Taphonomic Controls on a Multi-Element Skeletal Fossil Record

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Abstract

Animals with multi-element skeletons, including the vertebrates, echinoderms, and arthropods, are some of the most biodiverse and ecologically important animal groups. Understanding the relative impact of the myriad geological and biological factors which impact on the quality of multi-element skeletal fossils is thus crucial for disentangling perceived changes in biodiversity through time and shedding light on gaps in the fossil record. We have characterised the specimen-level taphonomic history of virtually the entire Palaeozoic fossil record of echinoids, the class of echinoderms which includes the living sea urchins. We find that the majority of this fossil record consists of disarticulated skeletal elements and as preservational quality increases, so does the proportion of specimens which can be identified with higher taxonomic precision. We then assessed the relative impacts of multiple geological and biological factors on our specimen quality, identifying that fine-grained host matrix, as well as siliciclastic lithology are the biggest factors in determining quality of fossil echinoid preservation, while aspects intrinsic to specific taxonomic groups also play a role. Differential sampling of the fossil record seems to play little role in influencing the distribution of taphonomic grades, and fluctuations in the North American record of Siliciclastic rocks are positively correlated with fluctuations in taphonomic grades. Our results highlight that the factors controlling the animal macrofossil record are varied, and that the interplay between these variables, taphonomic grade, and taxonomic precision impacts on our ability to use the fossil record to understand macroevolution.

Key words: Taphonomy, Rock Record, Echinoidea, Echinodermata, Palaeozoic

Not all fossils are preserved equally. This variable preservation impacts our ability to accurately comprehend the ancient past: for example, a single disarticulated tooth and a complete, articulated skeleton provide different amounts of data about the ecology, diversity, and evolutionary history of *Tyrannosaurus rex.* Animals with multi-element skeletons such as vertebrates, echinoderms, and arthropods, are abundant in the fossil record and are a treasure trove of information about how macroevolutionary processes in deep time underlie the origins of modern biodiversity (Legg *et al.* 2013; Mongiardino Koch and Thompson 2021; Kuo *et al.* 2023; Hopkins and Smith 2015). Multi-element skeletons consist of hundreds to thousands of variably-sized parts, which disarticulated rapidly upon death, except in exceptional circumstances (Donovan 1991; Nebelsick 1996). Understanding the controls on differential preservation of multi-element skeletons is thus crucial for our understanding of deep-time biodiversity change.

Differential quality in fossil preservation has important influences on our perception of ancient biodiversity patterns, as well as our ability to accurately reconstruct evolutionary histories using these fossils (Smith, 2007; Mannion & Upchurch, 2010; Dean *et al.* 2016). The varied environmental, biological, and geological processes which control the quality of fossil preservation are thus critical for an accurate perception of ancient biodiversity (Nebelsick 1996; Hendy 2011; Allison and Bottjer 2011; Smith *et al.* 2001; Butts and Briggs 2011; Nanglu and Cullen 2023; Dean *et al.* 2019). The majority of taphonomic studies which seek to assess the role of these myriad geological and biological controls on fossil preservation focus in exceptional detail on particular localities or basins, interrogating the respective roles of local processes such as depositional, geochemical and diagenetic conditions (Anderson *et al.* 2021; Briggs *et al.* 1996; von Bitter *et al.* 2007). However, in addition to these local signals, broader “megabiases” are also known to influence the fossil record; these include factors such as the age of fossil-bearing deposits (Signor *et al.* 1982; Dean *et al.* 2020), anatomical differences within and between taxonomic groups that influence preservation (Butts and Briggs 2011; Cherns and Wright 2000; Wright *et al.* 2003; Dean*, et al.* 2019; Kowalewski and Flessa 1996), preferential preservation within particular lithologies (Hendy 2011; Cleary *et al.* 2015), spatial variation in the quality of fossil preservation (Dean *et al.* 2019) or spatial sampling heterogeneity more generally (Antell *et al.* 2024; Benson *et al.* 2016; Close *et al.* 2020; Benson *et al.* 2021; Jones *et al.* 2021). While local environment and large-scale factors undoubtedly both influence fossil preservation, their impact on both the preservation and evolutionary history of specific taxonomic groups is more difficult to ascertain, due to the difficulty of collecting relevant specimen-level information across the entire fossil record of a group of organisms. Subsequently, the relative importance of these different factors on influencing fossil preservation, and subsequently our understanding of observed fluctuations in palaeodiversity, remains poorly constrained.

To characterise global and long-term trends in fossil preservation, and better understand the biological and geological factors which influence fossil preservation throughout deep-time, we herein assess the taphonomic quality of the entire known Palaeozoic fossil record of an invertebrate fossil group with multi-element skeletons. Echinoids are a class of echinoderms which includes the living sea urchins, sand dollars, and heart urchins, and have a fossil record dating back to the Ordovician period (Thompson *et al.* 2022). In contrast to the post-Palaeozoic echinoids, which are renowned for their exceptionally well-sampled fossil record (Foote and Sepkoski 1999), most Palaeozoic echinoid taxa lacked the microstructural interlocking of skeletal plates found in post-Palaeozoic echinoids (Smith 1980; Grun and Nebelsick 2018). This made them prone to disarticulation following death and thus the fossil record of Palaeozoic echinoids exhibits a wide range in preservational quality, from single disarticulated plates (Thompson and Denayer 2017), to articulated individuals preserving most or all of the original skeleton (Schneider *et al.* 2005). Furthermore, while post-Palaeozoic echinoids were abundant members of Mesozoic and Cenozoic ecosystems, their Palaeozoic precursors were comparatively rarer (Schneider 2008), meaning that a near-exhaustive sampling of their occurrence in museum collections is feasible. This variation in preservational state and tractability of building a large near-exhaustive database makes Palaeozoic echinoids an excellent model system to identify the differential importance of factors controlling preservational quality in the fossil record.

Building on previous work (Thompson & Bottjer, 2019, Thompson *et al.* 2022) we have produced the most complete specimen-level taphonomic dataset of a temporally and geographically widespread Palaeozoic fossil invertebrate group to date, containing virtually every record of Palaeozoic echinoids (3447 specimens total) collected from the general literature and thirty-three museums around the globe. Each specimen is designated with a taphonomic grade, and is associated with lithological, environmental and geographic information. We then use a variety of statistical and modelling procedures to establish the relative influence of various geological, geographical and biological controls on preservational state through space and time. Lastly, we use this information to refine our understanding of the critical early evolutionary history of echinoids, and the relative impacts of environmental variables on fossil preservation more broadly.

Material and Method

Fossil dataset

To quantify the preservation of the Palaeozoic echinoid fossil record, we devised a semi-quantitative index to describe the taphonomic grade (TG) of fossil specimens from museum collections and the literature. We visited thirty-three museum collections and, where possible, photographed each specimen and assigned it to one of five taphonomic grades (TG1-5) based upon its completeness (Fig. 1A). These taphonomic grades mirror series of disarticulation and disintegration identified from experiments with living echinoids (Kidwell and Baumiller 1990; Greenstein 1991), and modified for the distinct body plans of Palaeozoic echinoids which lack stereomic interlocking. The lowest taphonomic grade (TG1) represents single, disarticulated skeletal ossicles (including lots in collections of multiple ossicles which we treat conservatively to represent a single disarticulated specimen) while the second lowest grade (TG2) represents disarticulated but associated ossicles. These lowest two taphonomic grades usually consist of disarticulated coronal plates and spines, though more rarely include elements of the Aristotle's lantern. TG3 is the middle taphonomic grade, and represents fragments of articulated or semi-articulated test. TG4 represents articulated tests which have become denuded of spines and represents minimal degradation post-mortem (Kidwell and Baumiller 1990). Finally our highest taphonomic grade, TG5, consists of articulated tests with attached spines, representing highest quality preservation.

