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1 **Does exceptional preservation distort our view of disparity in the fossil**
2 **record?**

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10

11 **ABSTRACT**

12 How much of evolutionary history is lost because of the unevenness of the fossil record?

13 Lagerstätten, sites which have historically yielded exceptionally preserved fossils, provide
14 remarkable, yet distorting insights into past life. When examining macroevolutionary trends
15 in the fossil record, they can generate an uneven sampling signal for taxonomic diversity; by
16 comparison, their effect on morphological variety (disparity) is poorly understood. We show
17 here that lagerstätten impact the disparity of ichthyosaurs, Mesozoic marine reptiles, by
18 preserving higher diversity and more complete specimens. Elsewhere in the fossil record,
19 undersampled diversity and more fragmentary specimens produce spurious results. We
20 identify a novel effect, that a taxon moves towards the centroid of a Generalised Euclidean
21 dataset as its proportion of missing data increases. We term this effect ‘centroid slippage’, as
22 a disparity-based analogue of phylogenetic stemward slippage. Our results suggest that
23 uneven sampling presents issues for our view of disparity in the fossil record, but that this is
24 also dependent on the methodology used, especially true with widely used Generalised
25 Euclidean distances. Mitigation of missing cladistic data is possible by phylogenetic gap
26 filling, and heterogeneous effects of lagerstätten on disparity may be accounted for by
27 understanding the factors affecting their spatiotemporal distribution.

28

29 **Keywords:** Lagerstätten, disparity, missing data, centroid slippage, Generalised Euclidean
30 Distance

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41 Palaeontologists express different attitudes to lagerstätten, deposits which have historically
42 yielded exceptionally preserved fossils. Most see them as opportunities to encounter the true
43 richness of past life, others as statistical outliers that distort the story presented by the fossil
44 record [1]. The distortion is potentially huge; for example, only 10% of the Burgess Shale
45 fauna would be seen under ‘normal’ conditions of fossilisation [2]. Alternatively, younger
46 lagerstätten like Holzmaden or Jehol do not exhibit such high levels of biological novelty and
47 many lagerstätte taxa co-occur in deposits lacking exceptional preservation. Understanding
48 how lagerstätten bias the fossil record is therefore crucial to accurately reconstructing
49 biodiversity through deep time.

50 The effects of lagerstätten sampling on taxonomic diversity are well documented [1,3,4],
51 but do not necessarily extend to morphological variety (disparity), as these measures of
52 biodiversity are generally decoupled [5,6,7]. Morphometric disparity analyses directly
53 compare physical shapes between taxa, but their application in palaeontology is limited by
54 the pervasive issue of missing anatomical data [8]. Cladistic disparity analyses use
55 differential character states between taxa as a proxy for disparity, producing similar results to
56 the morphometric approach [9] and readily accommodating missing character data. While
57 that same missing data negatively affects measurement of disparity, lagerstätten positively
58 affect character completeness [10,11,12]. Lagerstätte biases may therefore relate to the
59 problem of missing data, introducing methodological issues to cladistic disparity analyses
60 that are linked to biases in the geological record. Ciampaglio *et al.* [13] examined the effects
61 of missing data on disparity by using artificial cladistic data sets that were up to 25%
62 incomplete. Smith *et al.* [14] address the impacts of missing data at greater percentages,
63 finding that disparity for a variety of metrics decreases as the proportion of missing cladistic
64 data increases; this analysis, however, was performed on fossil data sets rather than artificial
65 data sets where the true (complete data) disparity value can be measured. Consequently, the
66 theoretical impacts of missing data at the highest percentages remain unexplored.

67 Several morphometric disparity studies have excluded lagerstätten taxa from their analyses
68 [15,16,17,18]. Each found little evidence for lagerstätten biases, but these conclusions cannot

69 necessarily be extended to cladistic disparity analyses. Lagerstätten bias the cladistic disparity
70 of pterosaurs, flying reptiles with delicate, hollow bones [4]. While diversity and disparity
71 may be decoupled, their fossil record is strongly dependent on lagerstätten [19]; such deposits
72 undoubtedly record a sizeable proportion of their disparity. Butler *et al.* [4] also used
73 phylogenetic correction to infill missing character states in their cladistic matrix, preventing
74 investigation of the potential interrelationship between lagerstätten, missing data and
75 disparity. Brusatte *et al.* [20] found that phylogenetic correction for missing data in
76 pterosaurs alters the results of disparity analysis in diverse ways depending on the data sets,
77 phylogenetic trees and disparity comparisons used, and does not simply inflate disparity
78 estimates. However, they caution against phylogenetic correction, except for clades with a
79 large amount of missing data or patchy fossil records. It is, therefore, worth exploring the
80 fossil records of clades not composed predominantly of lagerstätten to understand the
81 interlinked effects of methodology, missing data and exceptional preservation on disparity.

82 Ichthyosaurs, swimming reptiles with large, robust skeletons, occupied shallow and deep
83 marine environments with high preservation potentials, giving them a rich fossil record.
84 Ichthyosaurs were among the most significant groups to radiate in the oceans after the
85 Permian–Triassic mass extinction. New taxa described from the Panxian, Luoping, Xingyi,
86 and Guanling lagerstätten of China [21], alongside longer-known materials from the Besano
87 lagerstätte of Italy and Switzerland and the well-established global record of Triassic
88 ichthyosaurs [22], document rapid accumulation of disparity and anatomical innovations
89 through the Triassic [23]. Despite reduction in ecomorphospace by the Triassic–Jurassic
90 extinction [24], ichthyosaurs remained ecologically prominent throughout most of the
91 Mesozoic [25]. With their rich fossil record, comprising lagerstätten and non-lagerstätten
92 deposits, ichthyosaurs make a suitable case study to investigate the impacts of exceptional
93 preservation on our view of disparity.

94 We also examine disparity in artificial cladistic data sets, allowing for measurement of the
95 true disparity signal, followed by the random removal of 0 to 100% of characters to ascertain
96 the impact of higher levels of missing data. Ichthyosaur disparity is calculated here from a
97 moderately incomplete data set (52% missing characters) without any phylogenetic correction
98 method, and so our analysis of the effects of missing data provides a means of critiquing the
99 signal that emerges.

