



## Preservational bias controls the fossil record of pterosaurs

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# *Preservational bias controls the fossil record of pterosaurs*

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**Abstract:** Pterosaurs, a Mesozoic group of flying archosaurs, have become a focal point for debates pertaining to the impact of sampling biases on our reading of the fossil record, as well as the utility of sampling proxies in palaeodiversity reconstructions. The completeness of the pterosaur fossil specimens themselves potentially provides additional information that is not captured in existing sampling proxies, and might shed new light on the group's evolutionary history. Here we assess the quality of the pterosaur fossil record via a character completeness metric based on the number of phylogenetic characters that can be scored for all known skeletons of 172 valid species, with averaged completeness values calculated for each geological stage. The fossil record of pterosaurs is observed to be strongly influenced by the occurrence and distribution of Lagerstätten. Peaks in completeness correlate with Lagerstätten deposits, and a recovered correlation between completeness and observed diversity is rendered non-significant when Lagerstätten species are excluded. Intervals previously regarded as potential extinction events are shown to lack Lagerstätten and exhibit low completeness values: as such, the apparent low diversity in these intervals might be at least partly the result of poor fossil record quality. A positive correlation between temporal patterns in completeness of Cretaceous pterosaurs and birds further demonstrates the prominent role that Lagerstätten deposits have on the preservation of smaller bodied organisms, contrasting with a lack of correlation with the completeness of large-bodied sauropodomorphs. However, we unexpectedly find a strong correlation between sauropodomorph and pterosaur

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3 completeness within the Triassic–Jurassic, but not the Cretaceous, potentially relating to a  
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5 shared shift in environmental preference and thus preservation style through time. This study  
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7 highlights the importance of understanding the relationship between various taphonomic  
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9 controls when correcting for sampling bias, and provides additional evidence for the  
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11 prominent role of sampling on observed patterns in pterosaur macroevolution.  
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16 **Key words:** Fossil record completeness; Lagerstätten, Mesozoic; Pterodactyloidea;  
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18 Pterosauria; Sampling bias  
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23 PTEROSAURS were a group of Mesozoic flying archosaurs that went extinct at the  
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25 Cretaceous/Paleogene (K/Pg) mass extinction 66 Ma, approximately 150 myr after their first  
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27 appearance in the fossil record (Wellnhofer 1991; Unwin 2003, 2005; Barrett *et al.* 2008;  
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29 Dalla Vecchia 2013; Witton 2013). They show high taxonomic (Unwin 2005; Butler *et al.*  
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31 2009, 2013; Witton 2013) and morphological diversity (Prentice *et al.* 2011; Foth *et al.* 2012;  
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33 Butler *et al.* 2012), with a global distribution by at least the Early Jurassic (Barrett *et al.* 2008;  
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35 Upchurch *et al.* 2015). A number of studies have evaluated evidence for fluctuations through  
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37 time in pterosaur diversity, including discussion of their possible competitive replacement by  
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39 birds (e.g. Unwin 1987, 2005; Buffetaut *et al.* 1996; Slack *et al.* 2006; Butler *et al.* 2009,  
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41 2012, 2013; Dyke *et al.* 2009; Benton *et al.* 2011; Andres 2012; Benson *et al.* 2014).  
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46 Whereas pterosaur remains have been found in hundreds of localities, and on all  
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48 continents throughout the Mesozoic (Barrett *et al.* 2008; Upchurch *et al.* 2015), their often-  
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50 fragmentary state means that many specimens do not yield sufficient morphological data to  
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52 determine their taxonomic status. Pterosaur skeletons were adapted for flight and, as such, are  
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54 light, thin-walled and highly fragile; preservation of complete specimens within high-energy  
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56 depositional settings is rare (Wellnhofer 1991). Consequently, our knowledge of pterosaur  
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3 anatomy and species richness is dominated by Lagerstätten (Buffetaut 1995; Butler *et al.*  
4 2009), formations with unusually good fossil preservation (Seilacher 1970), of which several  
5 pterosaur-bearing units are known, including the Late Jurassic Solnhofen Limestone of  
6 Bavaria in Germany (e.g. Wellnhofer 1970, 1975), and the Early Cretaceous Jehol Group of  
7 China (e.g. Wang & Zhou 2006). Approximately a dozen of these formations account for  
8 ~50% of the total known species of pterosaurs (Benton *et al.* 2011). Previous palaeodiversity  
9 studies have shown that these Lagerstätten deposits can have a large influence on observed  
10 diversity for time periods in which they appear (Benson and Butler 2011), potentially  
11 distorting our understanding of patterns of diversity change through time. As such, their  
12 predominance as our main window onto pterosaur evolution might mask true diversity  
13 patterns throughout the Mesozoic: i.e. highly heterogeneous sampling might produce episodic  
14 peaks of observed diversity during periods containing Lagerstätten, whereas time intervals  
15 dominated by fragmentary or less diagnosable material might produce troughs in recorded  
16 diversity which do not necessarily reflect real diversity changes (Wellnhofer *et al.* 1991;  
17 Buffetaut 1995; Butler *et al.* 2009, 2013; Benton *et al.* 2011, 2013; Prentice *et al.* 2011; but  
18 see Dyke *et al.* 2009).

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38 It has become increasingly apparent that biases in our sampling of the fossil record,  
39 resulting from geological, taphonomic and anthropogenic processes, might distort observed  
40 patterns of diversity (e.g. Raup 1976; Alroy *et al.* 2001; Smith 2001; Peters and Foote 2001;  
41 Peters 2005; Smith and McGowan 2005). Ameliorating for such biases is crucial to enable  
42 exploration of diversity through deep time. Sampling proxies, representations of bias  
43 introduced to the fossil record through anthropogenic or geological processes, have become a  
44 common, albeit controversial, method used to ‘correct’ for biased signals recorded in the  
45 geological record. Butler *et al.* (2009) presented a detailed examination of pterosaur species  
46 and genus level diversity through time, and attempted to account for sampling bias by  
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3 comparing diversity with the numbers of geological formations preserving pterosaur remains  
4 (pterosaur-bearing formations: PBFs). A strong correlation was found between temporal  
5 variation in the number of PBFs and diversity over time for both taxonomic and phylogenetic  
6 diversity estimates (TDEs and PDEs respectively). Butler *et al.* (2009) suggested that these  
7 correlations could potentially be explained by one of two hypotheses: that either a significant  
8 portion of the observed diversity curve for pterosaurs is controlled by sampling variation, or  
9 that diversity is accurate, with diversity and sedimentary rock preservation covarying in  
10 response to a third driving factor (e.g. sea level). Butler *et al.* (2009) favoured the sampling  
11 bias hypothesis, but voiced caution with regard to their attempts to ‘correct’ diversity patterns  
12 using PBFs, because this approach did not account for the presence or absence of  
13 Lagerstätten.  
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27 However, the use of formations as a sampling proxy (for both raw numbers of  
28 formations and counting only fossiliferous formations) has been criticized by several authors  
29 (e.g. Crampton *et al.* 2003; Benton *et al.* 2011, 2013; Dunhill *et al.* 2012, 2013, 2014). Benton  
30 *et al.* (2011) argued that: (1) in many cases formation counts will always correlate with fossil  
31 counts, irrespective of the degree of sampling, rendering PBFs redundant with pterosaur  
32 diversity; and (2) absent results (either potential future sites of pterosaur recovery or sites  
33 which failed to produce pterosaurs but still represent a sampling attempt) are ignored: if  
34 sampling in these formations is insufficient, this can create an additional bias (see also  
35 Upchurch *et al.* 2011 for further debate). Butler *et al.* (2013) revisited the analyses of Butler  
36 *et al.* (2009), using new sampling proxies of pterosaur-bearing collections (PBCs), as well as  
37 dinosaur-bearing formations and collections (DBFs and DBCs respectively), the latter two  
38 representing attempts to quantify ‘global’ sampling and utilize sampling metrics independent  
39 of the pterosaur fossil record. DBFs and PBFs were found to correlate with one another at  
40 least within the Cretaceous, suggesting that PBFs at least partially reflect a ‘global’ sampling  
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3 proxy (Butler *et al.* 2013). Butler *et al.* (2013) concluded that whereas ‘true’ pterosaur  
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5 diversity might be impossible to ever fully reconstruct, current formation-based proxies  
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7 enable an incomplete, but informative picture of broad scale patterns of species richness  
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9 throughout the Mesozoic.  
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12 The completeness of the fossil material of a taxonomic group is likely to exert a direct  
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14 influence on the observed species richness of that group through time, and thus represents an  
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16 additional metric that might capture otherwise neglected aspects of sampling bias (Mannion  
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18 and Upchurch 2010a; Brocklehurst *et al.* 2012; Walther and Fröbisch 2013; Brocklehurst and  
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20 Fröbisch 2014; Cleary *et al.* 2015). Time bins with low average completeness values of  
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22 specimens will potentially yield less taxonomically diagnosable specimens. Observed  
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24 diversity could therefore be: (1) reduced, as collected remains cannot confidently be assigned  
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26 to a species; or (2) increased, as a result of assigning partial remains of one taxon to multiple  
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28 species (Mannion and Upchurch 2010a). Alternatively, periods of high completeness levels  
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30 (including times in which Lagerstätten are present) should allow for clear recognition and  
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32 identification of species, resulting in heightened observed diversity.  
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37 Only one previous study has attempted to examine the completeness of the pterosaur  
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39 fossil record. Dyke *et al.* (2009) compiled a dataset of 66 genera, comprising 101 species, to  
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41 calculate completeness over geological stage-level time bins, using three-categories of  
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43 preservation, based on: (1) one bone; (2) more than one bone; and (3) more than one  
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45 individual, each known from more than one bone. Although this approach utilized semi-  
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47 quantitative values, these appear to be assigned as arbitrary metrics; the application of  
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49 alternative preservation categories might have a notable impact on the resultant data,  
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51 irrespective of actual fossil record quality or methodology. The low number of categories  
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53 assigned (three unevenly assigned metrics relating to potential states of completeness) is  
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55 coarse-grained and it is possible that underlying trends and subtle variations in fossil record  
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3 quality might be obscured. In light of these potential weaknesses, as well as the recent spate  
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5 of newly described pterosaur taxa (e.g. Manzig *et al.* 2014; Wang *et al.*, 2014a,b), a re-  
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7 evaluation of the completeness of the pterosaur fossil record is timely.  
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10 Here, an extensive new dataset of pterosaur completeness is presented, utilizing a  
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12 recently devised quantitative metric (Mannion and Upchurch 2010a), and comprising  
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14 completeness values for 172 valid species of pterosaurs. The impact of completeness on our  
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16 reading of the pterosaur fossil record is evaluated via statistical comparisons with various  
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18 sampling proxies and sea level, as well as a ‘corrected’ diversity estimate. Pterosaur  
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20 completeness is also compared to comparable datasets for Mesozoic birds and  
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22 sauropodomorph dinosaurs in order to assess how completeness varies between different body  
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24 plans and sizes through time. In addition, we make comparisons between our results and those  
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26 of Dyke *et al.* (2009), to test for differences between these two approaches to assessing  
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28 completeness. Four main aims form the focus of this study: (1) to determine the potential  
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30 impact of pterosaur completeness on ‘key’ intervals of pterosaur history; (2) to determine  
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32 whether completeness acts as a controlling mechanism on observed pterosaur diversity; (3) to  
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34 assess the impact of Lagerstätten on the pterosaur fossil record through time; and (4) to  
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36 compare the fossil record of small bodied (i.e. pterosaurs and birds) and large-bodied  
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38 (sauropodomorphs) organisms to test for differences in preservational bias.  
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## 45 **MATERIALS AND METHODS**