By basing our analyses on specific specimens from museums and the literature, we are able to link geological variables of the rock matrix, such as grain size and lithology directly with the fossils they entomb. As such, following Thompson and Bottjer (2019) the associated lithology and grain size were recorded for each specimen, alongside data on taxonomy (including most-specific taxonomic rank possible), stratigraphic provenance and locality of collection. These data were further bolstered with data collected from the general literature, as well as all available stratigraphic, taxonomic, lithological and taphonomic data available for each published specimen. All data were collected by one individual (J.R. Thompson), who also vetted all the taxonomic designation of all specimens; as such, there is consistency in approach across the dataset, reducing a potential source of bias (Wagner *et al.* 2007). Specimens without precise geographic co-ordinates were georeferenced by locating text-based locality descriptions on Google Maps (available from http://google.com/maps); we additionally included the likely precision of this estimate in the degrees-minutes-seconds format. Palaeo-coordinates for these locations were obtained using the ‘PALAEOMAP’ rotation model through the GPlates API, using the ‘palaeorotate’ function of the ‘palaeoverse’ package (Jones *et al.,* 2023). Data were additionally assigned to stage, series and period level time bins using the ‘majority’ method of the ‘bin_time’ function from the ‘palaeoverse’ package (Jones *et al.,* 2023). Our final dataset utilised for analysis contains 3447 unique specimens across 37 countries, and spans approximately the first 300 million years (Ordovician to Permian) of the evolutionary history of echinoids. It is available as supplementary information at https://github.com/ChristopherDavidDean/Echino_taph.

Multiple logistic regression

To assess the primary controls on the differential fossil preservation seen in our dataset, we used multiple logistic regression, coding each TG as a binary response variable and including lithology (carbonate vs. siliciclastic), grain size (fine-grained vs. coarse grained), age (midpoint of the stage to which the specimen belonged), latitude of the locality of collection, and palaeolatitude as predictor variables. Due to low numbers of occurrences for various families across taphonomic grades, we did not include taxonomic information as a response variable. We are primarily interested in reporting effect sizes, which are gauged by the magnitude of regression coefficients. When interpreting results, note that the chosen taphonomic grade is compared against all other grades (e.g. specimens with a taphonomic grade of 5 [1], vs. all other taphonomic grades [0]) so that positive regression coefficients indicate greater odds of sampling the specific taphonomic grade of choice, and log-odds below 0 indicate reduced odds of sampling. For binary covariates, we report the log odds of one level relative to the other (for instance, fine grained vs. coarse grained), so positive regression coefficients represent greater odds of the named factor influencing the presence of a particular taphonomic grade. An interaction term consisting of a combination of lithology and grain size was additionally added to test for interactions between the covariates. We used the ‘dredge’ function of the package ‘MuMin’ (Bartoń 2023) to obtain information about the full model set and the small sample size corrected Akaike Information Criterion (AICc) for final model selection, with lower scores indicating a better model fit (Burnham and Anderson 2001). Here we present models with the lowest AICc scores, and only report factors with statistically significant results ($p < 0.05$); full results can be found within Supplementary Information 2 at https://github.com/ChristopherDavidDean/Echino_taph.

Statistical Tests

We used Pearson’s chi-squared tests to establish whether there were statistically significant differences between taphonomic grades with respect to lithology, grain size and time intervals. Mosaic plots of these results were produced using the ‘mosaic’ function of the ‘vcd’ package (Meyer *et al.* 2006). To test whether preservational state showed a correlation with specific variables through time, we used Spearman's rank correlation tests corrected for large sample sizes with the Benjamini Hochberg procedure (Benjamini and Hochberg 1995) to characterise the strength of correlations between the abundance of taphonomic grades, the available rock record, sampling proxies and genus-level diversity at the stage level. The abundance of carbonate and siliciclastic rocks in North America was obtained from Macrostrat (Peters *et al.* 2018), a database of geological data which includes compilations of the spatial and temporal distribution of North American sedimentary rocks, and was compared to the abundance of North American occurrences (downgraded from the specimen level dataset) of each taphonomic grade from our dataset. This provided a picture of the role of the rock record on the abundance of our preservational states. We used the number of Palaeozoic echinoid, Echinoderm, and invertebrate collections from the Paleobiology Database (PBDB; https://paleobiodb.org/) as potential general sampling proxies; we used the latter two as proxies approaching a 'global' sampling signal to reduce the possibility of redundancy (Benton *et al.* 2011). These collections were obtained from PBDB downloads. Species and period level correlations can be found in Supplementary Information 2 at https://github.com/ChristopherDavidDean/Echino_taph.

All statistical tests were implemented in R, and lithological data from Macrostrat was obtained in R via the Macrostrat API. Counts for global invertebrate collections were obtained by downloading all Palaeozoic invertebrate records from the PBDB (on 08/11/2022). Genus level diversity for echinoids was established using the 'binstat' function of the divDyn package (Kocsis *et al.* 2019). Associated R scripts can be found in Supplementary Information at https://github.com/ChristopherDavidDean/Echino_taph.

RESULTS

Differences in quality of fossil preservation

Our analyses highlight striking differences in the quality of fossil preservation across the Palaeozoic history of echinoids. The majority of known echinoid specimens are disarticulated (Fig. 1C), with the taphonomic grades in our dataset representing disarticulated remains equating to 61% of the total dataset (TG1: 38%; TG2: 23%). These are twice as abundant than TG4 and TG5, which represent those specimens which are best-preserved (TG4: 14%; TG5: 15%).

Across all taphonomic grades Palaeozoic echinoid fossils are significantly more abundant in fine-grained than coarse-grained rocks (Figure 2B,D; X-squared = 159.08, df = 4, p-value < 2.2e-16). Mosaic plots reveals that in particular taphonomic grades TG4 and TG5 are noticeably less common than expected in coarse-grained rocks, whereas disarticulated remains (TG1 and TG2) occur more likely than expected in coarse-grained rocks (Fig. 2D). Echinoid fossils are also significantly more abundant in carbonate rocks than siliciclastics (Figure 2A,C; X-squared = 182.6, df = 4, p-value < 2.2e-16). Disarticulated plates (TG1 and TG2) occur less frequently than expected in siliciclastic rocks, whereas individuals with the highest taphonomic grade (TG5) occur more frequently than expected in siliciclastic rocks and less than expected in carbonates (Fig. 2C).

Taphonomic grades are not distributed evenly with respect to the lowest taxonomic rank to which a specimen can be assigned (Fig. 3A; X-squared = 1540.9, df = 12, p-value < 2.2e-16). At TG1, a higher proportion of specimens are only assignable at the class level (Echinoidea) than at any other taphonomic grades. At this grade, specimens assignable to the species level occur less frequently than expected, while specimens which can be assigned to higher taxonomic levels occur more frequently than expected (Fig. 3C). As preservational score increases, so too does the proportion of specimens assignable to a lower taxonomic rank, with specimens only assignable to higher taxonomic ranks occurring less-frequently than expected. Likewise specimens which can be attributed to the species-level occur more frequently than expected at TG3-TG5 (Fig. 3C).