100

101 **2. Materials and methods**

102 **(a) Character and distance matrices**

103 In cladistic disparity analyses, character-taxon cladistic matrices are converted to taxon-taxon
104 distance matrices and then ordinated, allowing disparity metrics to be calculated as summary
105 statistics from the ordination space. Most studies use either Generalised Euclidean Distance
106 (GED) or Gower Coefficient Distance (GCD) matrices. The former has proved popular
107 because incomparable distances are mathematically infilled; complete data sets allow for a
108 greater range of subsequent analytical techniques. Lloyd [26], however, cautioned that this
109 approach may result in illogical data that could negatively impact a disparity study. GCD has
110 become increasingly popular as it has the advantage of accounting for the effects of missing
111 data at the cost of removing taxa which do not share any characters and so are incomparable.
112 Maximum Observable Rescaled Distance (MORD) operates in a similar way to GCD [26];
113 however, this has not yet been widely utilised as it has only recently been developed. Here,
114 we use disparity metrics calculated from all three distances to ascertain how the choice of
115 distance matrix may affect measurements of disparity as GCD and MORD matrices are
116 designed to more readily accommodate missing data.

117 Our chosen cladistic matrix is modified from Moon [27] and comprises 112
118 ichthyosauriforms scored for 287 discrete characters, where characters 100, 204, 205 and 218
119 are ordered. *Phalarodon major* was removed as it is a nomen dubium [28] and the character
120 states for *Suevoleviathan integer* and *S. disinteger* were combined as the latter is a junior
121 synonym of the former [29]. GED, GCD and MORD distance matrices were generated from
122 this using the MorphDistMatrix function of the Claddis package [26] in R (v3.2.2) [30]. In
123 the GCD and MORD matrices, 14 taxa had incomparable distances and were removed prior
124 to ordination. While GED matrices are commonly employed for the specific reason that they
125 do not require taxon removal, those same taxa were then removed from the GED matrix to
126 give taxon parity in subsequent statistical tests.

127

128 **(b) Ordination**

129 Each distance matrix was subjected to principal coordinates analysis (PCO) in R (v3.2.2)
130 [30]. PCO may introduce negative eigenvalues into the resultant data; thus, their
131 corresponding axis lengths, as the square roots of those eigenvalues, are imaginary. Negative
132 eigenvalue correction, utilising either the Lingoes [31] or Cailliez [32] methods, are used to
133 avoid this issue and are commonly employed in PCO analyses. Such methods, however,
134 reduce the amount of variation represented by lower ordination axes and so erode their
135 disparity signal [33]. As there is no consensus on the number of PCO axes to use in
136 subsequent analyses [26], this may be problematic for studies that focus on few axes, such as

137 the first three. To ascertain the impacts of negative eigenvalue correction, the squared
138 Pearson correlation between the pairwise distances in PCO space and the original distance
139 matrix was plotted, following the method of Kotrc and Knoll [33], along with the percentage
140 variance summarised by increasing numbers of PCO axes. This was conducted for each type
141 of distance matrix, with and without Cailliez negative eigenvalue correction.

142 Largely, as the number of uncorrected PCO axes increases, the degree of correlation with
143 the original distance matrix increases smoothly, plateauing as higher axes are included (Fig.
144 S1). By contrast, while inclusion of all corrected PCO axes produces a perfect correlation
145 with the original distance matrix, it fluctuates for lower numbers of axes. Even for
146 uncorrected GCD and MORD matrices, the correlation declines sharply over the first three
147 axes, those that are plottable and commonly used in the calculation of disparity metrics.

148 On the basis of these results, PCO without negative eigenvalue correction was performed
149 on each type of distance matrix. We used all positive PC axes in subsequent analyses to
150 maximise the correlation with its corresponding distance matrix and summarising the greatest
151 possible amount of variance on the lower axes, while excluding axes with negative
152 eigenvalues: 107 for GED, 62 for GCD and 62 for MORD.

153 The different degrees of correlation between the original distance matrices, and corrected
154 and uncorrected PCO matrices, warn against arbitrary selection of axes or selection based on
155 certain criteria, such as summarising a particular percentage of variance, as the chosen
156 number of axes may be poorly correlated with the original distance matrix. The sharp drop in
157 correlation over the first few axes even in the uncorrected PCO matrices further warns against
158 selection of axes without first determining how well they represent the original data.

159

160 (c) Disparity calculations

161 The selected taxa were sorted into 10 Ma time bins, spanning 250 Ma to 90 Ma, and the PCO
162 scores for each distance matrix subsampled for the taxa in each bin. Following the
163 recommendations of previous studies [34,35], a 10 Ma time bin length was selected as a
164 suitable trade-off between resolution and sample size. This approach was also selected, rather
165 than division into epochs, to avoid confounding effects associated with uneven time bin
166 lengths. Disparity metrics were then calculated using disparity function of the R package
167 dispRity [36]. The chosen metrics were the sums of ranges and variances, and the mean
168 distance from the centroid; 95% confidence intervals were calculated from 1000 bootstrapped
169 pseudoreplicates with replacement. PCO plots of morphospace for each bin were created

170 using the first two PCO axes. The same metrics and confidence intervals were then calculated
171 for a second data set pruned of taxa that occur in lagerstätte deposits.

172

173 **(d) Lagerstätten taxa**

174 The definition of a lagerstätte remains controversial. Sedimentological, geochemical and
175 taphonomic criteria have been described [37], but no consensus exists. The definition of a
176 lagerstätte may also include a historical component. Many classical lagerstätten have been
177 repeatedly sampled for decades or even centuries, partly due to the exceptional scientific and
178 aesthetic quality of their specimens, partly due to high specimen availability resulting from
179 systematic excavation in quarries or rapid erosional exposure (for example coastal settings).
180 Other factors may compound this historical component, for example the initial accessibility
181 of a locality or the effort invested in the subsequent preparation and description of any
182 collected specimens; all these elements are likely linked to some degree by the ‘bonanza
183 effect’ where palaeontologists preferentially sample and describe fossiliferous units of high
184 scientific potential over others [38], leading to sampling spikes for those units. Furthermore,
185 as lagerstätten show heterogeneous fidelity of preservation between clades, localities that
186 yield taxa used in our analysis may be considered lagerstätten for ichthyosaurs, but not for
187 other clades. Maisch [22] identified the Triassic Pardonet Formation and Hosselkus
188 Limestone, and the Middle Jurassic Los Molles Formation, amongst others, as ichthyosaur
189 lagerstätten, based on their relatively complete, well-preserved and well-sampled skeletons
190 despite the lack of classical indicators such as soft tissue preservation. Other ichthyosaur-
191 bearing horizons, particularly the Oxford Clay and Blue Lias formations, contain beds that
192 show exceptional preservation, and so are referred to as lagerstätte-grade by some authors;
193 however, other authors do not class them as such.