### 46 *Dataset*

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48 Data on all taxonomically diagnosable species of pterosaurs were compiled from Andres  
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50 (2010), Butler *et al.* (2013), *The Paleobiology Database* (PaleoDB: [www.paleobiodb.org](http://www.paleobiodb.org)),  
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52 and a comprehensive review of the literature. Collated information was thoroughly scrutinized  
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54 for potential synonyms and *nomina dubia*. The finalized dataset contains 135 genera,  
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3 comprising 172 species described between 1812 and 1<sup>st</sup> January 2014, along with  
4 stratigraphic ranges, completeness data, and environment of deposition (see Appendix S1).  
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7 Although this study presents the most complete compilation of pterosaur taxic  
8 diversity to date, only minor changes are noticeable between this and the dataset of Butler *et*  
9 *al.* (2013). As such, our focus is on comparisons between diversity and fossil record quality,  
10 rather than a re-evaluation of aspects of pterosaur diversity, and results relating only to  
11 diversity or residual diversity estimates are not discussed.  
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### 20 *Completeness metrics*

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22 The Character Completeness Metric (CCM) of Mannion and Upchurch (2010a) quantifies the  
23 potential phylogenetic data preserved in specimens; a percentage score is provided for the  
24 number of characters that can be coded for a specimen/taxon for phylogenetic analysis. This  
25 allows for adequate representation of individual skeletal elements that contain considerably  
26 more phylogenetically important information than others. CCM2 (*sensu* Mannion and  
27 Upchurch 2010a), combining the information of all specimens of a taxon to attain overall  
28 completeness, has been deemed more appropriate for comparisons between fossil record  
29 quality and diversity (Brocklehurst *et al.* 2012), and has thus been employed here. It is herein  
30 referred to just as the CCM. The phylogenetic data matrix presented in Butler *et al.* (2012  
31 [based on that of Andres, 2010]) which samples 101 pterosaur species, scored for 183  
32 characters (cranial = 107 characters, 59%; axial = 19 characters, 10%; appendicular = 57  
33 characters, 31%) is utilized using the same methodology as Walther and Fröbisch (2013),  
34 whereby the number of scorable characters was counted (See Supporting Information). The  
35 completeness of the remaining 71 taxa was determined via the literature, using this same  
36 character list. Completeness of sauropodomorphs and Mesozoic birds was extracted from  
37 Mannion and Upchurch (2010a) and Brocklehurst *et al.* (2012).  
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### *Sampling proxies and sea level*

Four time series are utilised as proxies to account for sampling biases within the Mesozoic rock record: PBFs, PBCs, DBFs, and DBCs (see Table 1). Formations represent a prospective site of fossil extraction and, although potentially influenced by external factors (e.g. human naming and collection bias, geographical bias, extent of outcrop, ability to preserve fossils adequate for taxonomic assignment), and despite criticism (Dunhill 2012; Benton *et al.* 2011, 2013), have been argued to provide an appropriate proxy for estimating temporal variation in the amount of rock available for sampling (Peters 2005; Upchurch *et al.* 2011; Butler *et al.* 2013). Collections incorporate all specimens collected from a stratigraphic horizon tied to a single location. DBFs and DBCs are proxies that capture a more global estimate of terrestrial sampling: dinosaurs were abundant and geographically diverse throughout the Mesozoic, living in nearly all terrestrial and coastal environments. The use of formations and collections in which pterosaur fossils could, but have not yet, been recovered, reduces the possibility of ‘redundancy’ with pterosaur diversity estimates (Benton *et al.* 2011; Butler *et al.* 2013). Two further proxies were utilized for appropriate comparisons with sub-divided environmental data series (see below): terrestrial and marine tetrapod-bearing collections (TTBCs and MTBCs, respectively).

All data for PBFs, PBCs, DBFs and DBCs were obtained from Butler *et al.* (2013), originally sourced from PaleoDB downloads, augmented with data from new collections/formations reported since this publication. Numbers of TTBCs and MTBCs were downloaded from the PaleoDB on the 8<sup>th</sup> June 2013. The Mesozoic sea level curve was sourced from data in Butler *et al.* (2011), based on Haq *et al.* (1987) and Miller *et al.* (2005).

### *Time Bins*

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3 Pterosaur fossil record quality was assessed through calculating a mean average value of  
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5 CCM scores and associated standard deviations for each Mesozoic stage-level time bin.  
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7 Stage-level bins were chosen to facilitate comparisons with the diversity and sampling proxy  
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9 data in Butler *et al.* (2013), the sea level data in Butler *et al.* (2011), and the completeness  
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11 data in Dyke *et al.* (2009). This approach resulted in a discrepancy when making comparisons  
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13 to the sub-stage level data for sauropodomorph completeness of Mannion and Upchurch  
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15 (2010a). To enable comparisons between datasets, sauropodomorph data were averaged to  
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17 produce artificial stage level bins, and resulting stages were assessed for any statistically  
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19 significant outlying results. Most bins showed minimal or no change; the average alteration to  
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21 completeness values across all time bins produced by this method is 1.39%. Original and  
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23 averaged values are presented in Appendix S1. Comparisons between pterosaur and bird  
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25 CCM were carried out for stages after the first appearance of birds (Tithonian onwards).  
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27 Species appearing within multiple time bins were considered independently and included in  
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29 the total count for each stage where they are present. All further time series data were  
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31 assigned to stage-level time bins.  
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36 No valid pterosaur taxa are known from the Aalenian (early Middle Jurassic).  
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38 Although this time interval might represent a genuine drop in diversity, pterosaurs clearly did  
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40 not become entirely extinct, and inclusion of this zero-data time bin has the potential to  
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42 artefactually influence the strength and significance of correlative tests. As such, we ran our  
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44 analyses both including and excluding the Aalenian.  
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#### 49 *Subdivisions of pterosaurs*

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51 To examine additional parameters which might influence or record otherwise neglected  
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53 aspects of pterosaur completeness through time, we subdivided our pterosaur dataset  
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3 according to Lagerstätten, environment, and taxonomy, and then calculated additional time  
4 series of completeness and diversity for these subsets (see Appendix S1).  
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10 *Lagerstätten*. To assess the impact of Lagerstätten on both pterosaur completeness and  
11 diversity, we separated species into those that were recovered from Lagerstätten, and those  
12 that came from other formations. Although formations such as the Calcare di Zorzino of Italy  
13 (Dalla Vecchia 2003) could potentially be classified as Lagerstätten, our list remains identical  
14 to that of Butler *et al.* (2013) for ease of comparison, and can be found in Appendix S1.  
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21 *Environments*. Pterosaurs were additionally grouped according to whether they were  
22 deposited and preserved within marine/coastal or terrestrial settings. Marine environments  
23 include lagoonal, coastal and open marine deposits, whereas terrestrial environments included  
24 lacustrine, fluvial, and floodplain deposits (for a full list of environments see Appendix S1;  
25 Environments). For ease, we subsequently refer to pterosaurs as either terrestrial or marine.  
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32 All data were sourced from the Paleodb and the relevant literature.  
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35 *Taxonomic groups*. Pterosaurs were taxonomically divided into Pterodactyloidea and non-  
36 Pterodactyloidea (the paraphyletic assemblage of early-branching pterosaur taxa that have  
37 historically been referred to as ‘rhamphorhynchoids’). The aim of this was to examine events  
38 around the Jurassic/Cretaceous (J/K) boundary, which has been suggested to mark a major  
39 extinction of non-pterodactyloids (e.g. Benson *et al.* 2014), as well as to consider any  
40 potential impact of palaeobiological changes on completeness metrics.  
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#### 49 *Pairwise statistical tests & Residual Diversity Estimates (RDE)*