The proportion of different preservational grades also varies temporally (Fig. 3B,D; X-squared = 875.85, df = 16, p-value < 2.2e-16). The Ordovician and Mississippian exhibit surprisingly well preserved records, with higher than anticipated counts of TG4 grade specimens and proportionally less TG1 grades (Fig. 3D). In contrast, the Permian record is shown to be poorly preserved, with a higher proportion of TG1 specimens than anticipated and significantly reduced TG5 specimens. Both the Silurian and Pennsylvanian have a significantly higher proportion of specimens at TG5.

Influences on the quality of fossil preservation

Comparisons of multiple logistic regression models using AICc consistently identify grain size and palaeo-latitude as predictor variables in the models which best explain preservational state for all five taphonomic grades (Table 1). Lithology is also a covariate in the best model in all grades except for TG3 and latitude, and age (Ma) also appear as covariates in the best model for different preservational states. In taphonomic grades corresponding to disarticulated and semi-articulated fossil remains (TG1 to TG3), log odds of fine grain size are negative (Fig. 4). Inversely, log odds of fine grain size are positive for articulated skeletal remains (TG4 and TG5). Of particular note, fine grain size has the highest positive log odds for any covariate in the best model for TG5, suggesting that the single biggest predictor for the high-quality preservation is an association with fine-grained sediments.

Siliciclastic lithology also shows positive log odds for well-preserved individuals (TG4 and TG5), and is higher than grain size for TG4. For disarticulated but associated plates (TG2), log odds for siliciclastic lithology are negative, implying higher odds of carbonate lithology accompanying this preservational state. Whilst age, latitude and palaeo-latitude all appear in a number of the top models, their log-odds are often near 0 or they are statistically insignificant, implying little influence on quality of preservation.

Comparing preservational state, the rock record and palaeodiversity

Because the results of our logistic regression and statistical tests suggest that preservational state varies systematically with respect to geological variables, we used Spearman's rank correlation to compare variation in the counts of Palaeozoic North American siliciclastic and carbonate units with the stage-level abundance of each taphonomic grade of North American Palaeozoic echinoids from our dataset (Table 2). Siliciclastic units report strong and statistically significant positive correlations with the abundance of all taphonomic grades, whereas carbonate units show overall weaker positive correlations, with only TG4 reporting a statistically significant result (Table 2). Disarticulated single plates (TG1) show the lowest strength of correlation across both siliciclastic and carbonate units.

To further explore the relationship between taphonomic grade and patterns of taxonomic diversity, we compared the abundance of different preservational states through time to standing diversity of Palaeozoic at the genus level (Table 3). At the stage level, no taphonomic grades show statistically significant positive correlations with genus-level diversity; however, TG5 shows a very strong and statistically significant correlation with diversity at the Period level.

We additionally tested the relationship between taphonomic grade and sampling proxies (Table 4). Preservation scores TG1-4 all show strong, positive and statistically significant correlations with counts of echinoid collections through time (Table 4); TG1&2 in particular show very strong correlations. Counts of TG1, 3 and 4 show positive and statistically significant correlations with total Echinodermata collections throughout the Palaeozoic, with TG1 showing the strongest overall. Conversely, correlations between preservation scores and counts of global collections are weak, and none are reported as statistically significant.

DISCUSSION

The taphonomic nature of the Palaeozoic echinoid fossil record

Our analyses highlight the factors which control the preservation of echinoids, an invertebrate class with multi-element, calcium carbonate skeletons, throughout the Palaeozoic. Simple quantification of different taphonomic grades indicates that the quality of preservation in the echinoid record is non-random, with the majority of recorded specimens belonging to taphonomic grades representing disarticulated plates (Fig. 3A). The prevalence of disarticulated material is in line with species-level analyses of echinoid taphonomic grades (Smith 2007; Greenstein 1992), which typically highlight the abundance of disarticulated spines. These results also align with studies of the vertebrate fossil record; where isolated or fragmentary remains are frequently more abundant than more complete fossils (Gardner *et al.* 2016; Schnetz *et al.* 2022; Brown *et al.* 2019). This is seemingly also the case with echinoids and suggests that a relatively low level of phylogenetically or taxonomically useful information is likely to be present in the majority of the sampled fossil record. While the disarticulated plates of Palaeozoic echinoids can often be recognised at the family level (Thompson and Denayer 2017), when we plot the proportion of specimens identifiable to different taxonomic ranks in each taphonomic grade using our taxonomically standardised database (Fig. 3A,C), it is clear that as taphonomic grade increases, so too does the proportion of total specimens identifiable to lower-level taxonomic ranks, such as species or genus.

A number of studies have highlighted the importance of so called “hidden diversity” that can be recognised from disarticulated skeletal elements and which have been proposed to will greatly increase our understanding of palaeobiodivesity of fossil groups (Twitchett and Oji 2005; Pietsch *et al.* 2019; Oji and Twitchett 2015; Martins *et al.* 2023). Because of the limited taxonomic utility of disarticulated specimens, for echinoids at least, it is unlikely that disarticulated specimens will significantly alter our understanding of deep time biodiversity change, and suggests that a minority of the record, those specimens from higher taphonomic grades, will be useful for analyses requiring higher taxonomic specificity. Notably, this contrasts with recent work on vertebrates, which has highlighted the utility of disarticulated skeletal elements for taxonomic identification and phylogenetic analysis (Cashmore *et al.* 2021; Woolley *et al.* 2022). The echinoid body plan is comprised of hundreds of skeletal elements, many of which are added indeterminately throughout growth (Smith 2005; Thompson *et al.* 2021), and almost all of which exist in multiples of at least five. Because of this, identifying homologous skeletal ossicles across different species from disarticulated remains is difficult. This is further complicated because of intraspecific and ontogenetic variation (Raup 1956; David and Laurin 1996). This situation contrasts to bilaterally symmetrical vertebrates where (with the exception of axial elements) in many species a single bone can be readily identified and provide precise taxonomic information due to bone-specific autapomorphies (Cashmore*, et al.* 2021). The taxonomic utility of disarticulated fossils, and thus the impact of taphonomic variables on fossil preservation, are likely to be felt differently across different taxonomic groups.

Our results furthermore show that different higher Palaeozoic echinoid taxa vary systematically in their preservation, and that taxon-specific differences in preservational quality may be related to factors intrinsic to the animals, such as differential aspects of skeletal anatomy. Different groups of Post-Palaeozoic echinoids, most classically the regular and irregular echinoids, are well known for their differential preservation in the fossil record (Greenstein 1993; Kier 1977), associated with differences in microstructural interlocking of test plates (Smith 1984; Grun and Nebelsick 2018). The relative over- and under-representation of particular families in different taphonomic grades suggests similar differences may exist for some Palaeozoic echinoid groups. One example is the Palaechinidae, which have characteristic tessellate test plating and are over-represented as articulated tests with denuded spines (TG4), or as fragments of tests (TG3). This is in stark contrast to other Palaeozoic families, such as the archaeocidarids, that have imbricate plating and are frequently preserved at the lowest taphonomic grades (Fig. 1C). This suggests that the tessellate plating in the Palaechinids may be less-prone to disarticulation, instead favouring fragmentation as is the case in many extant euechinoids (Kidwell and

Baumiller 1990). It further suggests the presence of micro-structural interlocking, as present in many crown group echinoids (Smith, 1980, Grun and Nebelsick, 2018), may have been present in Palaechinids.

