlation patterns between acanthodian completeness and average sea level. We could not find a significant relationship between freshwater acanthodian completeness and average sea level in any of the time series analyses, indicating that acanthodian skeletal preservation in freshwater environments is decoupled from sea level fluctuations.

Impact on phylogenetic assessments

Subsequent to Brazeau (2009) and Davis *et al.* (2012), who initially found large acanthodian subgroups branching from the chondrichthyan stem, most phylogenetic analyses of early gnathostomes over the past 10 years have placed all acanthodians on the chondrichthyan stem, therefore seemingly resolving the debate surrounding their overall taxonomic position (Zhu *et al.* 2013; King *et al.* 2016; Coates *et al.* 2018; Dearden *et al.* 2019; Frey *et al.* 2020; King & Rücklin 2020). However, relationships within the acanthodians are far from settled. Diplacanthiformes, Ischnacanthiformes and Acanthodiformes have been repeatedly recovered as well-resolved monophyletic orders, but it is likely that this reflects output from related (serially modified) morphological datasets; meanwhile, resolution of the climatiids is persistently poor at best (see e.g. Burrow *et al.* 2016; Coates *et al.* 2018; Dearden *et al.* 2019). Such instability is even more evident in the multitude of species that were not referable to a taxonomic rank beyond genus or family and were grouped into the *Incertae sedis* subgroup in our analysis,

comprising a disturbingly large proportion (one-third of the species) in the dataset. The craniocentric character sets employed for phylogenetic analyses contribute significantly to this lack of phylogenetic resolution (Davis *et al.* 2012, Zhu *et al.* 2013; Dupret *et al.* 2014; Brazeau & de Winter 2015; Giles *et al.* 2015; Long *et al.* 2015; King *et al.* 2016; Qiao *et al.* 2016; Zhu *et al.* 2016; Coates *et al.* 2018; Dearden *et al.* 2019). At least 65% of characters used in the data matrices are restricted to cranial features (including the jaws) whereas the postcranial skeleton comprises only 25% of characters, with the rest of the character list comprising histological properties that could be assigned to either cranial or postcranial skeleton. This is clearly problematic given our results on the relative percentages of the different skeletal regions in acanthodians, but difficult to avoid because of the data-rich skeletal and dental systems in vertebrate heads. In our entire dataset, the neurocranium represents less than 4% of recovered skeletal regions (Fig. 3). The palatoquadrate takes up 5% and the Meckel's cartilage 10%. In marked contrast, the 'character-poor' postcranial skeleton is recovered in over 80% of preserved skeletal regions in acanthodians. Our results emphasize how the currently used craniocentric character lists for phylogenetic analyses of acanthodians, chondrichthyans and early gnathostomes in general might be neglecting crucial information to better resolve the interrelationships of these taxa. However, postcranial data are limited and elusive, as exemplified by the still entirely unknown acanthodian pelvic skeleton.

Missing data are bound to diminish the quality of evolutionary hypotheses, ultimately resulting in loss of phylogenetic signal. Tests on a variety of datasets have shown that deletions of character information tend to result in stemward slippage (Sansom & Wills 2013). Thus, incomplete taxa are more prone to erroneously primitive placement in evolutionary trees. We do not propose that the set of least complete acanthodians harbours misidentified crown chondrichthyans. Nevertheless, the present quantified assessment provides both a basis and a prompt for further investigation of potential errors besetting current macroevolutionary hypotheses of early chondrichthyan evolution.

CONCLUSIONS

1. The acanthodian fossil record is mainly derived from isolated remains, including isolated scales and fin spines. Complete skeletons are rare.
2. Acanthodian skeletal and soft tissue completeness fluctuates throughout the Palaeozoic, with notable peaks in the Lochkovian, Givetian, Bashkirian–Moscovian and Asselian. The Silurian record captures the lowest mean completeness scores.

3. Soft tissue completeness of acanthodians is higher than skeletal completeness but both metrics reveal similar completeness patterns through time. This indicates that either metric can be used to accurately quantify the fluctuating quality of the acanthodian fossil record.
4. Acanthodian skeletal completeness correlates, albeit weakly, with time bin length: higher levels of completeness are associated with wider time bins. Soft tissue completeness correlates significantly with raw richness through time.
5. Among all vertebrate groups investigated thus far, acanthodians have one of the poorest skeletal completeness records. With bats (that have a significantly poorer record) they share a similarly shaped bottom-heavy distribution.
6. Acanthodiformes exhibit significantly higher skeletal and soft tissue completeness compared to other major acanthodian subgroups.
7. There is no significant difference between acanthodian record metrics from the northern hemisphere compared to the southern hemisphere. However, taxon distribution is very uneven with higher numbers in the northern hemisphere which probably results from sampling and/or geological biases.
8. Acanthodian skeletal and soft tissue completeness from freshwater sediments is initially higher in the Silurian and the Lower to Middle Devonian. Between the Givetian and Frasnian, a transition to more complete fossils from marine sediments occurs which lasts throughout most of the Carboniferous before reverting back to higher freshwater completeness in the Gzhelian and Asselian shortly before their extinction.
9. Acanthodian skeletons deposited in freshwater environments are significantly more complete than those in marine environments. This probably results from preservation under anoxic conditions (e.g. stratified lakes) and low turbulence. Soft tissue completeness, however, does not recover this trend.
10. Average sea level correlates significantly with skeletal and soft tissue completeness derived from marine but not freshwater deposits. The relationship is negative, with higher completeness recovered during times of low sea level. This pattern is consistent with previous reports on ichthyosaurs, plesiosaurs and sauropodomorphs and may be subject to both ecological and sampling biases.

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Author contributions. LS, IJS and RJB conceived the study. LS collected the data, performed the analyses and wrote the first draft. IJS provided the palaeoenvironmental data. IJS, RJB and MIC reviewed drafts of the paper. All authors contributed to writing the paper.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j0zpc86ff>

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12616>):

Appendix S1. Includes details of scoring for completeness metrics, Figures S0–S6 and Tables S1–S25.

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