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51 Jarque-Bera and Shapiro-Wilk tests were implemented to test for normality in all time series.  
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53 As pterosaur CCM scores were shown to not be normally distributed, statistical comparisons  
54 between time series were therefore calculated using non-parametric tests (Spearman’s rank  
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3 correlation coefficient and Kendall's tau rank correlation coefficient). In addition to  
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5 calculating raw taxic diversity, the residuals method of Smith and McGowan (2007) was used  
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7 to produce species diversity curves that are 'corrected' for sampling bias. Using this  
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9 approach, residual diversity estimates (RDEs) were calculated using all sampling proxies.  
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11 Data were detrended, and generalized differencing (McKinney 1990) was applied where  
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13 autocorrelation was detected. These analyses were implemented in Excel and PAST (Hammer  
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15 *et al.* 2001). Abbreviations for common terms used in this paper can be found within Table 1.  
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### 20 21 *Multiple Regression Modelling*

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23 For multivariate statistical approaches, stage duration was included as a non-optional  
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25 predictor in models to account for stage length variation, and Lagerstätten were coded as  
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27 present or absent using a binary variable in an attempt to account for their presence without  
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29 discarding data (see Benson and Butler 2011). Both linear modelling (multiple regression  
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31 models) and generalized least squares (GLS) models were applied to explore the possibility of  
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33 multiple explanatory variables, which can otherwise be missed through pairwise comparisons.  
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35 Multiple regression models allow for the sequential addition and removal of time series to  
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37 seek the model that best explains the chosen metric, with autoregressive terms included to  
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39 correct for serial correlation in time series data (Chatfield 2003). The order of the  
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41 autoregressive term for each model was selected by comparing AICc values at autoregressive  
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43 orders between zero and three.  
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48 GLS models take account of autocorrelation and permit specification of a non-  
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50 standard variance-covariance matrix, allowing non-independence of points within data series  
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52 according to specific models. The first-order autoregressive correlation model was used in  
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54 this case, which seeks autocorrelation at up to one lag in either direction, and minimizes the  
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56 error term (Box *et al.* 1994). Combinations of explanatory variables were compared using  
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3 AICc weights, as small sample sizes potentially reduce the efficiency of AIC for assessing the  
4 quality of model fitting (Burnham and Anderson 2001). R-squared, F-value or *p*-values were  
5 not computed for GLS models as their benefits are currently debated (e.g. Long and Freese  
6 2006). All multivariate analyses were implemented in R version 3.0.2 (R Development Core  
7 Team 2015), using the packages lmer version 0.9-22 (Zeileis and Hothorn 2002), nlme  
8 version 3.1-117 (Pinheiro *et al.* 2009), qPCR version 1.3-9 (Spiess and Ritz 2010), and tseries  
9 version 0.10-32 (Trapletti and Hornik 2009), and data were log<sub>10</sub> transformed prior to  
10 analysis (only stage duration and Lagerstätten presence/absence were not transformed). The  
11 Jarque–Bera test indicated that the residuals from these regression analyses were all normally  
12 distributed.

## 23 24 25 26 27 **RESULTS**

### 28 29 *Pterosaur completeness through time*

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32 Completeness scores and taxic diversity for each stage are plotted against time (Fig. 1). Initial  
33 completeness within the Late Triassic is high (~50%), followed by fluctuations through the  
34 Jurassic. After a Hettangian peak (84%), completeness declines to a Pliensbachian low (13%),  
35 prior to a peak in the Toarcian (62%). The remainder of the Jurassic exhibits varying levels of  
36 completeness, with a trough in the Bathonian (26%), and peaks in the Oxfordian (58%) and  
37 Tithonian (57%). Average completeness is generally lower in the Cretaceous than in  
38 preceding time intervals. Values fall dramatically across the J/K boundary (Berriasian =  
39 15%), before a gradual rise to an Aptian peak (43%), and subsequent decrease in the  
40 Cenomanian (11%). A second Cretaceous peak is reached in the Coniacian–Santonian  
41 (~40%), before a decline in the Campanian (25%) that is continued into the Maastrichtian  
42 (14%).

### *Sampling proxies through time*

PBFs, PBCs, DBFs and DBCs were plotted against time and compared with the pterosaur completeness curve (See Fig. 2A-C). PBF counts are low in the Triassic and Jurassic, averaging eight formations per stage, although a slight increase is observed towards the end of the Jurassic. PBCs exhibit strong, irregular peaks within the Toarcian and Kimmeridgian. Trends in PBCs and PBFs within the Cretaceous show a similar pattern to changes in completeness, mirroring the two broad peaks observed in completeness data; it should however be noted that these peaks appear to lag behind completeness values and, as such, correspond with intervals of lower completeness. This is also observable in the Late Jurassic, where troughs in completeness correlate with apparent peaks in PBF and PBC counts.

Whereas counts differ vastly between the two proxies, DBFs and DBCs exhibit a similar shape, and thus shall be discussed together. There is little clear similarity between pterosaur completeness and DBF/DBC curves throughout the Triassic or Jurassic; whereas completeness scores fluctuate, sampling proxy curves show a trend of gradual increase towards the Cretaceous. DBF/DBC counts seem to follow a similar shape to that of completeness within the Early and middle Cretaceous, although this appears as a one stage 'lag' behind completeness. A large discrepancy is observed in the Campanian and Maastrichtian between high values of DBFs/DBC and steadily declining pterosaur completeness.

### *Correlations between completeness, diversity and sampling*

All formation- and collection-based sampling proxies exhibit strong, positive and statistically significant correlations with species richness over geological time (see Table 2). Pterosaur completeness has a statistically significant positive correlation to both uncorrected diversity and residual diversity (calculated with PBFs, DBFs and DBCs) throughout the Mesozoic (see

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2  
3 Table 3) in all tests. The PBF-based residual diversity estimate produced the strongest  
4 correlation with pterosaur completeness, followed by DBF-based residuals, raw taxic  
5 diversity, and finally DBC-based residuals. Within the Triassic–Jurassic, a statistically  
6 significant, positive correlation is recovered between completeness and PBF-based residuals  
7 for all tests, and with taxic diversity and DBF-based residuals for the Kendall’s tau test.  
8  
9 Completeness shows a strong, positive correlation with raw taxic diversity, PBFs and DBFs in  
10 the Cretaceous, as well as with DBCs when using Spearman’s Rank. PBCs are not shown to  
11 have any statistically significant correlations with completeness.  
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### 23 *Comparisons with completeness of Sauropodomorpha and Aves*

24 Completeness values for sauropodomorph dinosaurs and Mesozoic birds were plotted against  
25 time to facilitate comparisons (see Fig. 3). Whereas both pterosaur and sauropodomorph  
26 completeness show a general decrease throughout the Mesozoic, comparisons between the  
27 two curves reveal little in the way of similarities on a stage to stage basis. The avian  
28 completeness curve bears a striking similarity to that of Pterosauria throughout the Tithonian–  
29 Cretaceous; only one discrepancy exists, when the bird fossil record quality dips compared to  
30 that of pterosaurs in the Albian (6% and 30% average completeness respectively).  
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41 Statistical comparisons between average completeness scores for pterosaurs, birds and  
42 sauropodomorph dinosaurs are shown in Table 4. Pterosaurs exhibit higher average  
43 completeness than avian species within stages where both are present, but lower than  
44 sauropodomorphs. When split between the Triassic–Jurassic and Cretaceous, pterosaurs  
45 display the lowest completeness values within both time intervals (48% and 28%  
46 respectively; it should be noted that the first appearance of birds in the Tithonian does not  
47 allow for comparison of Triassic–Jurassic completeness between pterosaurs and birds).  
48  
49 Pterosaur and avian completeness show a strong, positive and statistically significant  
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3 correlation within the Cretaceous and across all time bins in which they are present for all  
4  
5 statistical tests. Sauropodomorph completeness scores show no significant correlation to those  
6  
7 of pterosaurs across the Mesozoic and for the Cretaceous by itself; however, a statistically  
8  
9 significant positive correlation is found in analyses restricted to the Triassic–Jurassic  
10  
11 component of our sauropodomorph and pterosaur completeness values.  
12  
13

### 14 15 16 *Sensitivity tests*

17  
18 To examine the effect that stages with no data might have on correlation tests,  
19  
20 analyses were also run with the Aalenian excluded (Table 5). For the Mesozoic, the results of  
21  
22 correlation tests were the same as for the complete dataset, apart from with DBC-based  
23  
24 residuals, which did not produce a statistically significant result. When we restricted analyses  
25  
26 to the Triassic–Jurassic, only sauropodomorph completeness shows a statistically significant,  
27  
28 positive correlation with pterosaur completeness values, compared to positive correlations  
29  
30 between pterosaur completeness and taxic diversity, PBF residuals and DBF residuals with  
31  
32 the Aalenian included. Cretaceous comparisons were largely unchanged, with only DBC-  
33  
34 based residuals failing to recover a statistically significant result.  
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### 40 41 *Lagerstätten*

42  
43 Time-binned CCM values for species from Lagerstätten and species from non-Lagerstätten  
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45 deposits were each plotted against time (Fig. 4A). These were compared to overall pterosaur  
46  
47 completeness scores to visualize the occurrence of deposits of exceptional preservation on  
48  
49 temporal variation in the completeness of pterosaur remains (Fig. 4A). The removal of  
50  
51 Lagerstätten deposits decreased average completeness for each stage that they appear within.  
52  
53 The largest decreases appear within the Toarcian (from 62% to 26%) and Santonian (from  
54  
55 40% to 8%), corresponding to the Posidonienschiefer and Niobrara Chalk formations. Further  
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3 reductions are visible in the Oxfordian, Barremian, Aptian and Campanian. A very strong,  
4 highly statistically significant correlation occurs between Lagerstätten-only completeness and  
5 taxic diversity (Fig. 4B) for the Mesozoic (for all tests). This pattern is also observed when  
6 the Triassic–Jurassic and Cretaceous are analysed separately, although the latter is marginally  
7 weaker. No significant correlation is observed between Lagerstätten-excluded completeness  
8 and diversity for the Mesozoic or for the Triassic–Jurassic and Cretaceous.