194 Ultimately the issue under consideration is how lagerstätten impact our picture of
195 ichthyosaur disparity in terms of their contribution to character state codings. Thus, we define
196 a conservative list of lagerstätten which may have induced spikes in the availability of highly
197 codable specimens due to the balance of the historical (well sampled and documented) and
198 taphonomic (exceptionally preserved) factors outlined above. Any significant differences in
199 disparity metrics should therefore remain valid even with the elevation of existing deposits to
200 lagerstätte grade, the future discovery of new ichthyosaur taxa from lagerstätten, or the
201 discovery of new lagerstätten themselves. The chosen lagerstätten are the Early Triassic
202 Nanlinghu and Jialingjiang formations of China, the Middle and Late Triassic Guanling and
203 Xiaowa formations of China, the Middle Triassic Zhuganpo Member of the Falang Formation

204 of China, the Middle Triassic Besano Formation of Switzerland and Italy, the Early Jurassic
205 Posidonia Shale of Germany, the Early Jurassic Strawberry Bank Limestone, and Blue Lias
206 and Charmouth Mudstone formations of the UK, the Middle to Late Jurassic Oxford Clay of
207 the UK, the Late Jurassic Solnhofen Limestone of Germany, the Late Jurassic Kimmeridge
208 Clay Formation of the UK, the Early Cretaceous Vaca Muerta Formation of Argentina, and
209 the Early Cretaceous Toolebuc Formation of Australia. Out of the 112 taxa in this analysis,
210 37 are exclusively from lagerstätten (33%) and occur in bins 2–4, 6–8, 11–13, 15 – 16. As
211 there was no way to assess whether lagerstätte or non-lagerstätte specimens of the same taxon
212 provided particular character codings in the data set, we included co-occurring taxa in both
213 partitions of the data set. This represents a compromise reflecting the certain (lagerstätte-
214 exclusive taxa) and potential (co-occurring taxa) influences of lagerstätten on ichthyosaur
215 disparity, rather than the worst case scenario where lagerstätten also dominate the proportion
216 of known character states for co-occurring taxa. We also ran the following analyses where
217 only lagerstätten-exclusive taxa were removed from disparity calculations, thus representing
218 the best-case scenario.

219

220 **(e) Lagerstätten effects**

221 Statistically significant differences between time bins with and without lagerstätten taxa were
222 assessed in two ways. Firstly, disparity metrics from bins which contain lagerstätten and
223 those from the corresponding bins with lagerstätten taxa removed were extracted from the
224 overall time series and tested for significant differences using paired samples two-tailed T
225 tests and Wilcoxon Signed Ranks tests. Secondly, two-tailed Pearson and Spearman tests of
226 correlation with Holm correction [39] for false discovery rates were used to test whether the
227 removal of lagerstätten taxa affected the trend in each metric through time. Generalised
228 differencing [40] using Graeme Lloyd's gen.diff function [41], was performed on the raw
229 disparity metrics to detrend and remove short-term autocorrelation from the data.

230 Correlations were then tested for in the same manner. To relate missing data (see below) and
231 sample size biases to possible lagerstätte effects, the same tests as above were conducted on
232 diversity and mean character completeness time series, and an independent samples, two-
233 tailed T-test was used to test for a significant difference in completeness between lagerstätte
234 and non-lagerstätte taxa.

235

236 **(f) Missing data**

237 To assess how the proportion of missing data for a taxon in the original cladistic matrix might
238 affect its position in morphospace, Pearson and Spearman tests of correlation were used to
239 test for a relationship between the percentage of missing data from each taxon and their
240 Pythagorean distance from the origin of the PCO plots in n dimensions, where n is the
241 number of PCO axes. A linear model was then fitted to the data, showing that as the
242 percentage of missing data increases, the Pythagorean distance to the origin decreases (see
243 below). The procedure was repeated using just the first two axes to provide a means of
244 critiquing the PCO morphospace plots. Disparity metrics for each level of missing data were
245 also calculated, using the methodology described above (Fig. S2).

246 To ascertain whether the relationship is simply a quirk of the data set, the same procedure
247 was conducted on two other cladistic data sets taken from the literature: 81 non-avian
248 theropod dinosaurs coded for 413 characters taken from Nesbitt and Ezcurra [42], and 80
249 sauropterygians coded for 270 characters taken from Benson and Bowdler [43], as well as the
250 ichthyosaur cladistic matrix used in this study. Both data sets were downloaded from Graeme
251 Lloyd's website (<http://www.graemetlloyd.com/matr.html>) on 22/07/17, converted to
252 distance matrices and subjected to PCO without negative eigenvalue correction in R (v3.2.2)
253 [30] prior to the calculation of Pythagorean distances for each taxon and correlation with the
254 percentages of missing data (Fig. S3, S4, S5, S6).

255 The relationship between missing data and disparity was investigated further using
256 simulations. A single data set comprising 20 operational taxonomic units (OTU) coded for
257 300 unordered, binary, equally weighted characters with randomly assigned states generated
258 in R (v3.2.2) [30]. Within the same cladistic matrix, the 20 OTUs were duplicated ten times
259 and 10% through to 90% of character states were deleted for successive groups of 10 OTUs.
260 The cladistic matrix was converted to a GED matrix and subjected to PCO without negative
261 eigenvalue correction. The same relationship between missing data and Pythagorean distance
262 was tested for using the method above.