Factors influencing multi-element skeletal preservation

Because fossils at higher taphonomic grades impact more on our perceptions of palaeodiversity, we sought to identify the factors that influence the taphonomic grades of individual specimens, as well as their relative impact on preservational state. Our interrogation of the various factors affecting fossil preservation reveals that, while taxonomy position, grain size, and lithology all effect fossil preservation, of the factors included in our multiple logistic regression, the most important is grain size. Fossils at lower taphonomic grades are less likely to be associated with fine-grained sediments, while fossils at higher taphonomic grades are positively associated with fine-grained sediments (Fig. 4). After death, echinoid skeletons disarticulate rapidly (Kidwell and Baumiller 1990), and due to their porous test microstructure have low residence times on the seafloor relative to other more robust, taxa (Kowalewski *et al.* 2018). Rapid burial is thus generally evoked as the single most relevant factor in generating high-quality preservation of fossil echinoderms, as lower residence time on the seafloor is more likely to prevent disarticulation from disruption by scavengers, bioturbators, or erosion (Brett *et al.* 1997). Many of specimens in our dataset of the highest taphonomic grades are likely the result of obrution deposits where a layer of sediment has rapidly covered the animal during or soon after life (Brett and Seilacher 1991). These deposits are often associated with turbidites and tempestites (Ausich and Sevastopulo 1994), and often found in offshore slope or deltaic environments (Brett*, et al.* 1997; Brett and Seilacher 1991). While we did not attempt to characterise palaeoenvironment across our dataset due to the nature of historical museum collections data, many of the fine-grained occurrences in our dataset were likely deposited in deep-water settings. In contrast to fine-grained preservation associated with event beds, coarse-grained environments have been previously associated with, typically more near-shore, and higher-energy preservation of disarticulated echinoderms (Ausich and Sevastopulo 1994; Brett*, et al.* 1997) Recent experimental work has shown that during rapid burial, coarse-grained sediments are more likely to be associated with disarticulated or fragmentary echinoderm remains while finer-grained, more thixotropic sediments are more likely to impede movement during escape, and thus result in higher-quality preservation (Fraga and Vega 2024). While we have no examples of soft-tissue preservation in our dataset, rapid burial with fine-grained sediments has also been shown to be conducive to the high-quality soft-tissue preservation which characterises many Lagerstätte (Gaines *et al.* 2012; Allison 1988). Our global and temporally expansive analyses thus align with the numerous studies focusing on local sedimentological and geochemical conditions of numerous Lagerstätte and obrution deposits which have demonstrated the association between grain size taphonomic grade of fossil preservation.

At higher taphonomic grades, lithology also positively influences preservation, with well-preserved fossils associated with siliciclastic rocks. This mirrors a study of the ichthyosaur fossil record, which found the highest average completeness of specimens in fine grained siliciclastic (but not carbonate) sediments (Cleary*, et al.* 2015). Additionally, it has been noted that for similar depositional environments, siliciclastic settings tend to result in slightly better preserved fossil echinoderms than carbonate settings (Brett*, et al.* 1997) due to higher overall rates of sedimentation (Enos 1991; Schindelz 1980). The high rates of sedimentation in some siliciclastic environments, such as deltas, slopes, and channels, may explain this association in our dataset. Indeed many of our specimens at the highest taphonomic grades were recorded from well-known siliciclastic palaeoenvironments such as the deltaic Edwardsville Formation, the channel-shaped deposits of the Winchell Formation and the offshore downslope Ordovician Ladyburn Starfish beds (Lane 1973; Schneider*, et al.* 2005). In our dataset, however, the relationship between lithology and taphonomic grade breaks down at the lowest taphonomic grade (Fig. 4), suggesting that differences in lithology have little impact on dictating the distribution of disarticulated remains. This is likely because single disarticulated elements are more robust to biostratinomic processes such as transport and reworking (Brett*, et al.* 1997), and are thus more likely to be found across a range of environments. We suggest these are general patterns found across the marine skeletal fossil record, though further studies in other fossil groups will be necessary to very this.

We have also identified factors which have little bearing on the quality of fossil preservation. While these covariates are present in many of the best models identified for each preservational score, latitude, palaeolatitude, and fossil age all have little impact on fossil preservation based upon our analyses. Given that modern latitude has little to do with the original environmental conditions of a specific locality in the Palaeozoic, the lack of influence of latitude on specimen is not surprising. Furthermore, while variables linked to palaeolatitude, such as temperature, have been determined to influence specimen preservation in live-dead comparisons (Kidwell *et al.* 2005), and experiments (Kidwell and Baumiller 1990), given how global temperatures have fluctuated across different latitudes and times throughout the Palaeozoic (Goldberg *et al.* 2021; Korte *et al.* 2008), it is perhaps not surprising that specific latitudes are not associated with a given taphonomic grade or grades. In contrast, the age of fossil bearing-deposits has been identified as a megabias which influences the quality of the fossil record, and has been shown to influence taphonomic state of fossils in a non-random way (Hendy 2011). This impact of age on preservation is largely linked to specific intervals of time, such as the Neogene, with near-recent levels of fossil quality, and the Permian which is associated with high degrees of silicification (Butts and Briggs 2011; Hendy 2011). Age could play less of a role in our analysis because all of our fossils are all Palaeozoic, and the Permian in particular lacks many well-preserved Palaeooic echinoids (see discussion below). All in all, our analyses suggests that larger-scale determinants, such as latitude, palaeolatitude, and age have less of an impact on fossil preservation than more localised sedimentological and palaeoenvironmental factors, such as the above-discussed lithology and grain size.

Taphonomy, the rock record and perceived palaeodiversity

We found no overall correlation between the abundance of different taphonomic grades and taxonomic diversity at the stage and period levels (Table 3). This is in agreement with studies comparing patterns of skeletal completeness with raw taxonomic diversity, which have typically identified an absence of, or statistically weak, correlations between specimen or species quality and richness (Cashmore and Butler 2019; Cleary*, et al.* 2015; Schnetz*, et al.* 2022; Brown*, et al.* 2019), though see Dean *et al.* (2016) for a contrasting pattern observed in pterosaurs. The only exception to this in our dataset was a strong correlation between period-level genus richness and the abundance of fossils at the highest taphonomic grade, TG5. This implies that, at least at coarse temporal resolution, the abundance of well-preserved fossils could influence patterns of observed palaeodiversity. This is likely due to the aforementioned ability to more readily assign the best-preserved fossils to lower taxonomic levels (Fig. 3A,C). However, overall, it appears that quality of preservation does not significantly influence our understanding of Palaeozoic echinoid diversity.