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16 Two data series were examined to check for the influence of Lagerstätten on pterosaur  
17 completeness through deep time: Lagerstätten-only (Fig. 4C) and Lagerstätten-excluded (Fig.  
18 4D). For many stages, completeness values are zero for the Lagerstätten-only data series, due  
19 to their heterogeneous appearance in the fossil record. However, when Mesozoic  
20 completeness is averaged only from stages containing fossil remains, Lagerstätten-only  
21 deposits show a much higher average completeness (59%). Additionally, differences in  
22 Lagerstätten completeness between periods can be assessed: for Lagerstätten-only, within the  
23 Triassic–Jurassic, an extremely high CCM (71%) is observed. When looking at the  
24 Cretaceous, Lagerstätten-only completeness is much lower (40%). With Lagerstätten  
25 excluded from the completeness scores, no significant correlations between completeness and  
26 other variables were observed for the Mesozoic as a whole, within all tests (Table 6). For the  
27 Triassic–Jurassic, a positive, statistically significant result was recorded when compared to  
28 sauropodomorph completeness scores; no significant correlations were observed for all other  
29 variables in both the Triassic–Jurassic and the Cretaceous.

### 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 *Environmental variation*

51  
52 The completeness of pterosaurs from marine deposits closely follows overall pterosaur  
53 completeness from the Triassic until the Bathonian, at which point much lower completeness  
54 values are observed for marine pterosaurs (Fig. 5A). A sharp increase in marine pterosaur  
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3 completeness occurs from the Callovian, reaching a peak in the Tithonian (63%), which  
4  
5 corresponds with an increase in the taxic diversity of pterosaurs in marine deposits (Fig. 5B-  
6  
7 C). This increase is followed by a decline in completeness across the J/K boundary, into the  
8  
9 Berriasian. Marine and overall pterosaur completeness are similar for the rest of the  
10  
11 Cretaceous, although marine values are generally lower; only within the Santonian and  
12  
13 Campanian are there higher completeness values from marine specimens.  
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16  
17 Terrestrial pterosaur completeness and overall completeness values are not similar for  
18  
19 the Triassic and Early Jurassic, with terrestrial pterosaurs being less complete than the overall  
20  
21 pattern (Fig. 5A). A peak in terrestrial completeness is observed from the Bajocian–  
22  
23 Oxfordian, which matches closely with the overall pterosaur completeness curve; the end of  
24  
25 this peak coincides with an increase in terrestrial taxic diversity. Following a decline within  
26  
27 the Kimmeridgian and Tithonian, completeness values for terrestrial pterosaurs increase until  
28  
29 the Albian. Whereas high terrestrial completeness values are observed in tandem with high  
30  
31 terrestrial taxic diversity for the Barremian and Aptian (Fig. 5D), both the Hauterivian and  
32  
33 Albian exhibit only high completeness, with low taxic diversity. Following a period of no  
34  
35 recorded terrestrial specimens within the Turonian and Coniacian, completeness increases  
36  
37 towards the K/Pg boundary, the opposite of that seen for the total pterosaur completeness  
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39 curve.  
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44 Pterosaurs found within marine deposits are on average slightly more complete (31%)  
45  
46 than those from terrestrial deposits (25%), both as an average across all stages and when only  
47  
48 counting stages with pterosaurs recovered. This pattern is only partially supported when the  
49  
50 Mesozoic is subdivided: marine completeness is much higher than that of the terrestrial realm  
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52 in the Triassic–Jurassic (50% compared to 34%), but slightly lower within the Cretaceous  
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54 (22% compared to 27%).  
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3 Marine completeness is statistically significantly, positively correlated with both  
4 marine taxic diversity and marine TBCs for the Mesozoic in all tests (Table 7). This same  
5 pattern is also observed within the Triassic–Jurassic, in addition to a statistically significant,  
6 positive correlation with sauropodomorph completeness. No significant correlations appear  
7 within the Cretaceous. Terrestrial completeness exhibits a strong, positive, statistically  
8 significant correlation with terrestrial taxic diversity for the Mesozoic in all tests; this is also  
9 observed within the Triassic–Jurassic. Once again, no significant correlation appears within  
10 the Cretaceous with any variable.  
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### 20 21 22 *Taxonomic groups*

23  
24 The average completeness of non-pterodactyloid pterosaurs is much higher than that of  
25 Pterodactyloidea (45% versus 27%). Occurrences of non-Pterodactyloidea and  
26 Pterodactyloidea overlap only in the Late Jurassic (Figure 6); consequently, direct comparison  
27 of completeness values between the two groups is difficult. The first appearance of a possible  
28 pterodactyloid in the Oxfordian (Lü and Fucha, 2010) exhibits low completeness  
29 (*Archaeoistiodactylus linglongtaensis* [4.9%]; however, see Martill and Etches [2013] and  
30 Sullivan *et al.* [2014] regarding the affinities of this taxon). Subsequently, as pterodactyloid  
31 diversity increases within the following stages, their completeness values rise to a peak of  
32 56% in the Tithonian, immediately prior to the J/K boundary. Non-pterodactyloid pterosaurs  
33 exhibit high completeness values throughout the Late Jurassic, although no taxa survive  
34 across the J/K boundary (Unwin 2003; Butler *et al.* 2013; Andres *et al.* 2014).  
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49 Positive and statistically significant correlations exist between pterodactyloid  
50 completeness scores and both pterodactyloid taxic diversity and bird completeness scores  
51 (Table 8). Non-Pterodactyloidea completeness is statistically significantly positively  
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3 correlated with non-Pterodactyloidea taxic diversity (Kendall's Tau test only) and with  
4  
5 sauropodomorph completeness.  
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### 8 9 *Sea Level*

10  
11 There are no clear, shared patterns between pterosaur completeness and sea level changes: sea  
12  
13 level shows an overall rising trend towards the K/Pg boundary, whereas the completeness of  
14  
15 pterosaur specimens fluctuates widely (Figure 7). The correlation between sea level and  
16  
17 pterosaur completeness through time is weak and statistically insignificant for all comparisons  
18  
19 (See Tables 3, 5, 6, 7 & 8). Plots were also generated for groupings of marine and terrestrial  
20  
21 completeness and diversity against sea level (see Appendix S1, All Categories). None of these  
22  
23 showed evidence for correlation.  
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### 28 29 *Multiple Regression Models*

30  
31 Multiple regression model fitting procedures show that a combination of taxic diversity and  
32  
33 PBFs provides the best explanation for pterosaur completeness (Table 9). The relationship  
34  
35 between completeness and diversity is strongly positive, but interestingly the relationship  
36  
37 with formations is negative, suggesting that lower numbers of formations result in higher  
38  
39 average completeness. However, it should be noted that the  $p$ -value for this model is above  
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41 the 0.05 threshold, and thus the null model cannot be rejected.  
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46 Ranked by AICc value, the best fitting GLS model shows that a combination of DBFs  
47  
48 and Lagerstätten presence/absence is the best predictor of pterosaur completeness (Table 10;  
49  
50 for the full model, see Appendix S1: GLS Outputs). Out of the top five models, the time  
51  
52 series that appear are DBFs, PBFs, PBCs and Lagerstätten presence/absence, with the latter  
53  
54 appearing in four out of five. In the top twenty models, Lagerstätten presence/absence and  
55  
56 PBFs are the most commonly observed variables. The bottom five models all contain many  
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3 time series, and no discernable pattern is observed. However, in the bottom twenty models,  
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5 stage length, PBCs and taxic diversity are the most commonly observed data (See Appendix  
6  
7 S1).  
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11 *Diversity:* Additional GLS models were generated to test for the combination of variables  
12  
13 which best explains pterosaur taxic diversity (Table 11; for the full model, see Appendix S1:  
14  
15 GLS Outputs). By AICc value, the top GLS model shows a combination of Lagerstätten  
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17 presence/absence and PBFs as the best explanation for pterosaur diversity, with the former  
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19 also appearing in every one of the top twenty models.  
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## 25 **DISCUSSION**