263 Additional simulations were conducted to specifically focus on the relationship between
264 missing data and distance from the centroid. To ensure the accuracy of these simulations, 20
265 empirical cladistic matrices were downloaded from Graeme Lloyd's website on 01/05/18 and
266 the proportion of different character states assessed for each; the proportion of higher
267 character states was seen to decline in an approximate geometric relationship (Fig. S7).
268 Normal, Poisson and negative binomial distributions were then fitted to the distribution of
269 missing data in each matrix (Fig. S8) and the model fit assessed using the Akaike Information
270 Criterion. Negative binomial distributions performed the best, but only marginally compared

271 to normal distributions (Table S1). Simulated cladistic matrices covering a range of
272 dimensions were generated in R (v3.2.2). Each matrix was then assigned a different normal
273 distribution of missing data (this strategy was chosen for simplicity as a negative binomial
274 distribution tends towards normality for large sample sizes), and equal or geometric
275 distributions of unordered, randomly assigned character states for binary, ternary, quaternary,
276 quinary, and senary coding strategies. Each matrix was transformed, ordinated and analysed
277 using the methodology above.

278

279 **3. Results**

280 **(a) Lagerstätten biases**

281 Time bins with lagerstätten taxa show significantly lower values for each disparity metric
282 (Table 1; Fig. 1), when lagerstätte taxa are excluded. Morphospace occupation is similarly
283 reduced when lagerstätte taxa are excluded (Fig. 2). After generalised differencing, centroid
284 distances from GCD and MORD fail to correlate between lagerstätte and non-lagerstätte time
285 series using Pearson correlation; centroid distance from all three distances, and the sums of
286 variances from GED also fail using Spearman correlation (Table 2, 3). This shows that the
287 preservational biases of lagerstätten impact the long-term trend in disparity observed over
288 hundreds of millions of years. It should be noted, however, that while there is a statistical
289 difference between the time series, they broadly recover the same peaks and troughs in
290 disparity, aside from the late Early to Late Jurassic where lagerstätten dominate their fossil
291 record. An independent-samples, two-tailed T test showed a statistically significant
292 difference ($T = -3.47$, $df = 54.69$, $p < 0.005$, $n = 25, 40$) in the percentage completeness of
293 cladistic characters between the lagerstätte (57.4% complete) and non-lagerstätte taxa
294 (37.2.0% complete), and taxonomic diversity-per-bin shows significant differences within
295 lagerstätte bins when lagerstätte taxa are excluded (Table 1). Together, these results suggest
296 that lagerstätten affect disparity in two ways: through the preservation of more taxa; and
297 through the preservation of more complete specimens. Biases in individual disparity metrics
298 and morphospace plots, however, are partially dependent on the choice of distance matrix.

299 Reanalysis, excluding only lagerstätte-exclusive taxa from disparity calculations, had no
300 effect on the statistical significance or otherwise of our results, aside from significant
301 Spearman correlations for the GED-derived centroid distance after generalised differencing.
302 This demonstrates that the impacts of lagerstätten remain prevalent even for the best-case
303 scenario. The greater completeness of lagerstätte specimens, however, suggests that the true

304 impacts of lagerstätten on ichthyosaur disparity may lie somewhere between our comprise
305 and the worst-case scenario.

306

307 **(b) Missing data and centroid slippage**

308 A highly significant, negative relationship was found between the percentage of missing
309 characters for a taxon in a cladistic matrix and its Pythagorean distance to the origin of n -
310 dimensional principal coordinate (PCO) space derived from GED, where n is the number of
311 PCO axes examined (Table 4; Fig. 3). This trend holds true across simulated cladistic
312 matrices spanning a wide variety of dimensions, coding strategies and levels of missing data
313 (Fig. 4). For convenience, we term this effect ‘centroid slippage’ (PCO performed on a GED
314 matrix is mathematically equivalent to principal components analysis, where the centroid of
315 the dataset lies at zero on all axes). The effect of centroid slippage is nullified when GCD and
316 MORD are used. Together with the reduced impact of lagerstätten effects when alternative
317 distances are used, this highlights a key methodological issue for disparity analyses. In other
318 words, taxa move from their true positions in morphospace towards the centroid.

319 Generalised Euclidean Distance produces the most severe biases in disparity metrics and is
320 especially subject to centroid slippage, as gaps in the distance matrix are infilled with a
321 weighted mean fractional univariate distance based on the calculable distances [26]. The
322 limits of morphospace size are affected by the proportion of missing data for taxa comprising
323 the hull of the morphospace (Fig. 5), and trends in morphospace occupation by the dispersal
324 of taxa within that morphospace. Lagerstätten effects are part of this, with the higher
325 character completeness of their taxa often determining the bounds of morphospace in the bins
326 in which they occur, while their position relative to more incomplete taxa is warped as the
327 latter slip towards the centroid (Fig. 2).

328

329 **(c) Ichthyosaur disparity through time**

330 Despite their different responses to geological sampling biases, bivariate morphospace plots
331 and disparity metric time series from all three distance types converge upon trends in
332 disparity concordant with the findings of previous authors. Morphospace occupation was
333 greatest in the first 8.7 myr of the Triassic (Fig. 1, 2), during which time early ichthyosaurs
334 gained great ecomorphological diversity by radiating into ecological niches left vacant by the
335 Permian–Triassic mass extinction, plus possibly new, previously unoccupied ecospace [23].
336 Disparity rapidly decreased during the loss of circa-littoral and shallow water forms during
337 the Late Triassic and remained reduced in accordance with the conservative morphology of

338 Early Jurassic ichthyosaurs, despite their high diversity [24]. Overall, there was a shift in
339 morphospace occupation throughout the Mesozoic (Fig. 2), corresponding to the shift from
340 early elongate taxa to later thunniform taxa [41].

341

342 **4. Discussion**

343 Compared to the morphometric approach to disparity, the cladistic approach is an excellent
344 way of examining disparity in an incomplete fossil record, yet it is sensitive to the choice of
345 distance matrix and disparity metric. Gower Coefficient Distance is increasingly
346 recommended as it can account for the effect of missing data [44]; Lloyd [26] introduced
347 MORD which may perform even more strongly. While these latter distances will likely prove
348 preferable in future studies, two problems associated with GED may yet cause problems with
349 our current view of disparity in the fossil record, as this distance type is still commonly
350 employed in studies using the cladistic approach.