Comparisons between the number of collections and abundance of different taphonomic grades through time can reveal whether preservational quality is predominantly controlled by sampling variation. Whilst TG1-TG4 reported strong and statistically significant correlations with the number of echinoid collections through time, this was strongest for the lowest taphonomic grades; conversely TG5 showed a near miss for statistical significance, and the lowest strength of correlation (Table 4). This pattern indicates that the abundance of poorly preserved specimens closely mirrors echinoid sampling intensity, and that additional sampling will produce an equivalent amount of incomplete fossil material. At higher taphonomic grades, the strength of this correlation reduces, indicating that high quality preservation is less-influenced by sampling effort. This is likely because higher taphonomic grades likely are likely the result of event-based taphonomic conditions preserving ecological snapshots (Ausich 2016), as opposed to background conditions where specimens are exposed to a greater degree of biostratinomic processes (Brett*, et al.* 1997; Brett and Baird 1986). A more pronounced variation of this pattern is observed with comparisons to total

Echinodermata collections (Table 4). Conversely, the lack of significant correlations between total invertebrate collections and any taphonomic grades indicates that preservation is not dependent on ‘global’ measure of sampling intensity during the Palaeozoic, but more focused sampling on localities, formations and facies likely to record echinoderm fossils.

Because lithology was shown to positively influence the preservation of higher taphonomic grades, we compared the abundance of North American occurrences of different taphonomic grades to the abundance and outcrop area of carbonate and siliciclastic lithological units in Macrostrat (Table 2). Our results appear somewhat counterintuitive. Despite echinoid fossils being more abundant in carbonate rocks (Figure 1d, 2a) and overall showing an affinity for carbonate substrates (Thompson and Bottjer, 2019), variations in the number of siliciclastic units through time report stronger and more significant positive correlations with the abundance of different taphonomic grades than do carbonates (Table 2). This correlation is weakest at the lowest taphonomic grade, in agreement with our results obtained from multiple logistic regression, which found that lithology plays little role in preservation at lower grades, but that siliciclastic lithology influences higher taphonomic grades (Fig. 4). At higher taphonomic grades, the stronger positive correlations between siliciclastic sediment area and North American echinoid taphonomic grades may, as noted above, reflect higher rates of sedimentation in siliciclastic environments (Schindelz 1980; Enos 1991). Furthermore analyses of tropical mollusc death assemblages have shown higher rates of skeletal degradation and reduced skeletal condition in carbonate environments than in siliciclastic environments as a result of pore water chemistry and disturbance from bioeroders or bioturbators (Kidwell*, et al.* 2005; Best *et al.* 2007). These may explain why the distribution of North American taphonomic grades more-closely mirrors siliciclastics. Though we did not analyse secular variations in the abundance of fine-grained sediments through time we hypothesize, based on our analyses, that variations in the proportion of fine to coarse-grained rocks, coupled with rates of sedimentation as evident in siliciclastic settings, may be an overall regulator of fossil quality through time, at least for taxa with multi-element skeletons.

Taphonomic impact on the evolutionary history of echinoids

The Palaeozoic is a crucial interval for echinoids, encompassing both their initial diversification in their Ordovician (Thompson*, et al.* 2022), as well as the origin of the echinoid crown group in the late Palaeozoic (Mongiardino Koch and Thompson 2021; Thompson *et al.* 2020). Furthermore, the Permian, which yields some of the earliest crown group echinoids, includes species which have been used to calibrate divergence time estimates for the origin of the crown group echinoids (Koch *et al.* 2022; Thompson *et al.* 2015). Recent phylogenomic analyses have placed the origins of multiple extant echinoid groups in the Permian (Mongiardino Koch et al. 2022), despite the absence of these lineages from the Palaeozoic fossil record (Kier 1965). Identifying the number of lineages that survived the end-Permian mass extinction and subsequently diversified in the Mesozoic is a question with profound impacts on understanding the origins of modern echinoid biodiversity and the role of the end-Permian extinction in dictating their evolutionary history (Thompson *et al.* 2018; Thuy *et al.* 2017; Hagdorn 2017). While disarticulated remains are relatively abundant in the Permian, the lack of specimens at the highest taphonomic grades highlights that that majority of the sampled echinoid fossil record during the Permian are not identifiable to lower taxonomic ranks. There is also relative paucity of fine-grained or siliciclastic echinoid occurrences in our dataset which our analyses suggest are most strongly associated with high-quality preservation. Taken together, this suggests that differences in fossil preservation may explain the numerous ghost-lineages that plague our understanding of the evolutionary history of echinoids in the Late Palaeozoic and Early Mesozoic. More generally, this exemplifies how variations in the preservation of different environments in the fossil record can influence not only our perception of ancient biodiversity (Smith*, et al.* 2001), but also the factors which are conducive to the high-quality fossil preservation which is necessary to understand the origins of living clades.

CONCLUSION

Multi-element skeletons are abundant across the tree of life and their preservation in the fossil record sheds insight into fundamental mechanisms of macroevolution and the origin of diverse modern clades (Koch*, et al.* 2022; Simoes *et al.* 2018; Legg*, et al.* 2013; Hopkins and Smith 2015). Our results provide clear evidence of the dominant controls impacting the preservational quality of the known Palaeozoic fossil record for an entire major taxonomic group with a multi-element skeleton. We find that the majority of the Paleozoic echinoid fossil record is disarticulated, and that the dominant controls on fossil preservation are grain size and lithology. Counterintuitively, the abundance of North American siliciclastic rocks is more closely linked to fluctuations in fossil preservation than are those of carbonates. The influence of fossil preservation on our understanding of ancient biodiversity is likely to be mediated through the ability to more precisely identify well-preserved fossils. The geological and biological factors we herein implicate in controlling their fossil record are likely to be yet another mechanism by which perceived deep time fluctuations in biodiversity influenced by non-random fossil preservation.

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DATA ARCHIVING STATEMENT

Data for this study, including the underlying database for all analyses, data downloaded from the Paleobiology Database, as well as R scripts, and supplementary files are available at Github at: https://github.com/ChristopherDavidDean/Echino_taph