### 26 *Lagerstätten and comparisons with Dyke et al. (2009)*

27  
28 The strong heterogeneity of the sampling of the pterosaur fossil record likely introduces  
29  
30 extensive sampling bias to observed diversity patterns. How Lagerstätten deposits influence  
31  
32 patterns of completeness or observed diversity through time is poorly understood. A prior  
33  
34 investigation by Dyke *et al.* (2009) concluded that the numbers of pterosaur species were not  
35  
36 skewed towards specific stratigraphic intervals, although completeness of specimens through  
37  
38 time was influenced by Lagerstätten distribution.  
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43 Multiple lines of evidence collected in this study indicate that Lagerstätten have a  
44  
45 strong impact on the fossil record of pterosaurs. Results from the GLS models strongly  
46  
47 support this hypothesis and imply a joint influence on diversity and completeness from  
48  
49 Lagerstätten and formation numbers. No significant correlation is found between  
50  
51 completeness and PBFs, PBCs, DBFs or DBCs; whilst this indicates that there is no  
52  
53 relationship between these proxies and completeness, it does not contradict the existence of a  
54  
55 pervasive Lagerstätten influence. A single Lagerstätte will represent one formation with  
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3 numerous species and high completeness values. This formation might occur in a time  
4  
5 interval in which other PBFs are scarce. The apparent discrepancy between low numbers of  
6  
7 formations occurring at the same time as high apparent diversity and completeness results in  
8  
9 absence of correlation between metrics. The same is true for our results from multiple  
10  
11 regression modelling, specifically the negative relationship recovered between completeness  
12  
13 and PBFs, suggesting fewer sampled formations leads to higher completeness values  
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15 (although these results should be treated with caution due to lack of statistical significance).  
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18  
19 Additionally, when looking at visual evidence of the influence of Lagerstätten, peaks  
20  
21 in both average completeness and taxic diversity seem to correlate closely, or at least be  
22  
23 influenced by the presence or absence of Lagerstätten. This is especially evident when  
24  
25 looking at falls in diversity and completeness across stage boundaries where Lagerstätten are  
26  
27 absent. These lines of evidence suggest that Lagerstätten are a dominating influence on  
28  
29 completeness throughout the pterosaur fossil record, and confirm the hypothesis that  
30  
31 Lagerstätten effects on observed diversity are severe for small and/or delicate organisms  
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33 (Brocklehurst *et al.* 2012).  
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37 Within the last decade, there has been a marked increase in attempts to understand and  
38  
39 address the potential impacts that uneven sampling of the fossil record might have on species  
40  
41 richness through time (e.g. Alroy *et al.* 2001; Peters and Foote 2001; Smith 2001; Smith and  
42  
43 McGowan 2007; Benson *et al.* 2010; Mannion *et al.* 2011). Correlation between residual  
44  
45 diversity estimates and completeness recovered here could indicate that evolutionary factors  
46  
47 related to increased diversity and abundance would have had a direct impact on the  
48  
49 probability of recovering complete specimens. This study recovered a statistically significant  
50  
51 positive correlation between pterosaur completeness and uncorrected raw diversity, as well as  
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53 with residual diversity estimates produced using PBFs, DBFs and DBCs. As PBF-based  
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55 residuals showed the strongest and most statistically significant result, it is possible that  
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3 observed pterosaur completeness might be driven at least in part by genuine variation in  
4 species richness throughout time. Time periods during which pterosaur diversity was high  
5  
6 would likely result in a wider geographical distribution and higher abundance, and as such an  
7  
8 increased probability of high quality specimen preservation. Correlation with uncorrected  
9  
10 diversity indicates an underlying influence from sampling bias within the fossil record;  
11  
12 however, this appears to exert less control than the residual diversity estimate, implying that  
13  
14 'true' diversity (i.e. 'sampling-corrected' diversity) plays a more dominant role on  
15  
16 completeness.  
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21 Multivariate analyses produce partly contrasting results. Diversity did not appear in  
22  
23 the top five models when completeness was the independent variable, and vice versa. This  
24  
25 disparity with the results from pairwise comparisons to residual diversity estimates is likely  
26  
27 due to the fact that residual 'corrected' diversity does not include a correction for the presence  
28  
29 or absence of Lagerstätten; this is further exacerbated by the increased influence of  
30  
31 Lagerstätten-type deposits on small organisms. As such, it appears that diversity and  
32  
33 completeness are unlikely to exert much influence upon one another, and the correlation  
34  
35 recorded in pairwise comparison tests is a secondary effect of either Lagerstätten  
36  
37 presence/absence and/or PBFs driving both in tandem.  
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41  
42 Dyke *et al.* (2009) suggested two substantial areas of bias within the pterosaur fossil  
43  
44 record: high completeness within the Tithonian (latest Jurassic) and fragmentary fossil  
45  
46 material during the middle Cretaceous (Aptian–Cenomanian). Although comparison with the  
47  
48 completeness curve presented here yields remarkably similar Tithonian and middle  
49  
50 Cretaceous peaks and troughs, considerably more variation in fossil record quality is observed  
51  
52 within the current study, with numerous fragmentary remains within the Jurassic  
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54 (Pliensbachian and Callovian) and during the latest Cretaceous (Campanian–Maastrichtian).  
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3 Little further inference on patterns can be made, as significant changes in taxonomy  
4 have made comparison between Dyke *et al* (2009)'s results and ours problematic.  
5 Furthermore, the disparity between the opposing methods of using bone counts and character  
6 counts casts doubt on the few similarities that can be observed. As such, a better comparison  
7 with this study is likely to be produced when using the SCM method of measuring  
8 completeness, where a completeness score is based on the physical quantity and bulk of  
9 elements preserved, gauging an estimate as to how much of a complete skeleton is  
10 represented (see Mannion and Upchurch 2010a). However, despite this disparity between  
11 methods, our results challenge the idea that “the pterosaur fossil record is unbiased by sites of  
12 exceptional preservation (lagerstätte)” (Dyke *et al.* 2009, p890).  
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#### 27 *Potential Impact on Origins, Evolution and Extinctions*

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29 Completeness is high from the Norian to Hettangian (Late Triassic–earliest Jurassic), during  
30 the first appearance and radiation of pterosaurs (Andres 2012; Andres *et al.* 2014), potentially  
31 suggesting that specimen completeness is unlikely to be an important limiting factor in our  
32 understanding of taxonomic diversity at this time. Thus, the apparent rapid acquisition of high  
33 taxonomic diversity might be a genuine feature of the pterosaur fossil record, as implied by  
34 the interpretation of early pterosaur evolution as an adaptive radiation (Andres 2012). Whilst  
35 it could be argued that the Norian merely represents the first time bin with conditions suitable  
36 for pterosaur preservation, the first pterosaurs have all been found in marine formations, often  
37 in black shale lithologies, in Italy, Germany and Austria. Similar formations within the same  
38 geographical region and also preserving vertebrates are present within the Carnian (for  
39 example, the Polzberg Lagerstätte of the Reubgraben shales), yet yield no pterosaurs,  
40 providing a supportive taphonomic control. However, whereas currently recognized Norian  
41 diversity (eight species) approaches the average per stage for the Mesozoic (~9), species  
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3 numbers throughout the Rhaetian–Pliensbachian are low, and fluctuations in completeness  
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5 metrics might be driven by the relative preservation of individual, rarely discovered  
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7 specimens. For example, the apparent peak in completeness during the Hettangian results  
8  
9 from the discovery of a single species (*Dimorphodon macronyx* from the Lower Lias of  
10  
11 England) within a marine formation that is well known for exceptionally preserved vertebrate  
12  
13 specimens (Benton and Spencer 1995). The scarcity of pterosaur specimens from the  
14  
15 Rhaetian–Pliensbachian, and the low completeness values of Sinemurian and Pliensbachian  
16  
17 pterosaur species, makes it difficult to make inferences as to the impact of the  
18  
19 Triassic/Jurassic mass extinction event on pterosaur evolution (see also Butler *et al.* 2013).  
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25 The J/K boundary has previously been noted as a period of potential extinction and  
26  
27 faunal turnover for both marine and terrestrial groups (e.g. Raup & Sepkoski 1984; Upchurch  
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29 *et al.* 2011; Benson and Druckenmiller 2014), including pterosaurs (e.g. Butler *et al.* 2009;  
30  
31 Benson *et al.* 2014). Although the precise timing of their extinction is currently unknown,  
32  
33 unambiguously dated remains of non-pterodactyloids are not observed after the J/K, and there  
34  
35 is also an apparent decline in Pterodactyloidea species richness in the earliest Cretaceous.  
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37 However, the impact of fluctuations in completeness levels through this interval has not  
38  
39 previously been discussed in detail. There is a dramatic decline from 57% to 15% within  
40  
41 average completeness, as well as a decline within Pterodactyloidea completeness from 54% to  
42  
43 15%, between the Tithonian and Berriasian. When split into preservational environments,  
44  
45 pterosaurs appear to show varying completeness trends over the same interval: a decline is  
46  
47 evident for marine completeness and diversity (with completeness falling from 63% to 11%),  
48  
49 whereas terrestrial deposits show a slight increase in diversity and completeness (with  
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51 completeness rising from 10% to 20%). One potential cause of this drop in completeness  
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53 could be the lack of Lagerstätten reported in the Berriasian, in comparison to the Tithonian.  
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3 However, the same pattern of reduced completeness within the Berriasian is also observed  
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5 when Lagerstätten are removed (showing a drop from 40% to 15%). Two explanations are  
6  
7 possible: (1) the apparent low diversity of the earliest Cretaceous might be an artefact of a  
8  
9 decreased preservation potential and the absence of Lagerstätten, perhaps resulting from  
10  
11 global palaeoenvironmental change; or (2) the scrappy material by which currently known  
12  
13 earliest Cretaceous pterosaurs are diagnosed could reflect a genuine scarcity of pterosaurs  
14  
15 following a J/K extinction event. At present, these explanations cannot be readily  
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17 distinguished and might not be mutually exclusive; however, given the results discussed  
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19 above, it is likely that the first provides the more probable explanation.  
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23 A post-Albian reduction in pterosaur diversity has been equated with either a middle  
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25 Cretaceous extinction event, or a long-term Late Cretaceous decline (Unwin 2005; Butler *et*  
26  
27 *al.* 2009, 2013; Benson *et al.* 2014). A sudden decline in taxic diversity is observed during the  
28  
29 Cenomanian, accompanied by troughs in completeness in the Cenomanian and Turonian.  
30  
31 When split into environments, it is evident that the majority of this decline in completeness  
32  
33 can be attributed to declines in the completeness of terrestrial pterosaurs. Lagerstätten  
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35 deposits are also absent from this interval. Smith (2001) and Benson *et al.* (2013) have argued  
36  
37 that a reduction in available fossiliferous rocks masks true diversity at this time. Although  
38  
39 both a reduction in diversity and the loss of small-bodied pterosaurs clearly does occur  
40  
41 through this time interval, low completeness values might make this decline appear more  
42  
43 rapid and severe than was actually the case.  
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47 The record of pterosaurs during the Late Cretaceous has received particular interest  
48  
49 due to the concurrent radiation of birds, with claims of a correlated Late Cretaceous decline  
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51 within pterosaur diversity (Unwin 1987, 2005; Slack *et al.* 2006, Benson *et al.* 2014). A  
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53 steady decline in pterosaur completeness is recovered from the Santonian onwards; taxic  
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55 diversity first increases, then decreases through this interval. When split into environmental  
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3 groupings, marine completeness is observed to dramatically drop during this time interval,  
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5 whereas marine taxic diversity remains relatively level; terrestrial completeness increases  
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7 towards the Maastrichtian, whereas corresponding terrestrial diversity shows a peak followed  
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9 by a trough. However, a single species (*Quetzalcoatlus northropi*) produces an anomalously  
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11 high value for pterosaur completeness within the Maastrichtian; when removed, completeness  
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13 within the stage drops from 14% to 5%. Overall, these results indicate the poor quality of the  
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15 fossil record used for assessing pterosaur diversity within the Maastrichtian, especially within  
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17 the marine realm, and, as such, we urge caution when attempting to compare pterosaur taxic  
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19 diversity in this stage with that of other vertebrate groups. In general, the importance of  
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21 addressing environmental differences in taphonomy should be stressed when discussing the  
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23 dynamics of extinction events within groups of low species and specimen counts.  
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### 29 *Comparative Completeness*