351 Firstly, centroid slippage makes a taxon appear morphologically average, analogous to the
352 way in which missing data in phylogenetic studies causes stemward slippage [45], where the
353 incomplete taxon appears more plesiomorphic than is actually the case. By extension, just as
354 stemward slippage may confound the determination of phylogenetic relationships among a
355 set of taxa, centroid slippage will confound the morphological relationships among taxa,
356 affecting their relative positions in morphospace. Lagerstätte biases relate to this first issue
357 due to the greater completeness of their taxa.

358 The second issue is that, as PCO is a method used to visualise variance in a data set using
359 similarities and differences between groups of objects, centroid slippage may be problematic
360 for studies that attempt to use separation in morphospace as a proxy for ecomorphological
361 separation between clades. Highly incomplete taxa may be removed from the clusters to
362 which they are truly affiliated and pushed into another, or groups that are truly
363 morphologically separate may end up overlapping due to centroid slippage. More broadly, the
364 changing positions of taxa in all dimensions will alter the size and position of occupied
365 morphospace, strongly altering the disparity signal.

366 Focusing on the complete signal contained within the fossil record, the high number of
367 Triassic and Early Jurassic lagerstätten suggests that this part of ichthyosaur evolutionary
368 history can be interpreted with some confidence. In particular, their Jurassic fossil record is
369 composed predominantly of lagerstätten, giving high fidelity, yet also indicating the potential
370 severity of lagerstätte biases were these deposits absent. Ichthyosaur lagerstätten are fewer in
371 number from the Cretaceous onwards, and correspondingly interpretation of their

372 evolutionary history is less confident [24]. This is particularly problematic in the few million
373 years prior to their extinction during the mid-Cretaceous, where their fossil record is highly
374 fragmentary [25].

375 Butler *et al.* [4] demonstrated that the peaks and troughs in the record of pterosaur
376 disparity are largely artificial due to lagerstätte sampling. While the ichthyosaur fossil record
377 is less dependent on lagerstätten deposits, there is nevertheless a biased signal between bins
378 with and without lagerstätten. Lagerstätten vary in their depositional environments and are
379 geographically and temporally localised; thus, they only give a truer record of particular
380 ecosystems, but not necessarily a more complete global signal. Despite this, the disparity and
381 diversity signals they preserve are more complete and so are inherently more faithful than
382 bins without lagerstätte deposits; these latter must therefore be interpreted with caution.

383 Lagerstätten improve the fidelity of the disparity signal for a time bin by preserving a
384 greater range of species, and by preserving more complete specimens. Thus, while the bias of
385 missing species and missing data may affect bins containing lagerstätten less, the relative
386 increase in disparity in lagerstätte-containing bins will affect attempts to draw broad
387 conclusions about patterns of disparity through time; for example if linear models are fitted to
388 time series to try to discern an overall trend. An important point to consider is that while
389 lagerstätten provide more faithful preservation, they have differing impacts on different
390 groups. To an extent, this is dependent on the depositional environment of the ecosystem and
391 the ecological biases of the organisms within that ecosystem; for example, infaunal
392 organisms are typically more likely to be preserved than nektonic or pelagic species, and
393 shelf environments more likely to receive deposition than forests. As such, the distribution
394 and type of lagerstätten in time and space may have heterogeneous effects on the disparity of
395 different clades. Here we document a clear impact of lagerstätten on ichthyosaur disparity,
396 whereas a study of Palaeozoic echinoderms [46] found that lagerstätten had virtually no
397 effect on their overall disparity (strong effects were noted because of taphonomic
398 degradation, however, highlighting the problem of missing data). In turn, this poses
399 difficulties for associating changes in disparity within distinct groups to external causes or to
400 evolutionary interactions between those groups.

401 Together, these two points highlight the need to find ways to correct the biases imposed by
402 lagerstätten. The removal of highly incomplete taxa prior to analysis does not solve the
403 problem of missing data, merely sidestepping it at the cost of a straight reduction in disparity.
404 Phylogenetic correction is an alternative, but its utility is dependent on how well resolved the
405 chosen phylogenetic hypothesis is. As this is itself affected by the amount of missing data in

406 a cladistic matrix, the instability of phylogenetic and disparity analyses may trend together;
407 thus, the utility of phylogenetic correction will decline even as the disparity analysis calls
408 more strongly for correction. This is also the case for the use of gap weighting to infill
409 missing data. Smith *et al.* [14] note that these methods all affect the disparity signal
410 differently. They present a novel method of correction, which identifies linkage in the
411 presence or absence of characters in a data set, and then selectively removes additional data
412 to equalise the distribution of missing characters between the taxa, minimising the degree of
413 disparity reduction at varying levels of missing data. In turn, while the true disparity values
414 cannot be measured, relative changes in the size and occupation of morphospace through time
415 can be identified with greater confidence. Application of this method to future disparity
416 studies may help reduce the impact of the greater completeness of lagerstätte specimens.

417 The bias from preservation of a greater number of taxa is harder to mitigate, but may be
418 tackled through a better understanding of the factors that control the spatiotemporal
419 distribution of lagerstätten. Lagerstätten of similar ages, representing similar facies
420 environments, may occur in clusters resulting from deposition in a broad geographical region
421 where conditions were generally conducive to exceptional preservation [47]. Trends in the
422 size and distribution of these clusters through time result from fluctuations in the
423 environmental constraints required for their formation at local, regional and global scales
424 [47]. Preservational biases resulting in lagerstätten dominate in the marine environment,
425 while terrestrial lagerstätten are more strongly controlled by sampling biases [47]. Thus, it
426 may be possible to demonstrate more general links between these biases and the disparity
427 signal from the fossil record. The spatiotemporal distribution of lagerstätten may also provide
428 useful insight into the problem of missing data. Tutin and Butler [48] found a significant
429 relationship between skeletal completeness and character completeness metrics for
430 plesiosaurs, and between plesiosaur and ichthyosaur completeness, suggesting common
431 controls on skeletal preservation in both groups; this could feasibly include a lagerstätten
432 bias. Lagerstätte biases in completeness may not be present for all groups; however, Verriere
433 *et al.* [49] found no evidence for lagerstätte effects on parareptile diversity and in turn no
434 correlation between their diversity and skeletal or character completeness metrics.