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FIGURES

Figure 1

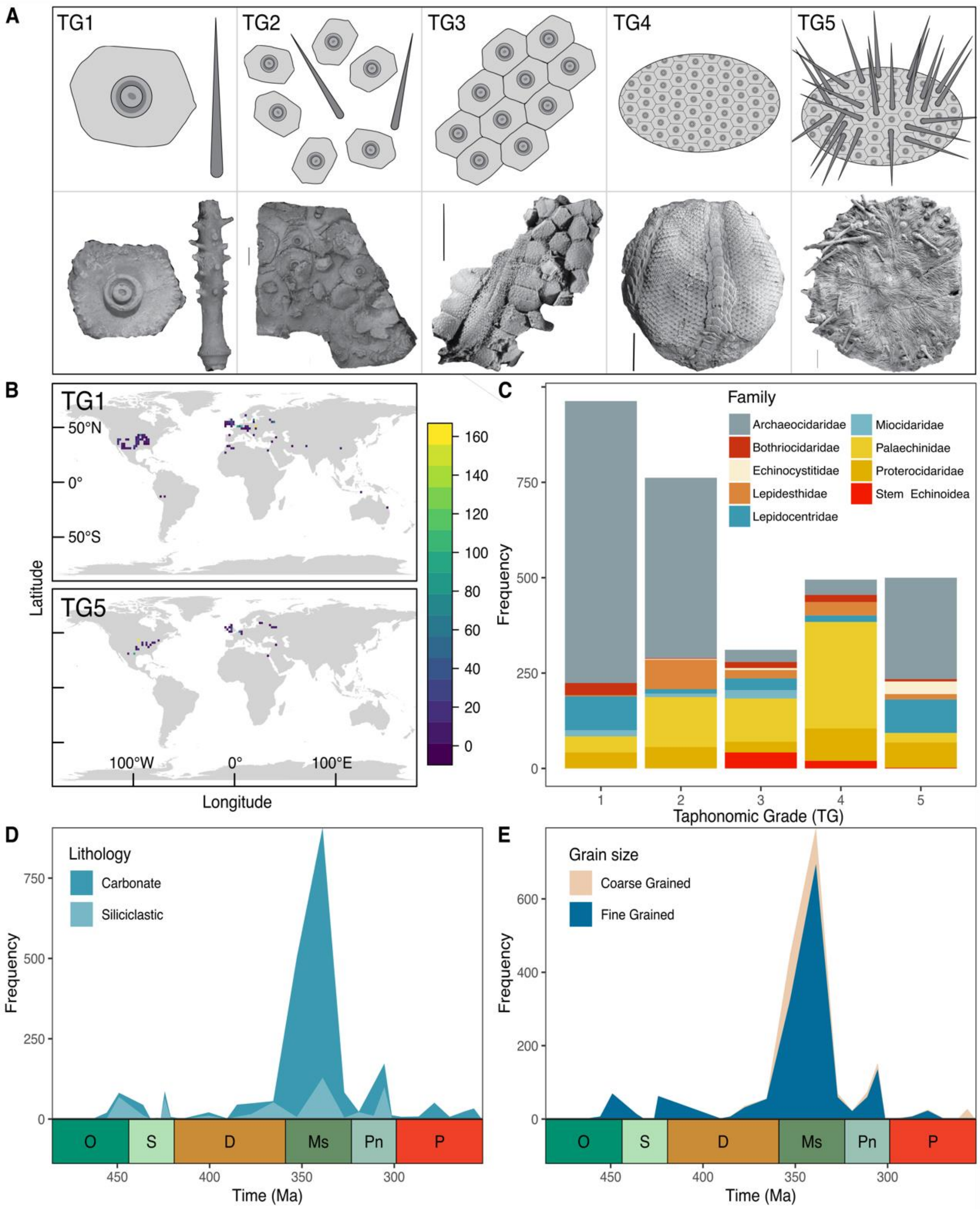

Figure 1. The distribution of different taphonomic grades spatially, taxonomically, and with respect to lithology and grain size. A: Illustrations and photographs of Palaeozoic echinoid fossils demonstrating examples of our different taphonomic grades. TG1 is specimen MCZ:IP:103620, a disarticulated spine and interambulacral plate of the archaeocidarid *Archaeocidaris* sp. TG2 is specimen LACMIP 2020, a pile of disarticulated interambulacral

plates and spines from *Archaeocidaris* sp. TG3 is specimen MCZ:IP:101936, a fragment of a test of the palaechinid *Maccoya intermedia* showing ambulacral and interambulacral plates. TG4 shows specimen YPM 26552, a denuded test of the lepidesthid echinoid *Lepidesthes colletti.* TG5 shows specimen NHMUK Pal E 76888, the holotype of *Archaeocidaris whatleyensis,* which is an articulated test preserved with covering spines. B: the differential global distribution of specimens of our lowest taphonomic grade (TG1, top) and our highest taphonomic grade (TG5, bottom). C: bar chart showing the differential frequency of taphonomic grades across our dataset broken down by family (or unit approximating family for stem echinoids). D: frequency of specimens associated with carbonate or siliciclastic sediments plotted through time. E: frequency of specimens associated with fine- or coarse-grained sedimentary rocks plotted through time.

Figure 2

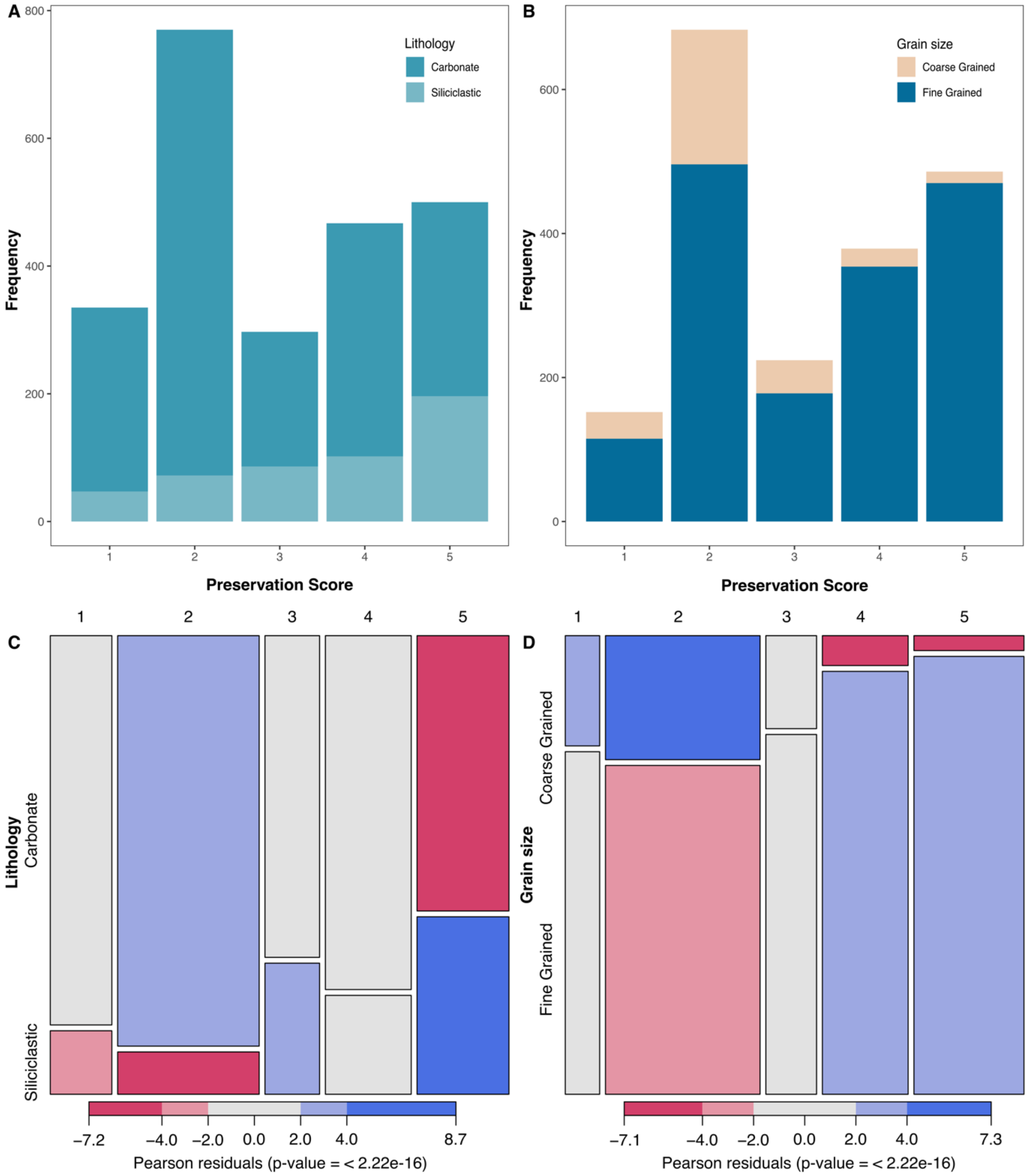

Figure 2. The distribution of different taphonomic grades according to lithology and grain-size. A: the frequency of different taphonomic grades according to carbonate or siliciclastic lithology. B: the frequency of different taphonomic grades according to grain size. C: mosaic plot showing the relative proportions of preservation scores within each lithological category, compared against expected levels, with colours relating to Pearson residuals from a log-linear model. D: mosaic plot showing the relative proportions of preservation scores within each grain size category, compared against expected levels, with colours relating to Pearson

residuals from a log-linear model. For mosaic plots, red indicates fewer observations than expected, whereas blue represents more observations than expected.