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31 A statistically significant, strong positive correlation was recovered when comparing  
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33 pterosaur and avian completeness within stage bins throughout the Mesozoic, but not with  
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35 sauropodomorphs. This result is in agreement with the hypothesis proposed by Brocklehurst  
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37 *et al.* (2012), whereby completeness is driven by differing taphonomical mechanisms between  
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39 large, robust organisms and smaller fragile animals. Radically different body plans result in  
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41 different methods of preservation and thus different completeness values. Both birds and  
42  
43 pterosaurs exhibit similar flight-adapted bodies, with thin-walled and fragile bones; as such,  
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45 similar modes of preservation within low energy depositional environments are common.  
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47 Both are often found as part and counter-part split blocks in Lagerstätten deposits, yielding  
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49 exceptionally preserved specimens; for example, Chinese Lagerstätten deposits, such as those  
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51 in the Jehol Group, are famous for containing exquisitely preserved bird and pterosaur  
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53 specimens (Wang *et al.* 2005; Wang & Zhou 2006). The control of Lagerstätten on the  
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3 completeness of these groups can be clearly observed in the single discrepancy between bird  
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5 and pterosaur completeness during the Albian, where birds are found to exhibit a much lower  
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7 completeness. This can be explained by the Crato Formation, which acts as a pterosaur  
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9 Lagerstätten, but for which bird specimens are only just starting to be discovered (Carvalho *et*  
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11 *al.*, 2015). As such, similar fossil record quality between pterosaur and avian species is to be  
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13 expected.  
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16 In contrast, the large, robust bones of sauropodomorphs are likely to be preserved  
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18 under different taphonomic settings. Despite the overall lack of correlation throughout the  
19  
20 Mesozoic, and the expectation of a taphonomic difference between pterosaurs and  
21  
22 sauropodomorphs, a positive correlation is present between pterosaur and sauropodomorph  
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24 completeness for the Triassic–Jurassic. Similar results are apparent when sauropodomorph  
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26 completeness is compared against non-Pterodactyloidea completeness, and the completeness  
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28 of pterosaurs found in marine environments from those stages (and remain when the Aalenian  
29  
30 is excluded). A potential cause for this surprising result might relate to environmental  
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32 preferences. It has previously been suggested that sauropods displayed differing habitat  
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34 preferences between non-titanosaurs and titanosaurs, with the former dominating during the  
35  
36 Jurassic and the latter during the Cretaceous (Butler and Barrett 2008; Mannion and Upchurch  
37  
38 2010b). Although both were fully terrestrial groups, non-titanosaurs seem to have spent a  
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40 greater amount of time in coastal environments than titanosaurs, which were more restricted  
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42 to inland settings. Pterosaurs have also been inferred to have inhabited increasingly terrestrial  
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44 environments through time (Butler *et al.* 2013); this appears to coincide with an increase in  
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46 diversity and disparity towards the end of the Jurassic (Prentice *et al.* 2011; Butler *et al.* 2012;  
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48 Foth *et al.* 2012) and the emergence of Pterodactyloidea (Andres *et al.* 2014). These results,  
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50 in combination with an observed increase in terrestrial completeness values across the J/K  
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52 boundary, suggest the possibility of an environmental-taphonomic shift, whereby  
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3 sauropodomorphs and pterosaurs often frequented coastal environments during the Triassic  
4 and Jurassic, before showing increased terrestrialisation in the Cretaceous. This shared  
5 environment preference during the Triassic and Jurassic potentially led to similar patterns of  
6 fossil completeness. Coastal areas will likely preserve fossils within a narrow range of  
7 conditions, such as lagoonal or estuarine depositional environments. Similar preservation  
8 mechanisms will therefore be recorded for both groups during this time, resulting in the  
9 observed statistically significant correlation. Increased exploration of a wider range of  
10 habitats may have occurred within both sauropods and pterosaurs in the Early Cretaceous.  
11 Terrestrial environments naturally exhibit a wider range of depositional settings  
12 (Behrensmeyer *et al.* 1992), many of which would be unsuitable for pterosaur preservation,  
13 but adequate for sauropodomorphs. As such, this might account for the divergence in  
14 correlation during the Cretaceous.  
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20 Several counterpoints are presented to this environmental shift hypothesis. Firstly, the  
21 observed pattern is not supported as statistically significant in all comparisons, and visual  
22 representations of the data show little in the way of correlation between the two data series  
23 throughout the Triassic–Jurassic. The general lack of co-occurrences of pterosaurs and  
24 sauropodomorphs in a single locality (see the PaleoDB) also suggests that the two groups  
25 were not tightly linked ecologically. Additionally, pterosaur diversity and completeness  
26 curves for both marine and terrestrial environments (Fig. 5A-D) exhibit little evidence for an  
27 increase within terrestrial diversity at the J/K boundary, whereas an increase in marine taxic  
28 diversity is observed within the Albian. However, divergence between marine completeness  
29 and taxic diversity during this stage is potentially due to taxonomic inflation caused by the  
30 Cambridge Greensand Formation, consisting of highly fragmentary remains (Unwin 2001).  
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32 Furthermore, the potential exists for discovering additional pterosaur-yielding terrestrial  
33 Lagerstätten within the Triassic and Jurassic, which currently remain unknown. Another point  
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3 to consider is the comparison between the nature of the characters used in calculation of the  
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5 CCM scores for the two groups. The phylogenetic matrix used to calculate the CCM scores of  
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7 pterosaurs is heavily biased towards cranial characters (making up 59% of the total  
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9 characters), whereas the sauropodomorph characters are assigned more evenly across the  
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11 skeleton (Mannion and Upchurch 2010a). As 56 species of pterosaur are known solely from  
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13 cranial material, with 13 of these appearing in the Triassic–Jurassic and 43 in the Cretaceous  
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15 (making up 22% and 39% of the pterosaurs found in those time bins respectively), this could  
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17 confound relationships between these groups. These factors make the testing of this  
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19 hypothesis difficult, and increased collection of both sauropodomorphs and pterosaurs for the  
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21 Jurassic–Cretaceous will be needed to fully explore this issue.  
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## 27 CONCLUSIONS

- 29 1. Completeness values for 172 species of pterosaur were generated using a Character  
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31 Completeness Metric (CCM), and tested for correlations with ‘raw’ and ‘corrected’  
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33 diversity, a variety of sampling proxies, and completeness of other vertebrate groups,  
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35 to address several critical questions relating to the fossil record of pterosaurs.  
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- 38 2. The earliest fossil record of pterosaurs is shown to be characterized by relatively high  
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40 levels of completeness, and thus data quality is high; however, taxon counts from the  
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42 Rhaetian–Bajocian (latest Triassic–early Middle Jurassic) are generally low. A decline  
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44 in completeness values is recovered across the J/K boundary, with low completeness  
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46 also characterizing the middle Cretaceous, meaning that apparent extinctions at these  
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48 times might at least partly reflect sampling artefacts. A taxic decline throughout the  
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50 Late Cretaceous is observed; however, the Maastrichtian exhibits extremely low  
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52 completeness, and thus taxic diversity is potentially unreliable.  
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3 3. CCM values of pterosaurs and birds exhibit a strong positive correlation throughout  
4 the Mesozoic, in contrast to sauropodomorph dinosaurs, supporting claims of  
5 taphonomic mode differences between large and small organisms affecting  
6 completeness. However, there is a correlation between pterosaur and sauropodomorph  
7 CCM when only the Triassic–Jurassic is examined. The absence of such a pattern in  
8 the Cretaceous might reflect a move within both groups to increased terrestrial  
9 habitation after the J/K boundary.  
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- 18 4. The fossil record of pterosaurs is strongly and pervasively affected by Lagerstätten  
19 deposits and heterogeneous sampling, which consequently drives both observed  
20 pterosaur taxic diversity and completeness through time.  
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36 publication number XXX.  
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### 49 **SUPPORTING INFORMATION**

50 Data for this study are available in the [Dryad Digital Repository]:

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52 <http://dx.doi.org/10.5061/dryad.td570>  
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### Tables and Figure Captions:

**Table 1:** All abbreviated terms discussed in the paper.

PBF	Pterosaur-Bearing Formations
PBC	Pterosaur-Bearing Collections
DBF	Dinosaur-Bearing Formations
DBC	Dinosaur-Bearing Collections
SCM	Skeletal Completeness Metric
CCM	Character Completeness Metric
RDE	Residual Diversity Estimate
TTBC	Terrestrial Tetrapod-Bearing Collections
MTBC	Marine Tetrapod-Bearing Collections

**Table 2:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between taxic diversity of pterosaurs and various sampling proxies.