435

436 **Competing interests.**

437 We declare we have no competing interests.

438

439 **Authors' contributions.**

440 J.F.S, T.L.S and B.C.M designed the analysis. J.F.S carried out the analysis. B.C.M provided
441 the cladistic data set. J.F.S and M.J.B wrote the paper, and all authors commented on the
442 paper.

443

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446

447 **Data accessibility.**

448 All additional data for this article are provided in the electronic supplementary material:

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454

455 This manuscript has not been published in whole or in part elsewhere and is not currently
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457

458 **References**

- 459 1. Benson, R., Butler, R., Lindgren, J., Smith, A. 2010 Mesozoic marine tetrapod diversity:
460 mass extinctions and temporal heterogeneity in geological megabiases affecting
461 vertebrates. *Proc. R. Soc. B* **277**, 829 – 834. (doi:10.1098/rspb.2009.1845)
- 462 2. Whittington, H., Conway Morris, S. 1985 Illustration in Briggs, D., Erwin, D., Collier, F.,
463 Clark, C. (eds). *Fossils of the Burgess Shale*. Smithsonian Institution Press, Washington,
464 418p
- 465 3. Benson, R., Butler, R. 2011 Uncovering the diversification history of marine tetrapods:
466 ecology influences the effect of geological sampling biases. *Geol. Soc. Spec. Publ.* **358**,
467 191 – 208. (doi:10.1144/SP358.13)
- 468 4. Butler, R., Brusatte, S., Andres, B., Benson, R. 2011 How do geological sampling biases
469 affect studies of morphological evolution in deep time? A case study of pterosaur
470 (Reptilia: Archosauria) disparity. *Evolution* **66**, 147 – 162, (doi:10.1111/j.1558-
471 5646.2011.01415.x)
- 472 5. Erwin, D. 2007 Disparity: morphological pattern and developmental context.
473 *Palaeontology* **50**, 57 – 73. (doi:10.1111/j.1475-4983.2006.00614.x)

- 474 6. Ruta, M., Angielczyk, D., Fröbisch, J., Benton, M. 2013 Decoupling of morphological
475 disparity and taxic diversity during the adaptive radiation of anomodont therapsids. *Proc.*
476 *R. Soc. B* **280**, 20131071. (doi:10.1098/rspb.2013.1071)
- 477 7. Benton, M., Forth, J., Langer, M. 2014 Models for the rise of the dinosaurs. *Curr. Biol.*
478 **24**, 87 – 95. (doi:10.1016/j.cub.2013.11.063)
- 479 8. Brown, C., Arbour, J., Jackson D. 2012. Testing of the Effect of Missing Data Estimation
480 and Distribution in Morphometric Multivariate Data Analyses. *Systematic Biol.* **61**, 941 –
481 954. (doi:10.1093/sysbio/sys047)
- 482 9. Hetherington, A., Sherratt, E., Ruta, M., Wilkinson, M., Deline, B., Donoghue, P. 2015
483 Do cladistic and morphometric data capture common patterns of morphological disparity?
484 *Palaeontology* **58**, 393 – 399. (doi:10.1111/pala.12159)
- 485 10. Brocklehurst, N., Upchurch, P., Mannion, P., O'Connor, J. 2012 The Completeness of the
486 Fossil Record of Mesozoic Birds: Implications for Early Avian Evolution. *PLoS ONE* **7**,
487 e39056. (doi:10.1371/journal.pone.0039056)
- 488 11. Cleary, T., Moon, B., Dunhill, D., Benton, M. 2015 The fossil record of ichthyosaurs,
489 completeness metrics and sampling biases. *Palaeontology* **58**, 521 – 536.
490 (doi:10.1111/pala.12158)
- 491 12. Dean, C., Mannion, P., Butler, R. 2016 Preservational bias controls the fossil record of
492 pterosaurs. *Palaeontology* **59**, 225 – 247. (doi:10.1111/pala.12225)
- 493 13. Ciampaglio, C., Kemp, M., McShea, D. 2001 Detecting changes in morphospace
494 occupation patterns in the fossil record: characterization and analysis of measures of
495 disparity. *Paleobiology* **27**, 695 – 715. (doi:10.1666/0094-
496 8373(2001)027<0695:DCIMOP>2.0.CO;2)
- 497 14. Smith, A., Rosario, M., Eiting, T., Dumont, E. 2014 Joined at the hip: linked characters
498 and the problem of missing data in studies of disparity. *Evolution* **68**, 2386 – 2400.
499 (doi:10.1111/evo.12435)
- 500 15. Friedman, M. 2010 Explosive morphological diversification of spiny-finned teleost fishes
501 in the aftermath of the end-Cretaceous extinction. *Proc. R. Soc. B* **277**, 1675 – 1683.
502 (doi:10.1098/rspb.2009.2177)
- 503 16. Anderson, P., Friedman, M., Brazeau, M., Rayfield, R. 2011 Initial radiation of jaws
504 demonstrated stability despite faunal and environmental change. *Nature* **476**, 206 – 209.
505 (doi:10.1038/nature10207)