Figure 3

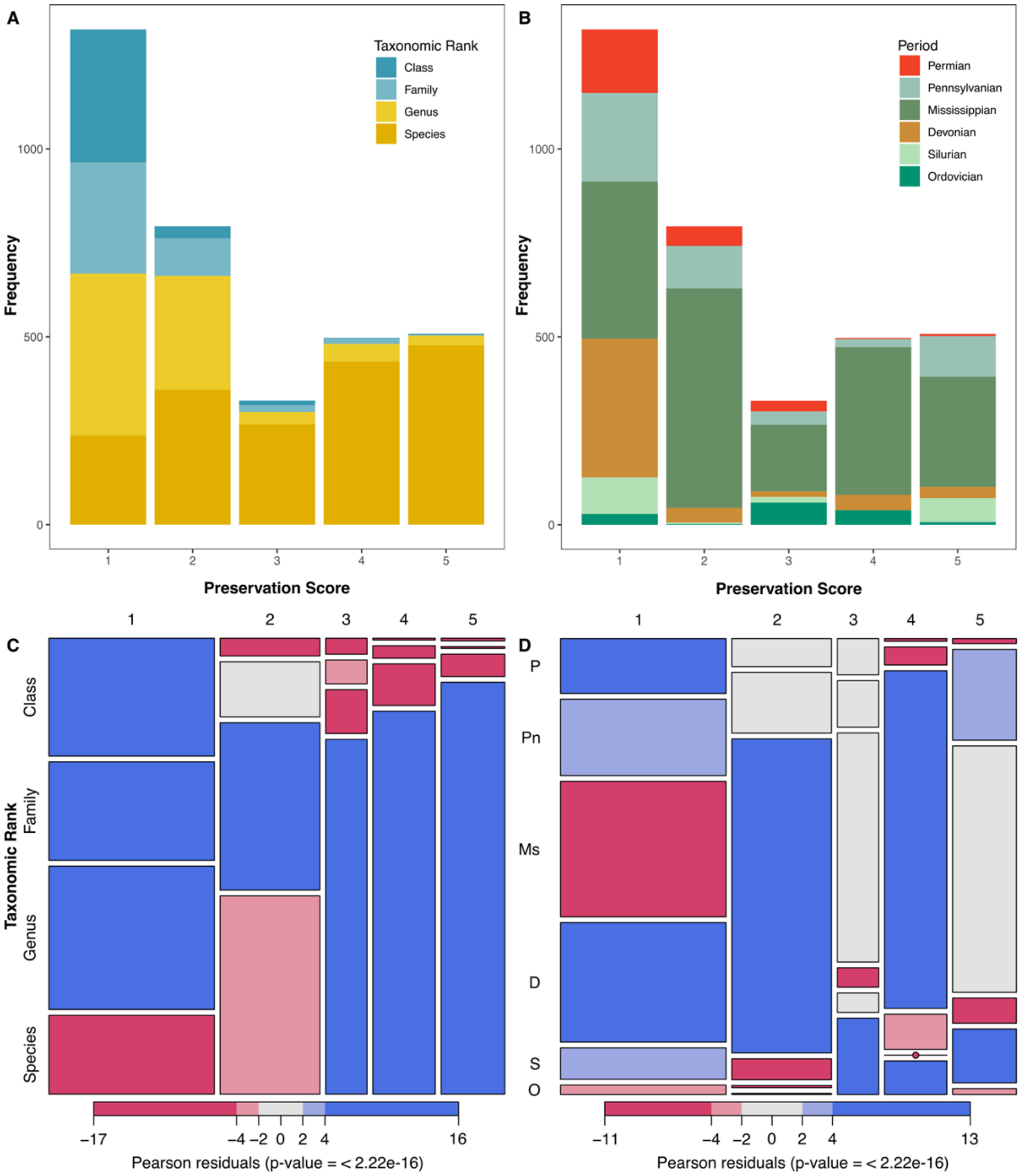

Figure 3. The distribution of specimens of different taphonomic grades according to the lowest assignable taxonomic rank and geological time. A: the distribution of specimens of different taphonomic grades according to the lowest taxonomic rank to which each specimen

could be assigned. B: the frequency of different taphonomic grades according to the Period of geological time from which they were sampled. C: mosaic plot showing the relative proportions of preservation scores within each taxonomic rank, compared against expected levels, with colours relating to Pearson residuals from a log-linear model. D: mosaic plot showing the relative proportions of preservation scores within geological Period, compared against expected levels, with colours relating to Pearson residuals from a log-linear model. For mosaic plots, red indicates fewer observations than expected, whereas blue represents more observations than expected.

Figure 4

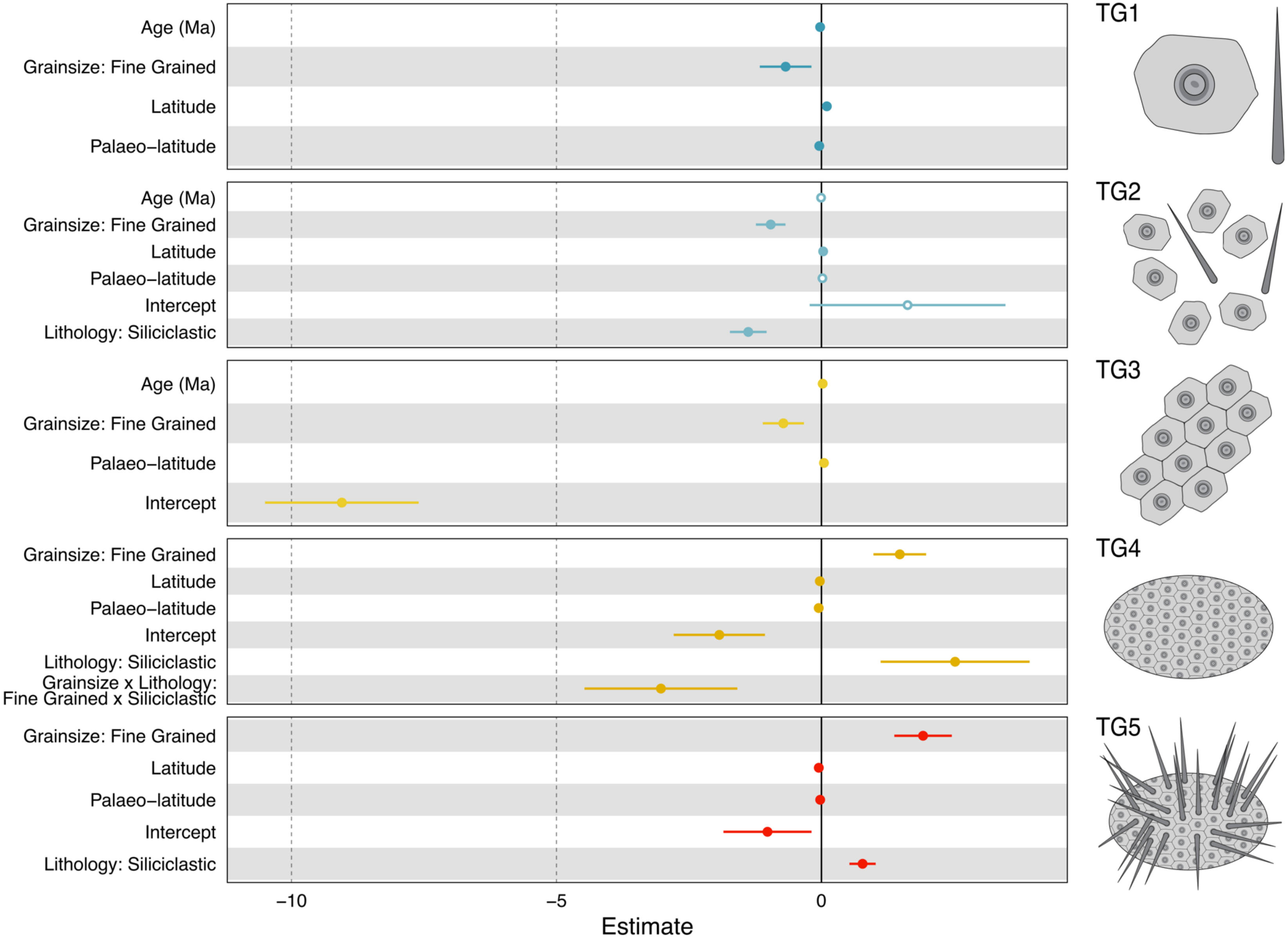
Age (Ma)
Grainsize: Fine Grained
Latitude
Palaeo–latitude
Age (Ma)
Grainsize: Fine Grained
Latitude
Palaeo–latitude
Intercept
Lithology: Siliciclastic
Age (Ma)
Grainsize: Fine Grained
Palaeo–latitude
Intercept
Grainsize: Fine Grained
Latitude
Palaeo–latitude
Intercept
Lithology: Siliciclastic
Grainsize x Lithology:
Fine Grained x Siliciclastic
Grainsize: Fine Grained
Latitude
Palaeo–latitude
Intercept
Lithology: Siliciclastic
−10
−5
0
Estimate
TG1
TG2
TG3
TG4
TG5