Taxic Div vs:	Spearman's rs	Kendall's tau
PBFs	0.51231 (p=0.00884)	0.34 (p=0.0172)
PBCs	0.56 (p=0.00360)	0.38 (p=0.00776)
DBFs	0.42154 (p=0.0358)	0.3 (p=0.0356)
DBC's	0.43846 (p=0.0283)	0.31333 (p=0.0281)

**Table 3:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between mean CCM values of pterosaurs and various sampling proxies, for the Mesozoic, the Triassic/Jurassic, and the Cretaceous.

CCM vs:	MESOZOIC		TRIASSIC/JURASSIC		CRETACEOUS	
	Spearman's rs	Kendall's tau	Spearman's rs	Kendall's tau	Spearman's rs	Kendall's tau
<i>Taxic Diversity</i>	<b>0.53 (p=0.00643)</b>	<b>0.413 (p=0.00378)</b>	0.456 (p=0.117)	<b>0.410 (p=0.0509)</b>	<b>0.650 (p=0.0220)</b>	<b>0.515 (p=0.0197)</b>
<i>PBFs</i>	-0.00538 (p=0.980)	-0.00667 (p=0.963)	-0.0110 (p=0.972)	-0.0256 (p=0.903)	0.0490 (p=0.880)	0.0606 (p=0.784)
<i>PBCs</i>	0.213 (p=0.306)	0.18 (p=0.207)	0.280 (p=0.354)	0.256 (p=0.222)	0.168 (p=0.602)	0.182 (p=0.411)
<i>DBFs</i>	0.287 (p=0.164)	0.207 (p=0.148)	0.467 (p=0.108)	0.333 (p=0.113)	0.238 (p=0.457)	0.182 (p=0.411)
<i>DBC's</i>	0.282 (p=0.173)	0.233 (p=0.102)	0.412 (p=0.162)	0.359 (p=0.0876)	0.273 (p=0.391)	0.182 (p=0.411)
<i>PBF Residuals</i>	<b>0.604 (p=0.0013924)</b>	<b>0.453 (p=0.0014918)</b>	-0.0110 (p=0.972)	-0.0256 (p=0.903)	<b>0.727 (p=0.00736)</b>	<b>0.576 (p=0.00917)</b>
<i>PBC Residuals</i>	0.211 (p=0.312)	0.127 (p=0.375)	0.280 (p=0.354)	0.256 (p=0.222)	0.238 (p=0.457)	0.091 (p=0.681)
<i>DBF Residuals</i>	<b>0.539 (p=0.00541)</b>	<b>0.427 (p=0.00279)</b>	0.467 (p=0.108)	0.333 (p=0.113)	<b>0.720 (p=0.00824)</b>	<b>0.515 (p=0.0197)</b>
<i>DBC Residuals</i>	<b>0.469 (p=0.018)</b>	<b>0.327 (p=0.0221)</b>	0.412 (p=0.162)	0.359 (p=0.0876)	<b>0.615 (p=0.0332)</b>	0.394 (p=0.0746)
<i>Sea Level</i>	0.0269 (p=0.898)	0.0333 (p=0.815)	0.00549 (p=0.986)	-0.0256 (p=0.903)	-0.182 (p=0.572)	-0.0606 (p=0.784)

Results in bold highlight statistical significance at  $p=0.05$

**Table 4:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between mean CCM values of pterosaurs, birds and sauropodomorphs, for the Mesozoic, Triassic/Jurassic, and the Cretaceous.

CCM vs:	MESOZOIC		TRIASSIC/JURASSIC		CRETACEOUS	
	Spearman's rs	Kendall's tau	Spearman's rs	Kendall's tau	Spearman's rs	Kendall's tau
<i>Sauropod CCM</i>	0.148 (p=0.479)	0.133 (p=0.350)	<b>0.670 (p=0.0122)</b>	<b>0.513 (p=0.0147)</b>	-0.510 (p=0.0899)	-0.212 (p=0.337)
<i>Aves CCM</i>	<b>0.758 (p=0.00267)</b>	<b>0.641 (p=0.00229)</b>	N/A	N/A	<b>0.804 (p=0.00161)</b>	<b>0.727 (p=0.000997)</b>

Results in bold highlight statistical significance at  $p=0.05$



**Table 5:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between mean CCM values of pterosaurs and various independent variables when the Aalenian is removed for the Mesozoic, Triassic/Jurassic, and the Cretaceous

AALENIAN REMOVED	MESOZOIC		TRIASSIC/JURASSIC		CRETACEOUS	
CCM vs:	Spearman's $r_s$	Kendall's $\tau_{\text{au}}$	Spearman's $r_s$	Kendall's $\tau_{\text{au}}$	Spearman's $r_s$	Kendall's $\tau_{\text{au}}$
<i>Taxic Diversity</i>	<b>0.412 (p=0.0453)</b>	<b>0.304 (p=0.0372)</b>	0.322 (p=0.308)	0.303 (p=0.170)	<b>0.587 (p=0.0446)</b>	0.424 (p=0.0549)
<i>PBFs</i>	-0.183 (p=0.393)	-0.116 (p=0.427)	-0.224 (p=0.484)	-0.182 (p=0.411)	-0.0559 (p=0.863)	-0.0303 (p=0.891)
<i>PBCs</i>	0.142 (p=0.50883)	0.130 (p=0.372)	0.133 (p=0.680)	0.121 (p=0.583)	0.14 (p=0.665)	0.152 (p=0.493)
<i>DBFs</i>	0.163 (p=0.448)	0.130 (p=0.372)	0.252 (p=0.43)	0.152 (p=0.493)	0.175 (p=0.587)	0.212 (p=0.337)
<i>DBC</i> s	0.133 (p=0.535)	0.123 (p=0.399)	0.28 (0.379)	0.273 (p=0.217)	0.161 (p=0.618)	0.121 (p=0.583)
<i>Sauropod CCM</i>	0.027 (p=0.901)	0.029 (p=0.843)	<b>0.657 (p=0.0202)</b>	<b>0.455 (p=0.0397)</b>	-0.476 (p=0.118)	-0.212 (p=0.337)
<i>Aves CCM</i>	<b>0.841 (p=0.000319)</b>	<b>0.667 (p=0.00151)</b>	N/A	N/A	<b>0.839 (p=0.000643)</b>	<b>0.697 (p=0.00161)</b>
<i>Sea Level</i>	0.0548 (p=0.799)	0.0362 (p=0.804)	0.126 (p=0.697)	0.0909 (0.681)	-0.23077 (p=0.47053)	-0.152 (p=0.493)
<i>PBF Residuals</i>	<b>0.461 (p=0.0234)</b>	<b>0.333 (p=0.0225)</b>	0.54)	0.273 (p=0.217)	<b>0.73427 (p=0.0065435)</b>	<b>0.515 (p=0.197)</b>
<i>PBC Residuals</i>	0.183 (p=0.393)	0.159 (p=0.275)	0.147 (p=0.649)	0.152 (p=0.493)	0.18881 (p=0.55674)	0.152 (p=0.493)
<i>DBF Residuals</i>	<b>0.422 (p=0.0401)</b>	<b>0.319 (p=0.0291)</b>	0.364 (p=0.225)	0.333 (p=0.131)	<b>0.580 (p=0.0479)</b>	<b>0.394 (p=0.0746)</b>
<i>DBC Residuals</i>	0.335 (p=0.11)	0.232 (p=0.1124)	0.203 (p=0.527)	0.182 (p=0.411)	0.392 (p=0.208)	0.242 (p=0.273)

Results in bold highlight statistical significance at  $p=0.05$

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**Table 6:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between CCM values of pterosaurs and various proxies within Lagerstätten only and Lagerstätten removed subgroups for the Mesozoic, Triassic/Jurassic, and the Cretaceous.