- 506 17. Smithwick, F., Stubbs, T. 2018 Phanerozoic survivors: Actinopterygian evolution through
507 the Permo-Triassic and Triassic-Jurassic mass extinction events. *Evolution* **72**, 348 – 362.
508 (doi:10.1111/evo.13421)
- 509 18. Clarke, J., Friedman, M. 2018 Body-shape diversity in Triassic–Early Cretaceous
510 neopterygian fishes: sustained holostean disparity and predominantly gradual increases in
511 teleost phenotypic variety. *Paleobiology* **94**, 1 – 32. (doi:10.1017/pab.2018.8)
- 512 19. Benton, M., Dunhill, A., Lloyd, G., Marx, F. 2011 Assessing the quality of the fossil
513 record: insights from vertebrates. In McGowan, A., Smith, A. (eds). Comparing the
514 geological and fossil records: implications for biodiversity studies. *Geol. Soc. Spec. Publ.*
515 **358**, 63 – 94. (doi:10.1144/SP358.6)
- 516 20. Brusatte, S., Montanari, S., Yi, H., Norell, M. 2011 Phylogenetic corrections for
517 morphological disparity analysis: new methodology and case studies. *Paleobiology* **37**, 1
518 – 22. (doi:10.1666/09057.1)
- 519 21. Benton, M., Zhang, Q., Hu, S., Chen, Z., Wen, W., Liu, J., Huang, J., Zhou, C., Xie, T.,
520 Tong, J., Choo, B. 2013 Exceptional vertebrate biotas from the Triassic of China, and the
521 expansion of marine ecosystems after the Permo–Triassic mass extinction. *Earth Sci. Rev.*
522 **137**, 85 – 128. (doi:10.1016/j.earscirev.2013.05.014)
- 523 22. Maisch, M. 2010 Phylogeny, systematics and origin of the Ichthyosauria – the state of the
524 art. *Palaeodiversity* **3**, 151 – 214
- 525 23. Stubbs, T., Benton, M. 2016 Ecomorphological diversifications of Mesozoic marine
526 reptiles: The roles of ecological opportunity and extinction. *Paleobiology* **42**, 547 – 573.
527 (doi:10.1017/pab.2016.15)
- 528 24. Dick, D., Maxwell, E. 2015 The evolution and extinction of the ichthyosaurs from the
529 perspective of quantitative ecospace modelling. *Biol. Lett.* **11**, 20150339.
530 (doi:10.1098/rsbl.2015.0339)
- 531 25. Fischer, V., Bardet, N., Guimar, M., Godefroit, P. 2014 High diversity in Cretaceous
532 ichthyosaurs from Europe prior to their extinction. *PLoS ONE* **9**, e84709.
533 (doi:10.1371/journal.pone.0084709)
- 534 26. Lloyd, G. 2016 Estimating morphological diversity and tempo with discrete character-
535 taxon matrices: implementation, challenges, progress, and future directions. *Biol. J. Linn.*
536 *Soc.* **118**, 131 – 151. (doi:10.1111/bij.12746)
- 537 27. Moon, B. 2017 A new phylogeny of ichthyosaurs (Reptilia: Diapsida). *J. Syst.*
538 *Palaeontol.* (doi:10.1080/14772019.2017.1394922)

- 539 28. MacGowan, C., Motani, R. 2003 *Ichthyopterygia*. Verlag Dr. Friedrich Pfeil, München,
540 175p
- 541 29. Maxwell, E 2018 Redescription of the 'lost' holotype of *Suevoleviathan integer* (Bronn,
542 1844) (Reptilia: Ichthyosauria). *J. Vertebr. Paleontol.* **38**, e1439833.
543 (doi:10.1080/02724634.2018.1439833)
- 544 30. R Core Team. 2013 R: A language and environment for statistical computing. R
545 Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- 546 31. Lingo, J. 1971 Some boundary conditions for a monotone analysis of symmetric
547 matrices. *Psychometrika* **36**, 195 – 203. (doi:10.1007/BF02291398)
- 548 32. Cailliez, F. 1983 The analytical solution of the additive constant problem. *Psychometrika*
549 **48**, 343 – 349. (doi:10.1007/BF02294026)
- 550 33. Kotrc, B., Knoll, A. 2015 A morphospace of planktonic marine diatoms. I. Two views of
551 disparity through time. *Paleobiology* **41**, 45 – 67. (doi:10.1017/pab.2014.4)
- 552 34. Foote, M. 1994 Morphological disparity in Ordovician–Devonian crinoids and the early
553 saturation of morphological space. *Paleobiology* **20**, 320 – 344.
554 (doi:10.1017/S009483730001280X)
- 555 35. Brusatte, S., Benton, M., Ruta, M., Lloyd, G. 2008 The first 50 Myr of dinosaur
556 evolution: macroevolutionary pattern and morphological disparity. *Biol. Lett.* **4**, 733 –
557 736. (doi:10.1098/rsbl.2008.0441)
- 558 36. Guillerme, T. 2018 dispRity: A modular R package for measuring disparity. *Methods*
559 *Ecol. Evol.* **9**, 1755 – 1763. (doi:10.1111/2041-210X.13022)
- 560 37. Allison, P. 1998 Konservat-Lagerstätten: cause and classification. *Paleobiology* **14**, 331 –
561 344. (doi:10.1017/S0094837300012082)
- 562 38. Raup, D. 1977 Systematists follow the fossils. *Paleobiology* **3**, 328 – 329.
563 (doi:10.1017/S0094837300005431)
- 564 39. Holm, S. 1979 A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**,
565 65 – 70. (doi:10.2307/4615733)
- 566 40. McKinney, M. 1990 Classifying and analyzing evolutionary trends. In McNamara, K.
567 (ed). *Evolutionary Trends*, Belhaven, London, 28 – 58
- 568 41. Lloyd, G. 2008 Generalized differencing of time series.
569 www.graemetlloyd.com/methgd.html
- 570 42. Nesbitt, S., Ezcurra, M. 2015 The early fossil record of dinosaurs in North America: a
571 new neotheropod from the base of the Upper Triassic Dockum Group of Texas. *Acta*
572 *Palaeontol. Pol.* **60**, 513 – 526. (doi:10.4202/app.00143.2014)