Figure 4. Forest plot showing best fitting model results for multiple logistic regression models for each taphonomic grade. Positive values indicate that the chance of observing a specimen at the associated taphonomic grade increases with the associated covariate, whereas negative values indicated the opposite. The output estimate is provided in log-odds scale.

TABLES

Table 1

Top ranked multiple logistic regression models for each Taphonomic grade. TG: Taphonomic Grade. df: Degrees of freedom. AICc: small sample corrected Akaike Information Criterion.

TG	*Model*	*df*	*Log-liklihood*	*AICc*	*Weight*
1	~ Age (Ma) + Palaeo−latitude + Grain size + Latitude + Lithology + Grain size:Lithology	7	-394.816	803.7	0.675
2	~ Age (Ma) + Palaeo−latitude + Grain size + Latitude + Lithology	6	-974.809	1961.7	0.306
3	~ Age (Ma) + Palaeo−latitude + Grain size	4	-569.936	1147.9	0.395
4	~ Palaeo−latitude + Grain size + Latitude + Lithology + Grain size:Lithology	6	-796.565	1609.2	0.618
5	~ Age (Ma) + Palaeo−latitude + Grain size + Latitude + Lithology	5	-897.518	1805.1	0.302

Table 2

Spearman's rank correlations between Taphnomic Grade and counts of North North American siliclastic and carbonate rock units in Macrostrat through time. TG: Taphonomic grade. BH: Benjamini Hochberg corrected p-value. Signif.: statistical significance, evaluated using Benjamini Hochberg corrected p-value < 0.05.

Temporal Resolution	*TG*	*vs. (test)*	*Rho*	*p*	*BH*	*Signif.*
Stage	1	Macrostrat carbonate (count)	0.312	0.056	0.137	
Stage	2	Macrostrat carbonate (count)	0.332	0.042	0.111	
Stage	3	Macrostrat carbonate (count)	0.346	0.033	0.092	
Stage	4	Macrostrat carbonate (count)	0.439	0.006	0.024	*
Stage	5	Macrostrat carbonate (count)	0.365	0.024	0.078	
Stage	1	Macrostrat silicilcastic (count)	0.49	0.002	0.008	*
Stage	2	Macrostrat siliciclastic (count)	0.644	0.00001	0.0003	*
Stage	3	Macrostrat siliciclastic (count)	0.524	0.001	0.005	*
Stage	4	Macrostrat siliciclastic (count)	0.627	0.00003	0.0003	*
Stage	5	Macrostrat siliciclastic (count)	0.548	0.0004	0.003	*

Table 3

Spearman's rank correlations between Taphonomic Grade and generic diversity at Stage and Period temporal resolutions. TG: Taphonomic grade. BH: Benjamini Hochberg corrected p-value. Signif.: statistical significance, evaluated using Benjamini Hochberg corrected p-value < 0.05.

Temporal Resolution	***TG***	***vs. (test)***	***Rho***	***p***	***BH***	***Signif.***
Stage	1	Diversity (genera)	0.462	0.047	0.119	
Stage	2	Diversity (genera)	0.541	0.017	0.058	
Stage	3	Diversity (genera)	0.343	0.151	0.280	
Stage	4	Diversity (genera)	0.258	0.286	0.391	
Stage	5	Diversity (genera)	0.402	0.088	0.196	
Period	1	Diversity (genera)	0.618	0.191	0.340	
Period	2	Diversity (genera)	0.618	0.191	0.340	
Period	3	Diversity (genera)	0.224	0.670	0.734	
Period	4	Diversity (genera)	0.265	0.612	0.690	
Period	5	Diversity (genera)	0.971	0.001	0.006	*

Table 4

Spearman’s rank correlations between Taphonomic Grade and counts of collections through time. TG: Taphonomic grade. BH: Benjamini Hochberg corrected p-value. Signif.: statistical significance, evaluated using Benjamini Hochberg corrected p-value < 0.05. echinoid and global collections, and counts of North American siliclastic and carbonate rock units.

Temporal resolution	*TG*	*vs. (test)*	*Rho*	*p*	*BH*	*Signif.*
Stage	1	Echinoid collections	0.776	0.00000046	0.00002	*
Stage	2	Echinoid collections	0.823	0.00000002	0.000002	*
Stage	3	Echinoid collections	0.645	0.0001	0.001	*
Stage	4	Echinoid collections	0.685	0.00003	0.0003	*
Stage	5	Echinoid collections	0.436	0.016	0.058	
Stage	1	Echinodermata collections	0.589	0.00011	0.0012	*
Stage	2	Echinodermata collections	0.361	0.031	0.091	
Stage	3	Echinodermata collections	0.562	0.00036	0.0025	*
Stage	4	Echinodermata collections	0.539	0.0007	0.0044	*
Stage	5	Echinodermata collections	0.298	0.077	0.18	
Stage	1	Global collections (pbdb)	0.207	0.212	0.352	
Stage	2	Global collections (pbdb)	0.0481	0.774	0.815	
Stage	3	Global collections (pbdb)	0.324	0.047	0.119	
Stage	4	Global collections (pbdb)	0.119	0.475	0.603	
Stage	5	Global collections (pbdb)	0.0113	0.947	0.958	