- 573 43. Benson, R., Bowdler, T. 2014 Anatomy of *Colymbosaurus megadeirus* (Reptilia,
574 Plesiosauria) from the Kimmeridge Clay Formation of the U.K., and high diversity
575 among Late Jurassic plesiosauroids. *J Vertebr. Paleontol.* **34**, 1053 – 1071.
576 (doi:10.1080/02724634.2014.850087)
- 577 44. Thorne, P., Ruta, M., Benton, M. 2011 Resetting the evolution of marine reptiles at the
578 Triassic-Jurassic boundary. *Proc. Natl. Acad. Sci. USA* **108**, 8339 – 8344.
579 (doi:10.1073/pnas.1018959108)
- 580 45. Sansom, R., Wills, M. 2013 Fossilization causes organisms to appear erroneously
581 primitive by distorting evolutionary trees. *Sci. Rep-UK* **3**, 2545. (doi:10.1038/srep02545)
- 582 46. Deline, B., Thomka, J. 2017 The role of preservation on the quantification of morphology
583 and patterns of disparity within Paleozoic echinoderms. *J Paleontol.* **91**, 618 – 632.
584 (doi:10.1017/jpa.2016.129)
- 585 47. Muscente, A., Schiffbauer, J., Broce, J., Laflamme, M., O'Donnell, K., Boag, T., Meyer,
586 M., Hawkins, A., Huntley, J., McNamara, M., MacKenzie, L., Stanley Jr, G., Hinman, N.,
587 Hofmann, M., Xiao, S. 2017 Exceptionally preserved fossil assemblages through geologic
588 time and space. *Gondwana Res.* **48**, 164 – 188. (doi:10.1016/j.gr.2017.04.020)
- 589 48. Tutin, S., Butler, R. 2017 The completeness of the fossil record of plesiosaurs, marine
590 reptiles from the Mesozoic. *Acta Palaeontol. Pol.* **62**, 563 – 573.
591 (doi:10.4202/app.00355.2017)
- 592 49. Verriere, A., Brocklehurst, N., Frobisch, J. 2016 Assessing the completeness of the fossil
593 record: comparison of different methods applied to parareptilian tetrapods (Vertebrata:
594 Sauropsida). *Paleobiology* **42**, 680 – 695. (doi:10.1017/pab.2016.26)
- 595
- 596

597 **Table 1.** Paired samples two-tailed T tests and Wilcoxon Signed Ranks (W) tests between
 598 disparity metrics (Sum V = sum of variances, Sum R = sum of ranges, Cent = mean distance
 599 from the centroid), and character completeness (Compl) and taxonomic diversity (Div), from
 600 time bins with lagerstätte taxa, and with those taxa removed (df = 9, p-values are *italicised*, T
 601 and W statistics are plain text).

		Sum V	Sum R	Cent	Compl	Div
T	GED	4.67, <0.005	11.01, <0.0001	5.80, <0.0005	-1.25, 0.24	4.11, <0.005
	GCD	5.08, <0.001	10.42, <0.0001	6.94, <0.0001	-	-
	MORD	4.94, <0.001	10.15, <0.0001	6.56, <0.0005	-	-
W	GED	55, <0.005	55, <0.005	55, <0.005	10, 0.16	45, <0.01
	GCD	55, <0.005	55, <0.005	55, <0.005	-	-
	MORD	55, <0.005	55, <0.005	55, <0.005	-	-

602

603 **Table 2.** Two-tailed tests of Pearson correlation between raw and generalised differenced
 604 (GD) disparity metric time series, and character completeness and diversity, with lagerstätte
 605 taxa present and removed (p-values are *italicised*). See Table 1 for column title abbreviations.

		Sum V	Sum R	Cent	Compl	Div
Raw	GED	0.79, <0.005	0.80, <0.005	0.78, <0.005	0.94, <0.0001	0.90, <0.0001
	GCD	0.92, <0.0001	0.82, <0.001	0.767, <0.01	-	-
	MORD	0.90, <0.0001	0.81, <0.001	0.65 <0.05	-	-
GD	GED	0.67, <0.05	0.74, <0.05	0.67, <0.05	0.93, <0.0001	0.92, <0.0001
	GCD	0.92, <0.0001	0.76, <0.01	0.45, 0.12	-	-
	MORD	0.89, <0.0005	0.76, <0.005	0.44, 0.13	-	-

606

607

608

609 **Table 3.** Two-tailed tests of Spearman correlation between raw and generalised differenced
 610 (GD) disparity metric time series, and character completeness and diversity, with lagerstätte
 611 taxa present and removed (p-values are *italicised*). See Table 1 for column title abbreviations.

		Sum V	Sum R	Cent	Compl	Div
Raw	GED	0.85, <0.005	0.81, <0.001	0.781 <0.005	0.94, <0.0001	0.85, <0.0005
	GCD	0.80, <0.005	0.75, <0.005	0.36, 0.20	-	-
	MORD	0.87, <0.0005	0.77, <0.005	0.32, 0.26	-	-
GD	GED	0.42, 0.14	0.66, <0.05	0.54, 0.12	0.98, <0.0001	0.90, <0.0005
	GCD	0.71, <0.05	0.65, <0.05	0.52, 0.07	-	-
	MORD	0.75, <0.01	0.64, <0.05	0.42, 0.16	-	-

612

613 **Table 4.** Two-tailed tests of Pearson and Spearman correlation between a taxon's percentage
 614 missing data and its Pythagorean distance from the origin of PCO space in n dimensions
 615 where n is the total number of PCO axes for each data set (p-values are *italicised*).

	Ichthyosauria	Sauropterygia	Dinosauria	Artificial
Pearson	-0.87, <0.0001	-0.91, <0.0001	-0.84, <0.0001	-0.98, <0.0001
Spearman	-0.89, <0.0001	-0.90, <0.0001	-0.88, <0.0001	-0.97, <0.0001

616

617

618

619 **Figure 1.** Comparisons of ichthyosaur diversity disparity through time, with and without
620 lagerstätte taxa. Time series of disparity metrics, along with taxonomic diversity, for each
621 time bin from 250 – 90 Ma. A. Taxonomic diversity; B. Sum of variances; C. Sum of ranges;
622 D. Mean distance from the centroid. Error bars represent the bootstrapped 95% confidence
623 interval.

624

625 **Figure 2.** Changing morphospace occupation of ichthyosaurs through geological time. 10
626 myr morphospace plots of the first two PCO axes of the ichthyosaur data set from 250 – 90
627 Ma.

628

629 **Figure 3.** The effect of missing data on distance from the morphospace origin. Linear
630 regressions between a taxon's percentage missing data and its Pythagorean distance from the
631 origin of PCO space on the first two PCO axes.

632

633 **Figure 4.** Simulation of the proportion of missing data versus distance from the morphospace
634 origin. Heatmaps of the relationship between a taxon's percentage missing data and its
635 Pythagorean distance from the origin of PCO space on the first two PCO axes, derived from
636 1,100 matrices and 100,000 taxa. The shift from blue to red indicates an increasing density of
637 points at a given coordinate.

638

639 **Figure 5.** Impact of missing data on morphospace. Morphospace plots of the first two PCO
640 axes of a simulated data set, artificially degraded for varying levels of missing data,
641 compared to the true morphospace for the complete simulation data set.