CCM vs:	MESOZOIC			
	LAGERSTÄTTEN ONLY		LAGERSTÄTTEN REMOVED	
	<i>Spearman's rs</i>	<i>Kendall's tau</i>	<i>Spearman's rs</i>	<i>Kendall's tau</i>
<i>Taxic Diversity</i>	<b>0.738 (p=0.0000258)</b>	<b>0.547 (p=0.000128)</b>	0.328 (p=0.109)	0.253 (p=0.0759)
<i>Lagerstätten presence/absence Tax. Div.</i>	<b>0.936 (p=0.0000000000633)</b>	<b>0.84 (p=0.0000000397)</b>	0.219 (p=0.292)	0.16 (p=0.262)
<i>Sauropod CCM</i>	-0.00308 (p=0.988)	-0.0133 (p=0.926)	0.182 (p=0.383)	0.147 (p=0.304)
<i>Aves CCM</i>	<b>0.615 (p=0.0252)</b>	<b>0.385 (p=0.0672)</b>	0.418 (p=0.156)	0.385 (p=0.0672))
<i>Sea Level</i>	0.236 (p=0.256)	0.18 (p=0.207)	-0.0654 (p=0.756)	-0.02 (p=0.744)

Results in bold highlight statistical significance at  $p=0.05$

CCM vs:	TRIASSIC/JURASSIC			
	LAGERSTÄTTEN ONLY		LAGERSTÄTTEN REMOVED	
	<i>Spearman's rs</i>	<i>Kendall's tau</i>	<i>Spearman's rs</i>	<i>Kendall's tau</i>
<i>Taxic Diversity</i>	<b>0.615 (p=0.0252)</b>	<b>0.385 (p=0.0672)</b>	0.302 (p=0.316)	0.231 (p=0.272)
<i>Lagerstätten presence/absence Tax. Div.</i>	<b>0.967 (p=0.0000000706)</b>	<b>0.897 (p=0.0000195)</b>	0.275 (p=0.364)	0.179 (p=0.393)
<i>Sauropod CCM</i>	0.445 (p=0.128)	0.333 (p=0.113)	0.489 (p=0.0899)	0.387 (p=0.0672)
<i>Aves CCM</i>	N/A	N/A	N/A	N/A
<i>Sea Level</i>	0.214 (p=0.482)	0.103 (p=0.626)	-0.0824 (p=0.789)	-0.103 (p=0.626)

Results in bold highlight statistical significance at  $p=0.05$

CCM vs:	CRETACEOUS			
	LAGERSTÄTTEN ONLY		LAGERSTÄTTEN REMOVED	
	<i>Spearman's rs</i>	<i>Kendall's tau</i>	<i>Spearman's rs</i>	<i>Kendall's tau</i>
<i>Taxic Diversity</i>	<b>0.755 (p=0.00451)</b>	<b>0.636 (p=0.00398)</b>	0.294 (p=0.354)	0.212 (p=0.337)
<i>Lagerstätten presence/absence Tax. Div.</i>	<b>0.944 (p=0.00000393)</b>	<b>0.848 (p=0.000123)</b>	0.105 (p=0.746)	0.0909 (p=0.681)
<i>Sauropod CCM</i>	-0.538 (p=0.0709)	-0.394 (p=0.0746)	-0.035 (p=0.914)	0.0303 (p=0.891)
<i>Aves CCM</i>	<b>0.622 (p=0.0307)</b>	<b>0.424 (p=0.0549)</b>	0.378 (p=0.226)	0.364 (p=0.0998)
<i>Sea Level</i>	0.119 (p=0.713)	0.121 (p=0.583)	-0.189 (p=0.557)	-0.121 (0.583)

Results in bold highlight statistical significance at  $p=0.05$

**Table 7:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between CCM values of pterosaurs and various proxies within marine and terrestrial subgroups for the Mesozoic, Triassic/Jurassic, and the Cretaceous.

	MESOZOIC		TRIASSIC/JURASSIC		CRETACEOUS							
	TERRESTRIAL	MARINE	TERRESTRIAL	MARINE	TERRESTRIAL	MARINE						
CCM vs:	Spearman's $r_s$	Kendall's $\tau_{au}$	Spearman's $r_s$	Kendall's $\tau_{au}$	Spearman's $r_s$	Kendall's $\tau_{au}$						
Taxic Diversity Env.	<b>0.587</b> ( <b>p=0.00204</b> )	<b>0.407</b> ( <b>p=0.00438</b> )	0.247 (p=0.234)	0.12 (p=0.4)	<b>0.555</b> ( <b>p=0.049</b> )	<b>0.385</b> ( <b>p=0.0672</b> )	0.269 (p=0.374)	0.154 (p=0.464)	0.531 (p=0.0754)	0.394 (p=0.0746)	0.028 (p=0.931)	0.0303 (p=0.891)
Taxic Diversity	<b>0.585</b> ( <b>p=0.00215</b> )	<b>0.44</b> ( <b>p=0.00205</b> )	<b>0.686</b> ( <b>p=0.00153</b> )	<b>0.527</b> ( <b>p=0.00224</b> )	<b>0.714</b> ( <b>p=0.00609</b> )	<b>0.538</b> ( <b>p=0.0104</b> )	<b>0.615</b> ( <b>p=0.0252</b> )	<b>0.513</b> ( <b>p=0.0147</b> )	0.413 (p=0.183)	0.364 (p=0.0998)	0.028 (p=0.931)	0.0303 (p=0.891)
Taxic Diversity TBCs	-0.0454 (p=0.829)	-0.0333 (p=0.815)	<b>0.536</b> ( <b>p=0.00573</b> )	<b>0.373</b> ( <b>p=0.0089</b> )	-0.209 (p=0.494)	-0.231 (p=0.272)	<b>0.626</b> ( <b>p=0.022</b> )	<b>0.462</b> ( <b>p=0.0281</b> )	0.413 (p=0.183)	0.303 (p=0.170)	0.294 (p=0.354)	0.212 (p=0.337)
Taxic Diversity Sauripod	-0.00615 (p=0.977)	-0.00667 (p=0.963)	0.283 (p=0.170)	0.187 (p=0.191)	-0.011 (p=0.972)	-0.0769 (p=0.714)	<b>0.571</b> ( <b>p=0.0413</b> )	<b>0.410</b> ( <b>p=0.0509</b> )	-0.266 (p=0.404)	-0.152 (p=0.493)	-0.21 (p=0.513)	-
Taxic Diversity CCM	0.209 (p=0.494)	0.154 (p=0.464)	0.473 (p=0.103)	0.308 (p=0.143)	N/A	N/A	N/A	N/A	0.238 (p=0.457)	0.182 (p=0.411)	0.476 (p=0.118)	0.333 (p=0.131)
Taxic Diversity Aves	0.162 (p=0.438)	0.107 (p=0.455)	-0.115 (p=0.583)	-0.113 (p=0.427)	0.368 (p=0.216)	0.256 (p=0.222)	-0.346 (p=0.247)	-0.333 (p=0.113)	-0.112 (p=0.729)	-0.0606 (p=0.784)	-0.042 (p=0.897)	-0.0909 (p=0.681)
Taxic Diversity Sea Level												

Results in bold highlight statistical significance at  $p=0.05$

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**Table 8:** Spearman's Rank and Kendall's Tau correlation coefficients and uncorrected probability values ( $p$ ) of statistical comparisons between CCM values of pterosaurs and various proxies within Pterodactyloidea and non-Pterodactyloidea subgroups.

CCM vs:	MESOZOIC			
	PTERODACTYLOIDEA		NON PTERODACTYLOIDEA	
	Spearman's $r_s$	Kendall's $\tau$	Spearman's $r_s$	Kendall's $\tau$
<i>Taxic Diversity</i>	0.389 (p=0.152)	0.352 (p=0.0671)	0.522 (p=0.0673)	<b>0.462 (p=0.00281)</b>
<i>Group Diversity</i>	<b>0.729 (p=0.00207)</b>	<b>0.6 (p=0.00182)</b>	0.121 (p=0.694)	0.128 (p=0.542)
<i>Sauropod CCM</i>	-0.482 (p=0.0688)	-0.314 (p=0.102)	<b>0.714 (p=0.00609)</b>	<b>0.564 (p=0.00727)</b>
<i>Aves CCM</i>	<b>0.758 (p=0.00267)</b>	<b>0.564 (p=0.00727)</b>	N/A	N/A
<i>Sea Level</i>	-0.114 (p=0.685)	-0.0476 (p=0.805)	0.0714 (p=0.817)	0.0256 (p=0.903)

Results in bold highlight statistical significance at  $p=0.05$

**Table 9:** Multiple regression results showing sampling proxy effects on pterosaur completeness.

	Full					Best			
	<i>Dependent</i>	<i>Independents</i>	$R^2$	$p$	$AIC$	<i>Independents</i>	$R^2$	$p$	$AIC$
CCM		Lagerstätten Presence/absence + PBFs + PBCs + DBFs + DBCs + Diversity + Stage Length	0.22	0.58	10.5	PBFs + Diversity	0.17	0.14	4.11

Details of full and best model selection process can be found in Supporting Information.

**Table 10:** Statistical comparison of the top twenty possible explanatory models for completeness of pterosaurs through the Mesozoic.

<i>Model</i>	<i>Parameters</i>	<i>df</i>	<i>Weighting</i>	<i>AICc</i>	<i>AIC</i>	<i>BIC</i>	<i>logLik</i>
112	DfL	5	0.11070917	-2.172124414	-3.372124414	2.518144738	6.686062207
119	LPf	5	0.079832147	-1.518163596	-2.718163596	3.172105555	6.359081798
99	LPcPf	6	0.068188103	-1.202851277	-3.308114435	3.760208547	7.654057217
120	PcPf	5	0.054518999	-0.755409579	-1.955409579	3.934859573	5.977704789
94	DfLPf	6	0.050394272	-0.598066097	-2.703329255	4.364993727	7.351664627
81	DcDfL	6	0.049432517	-0.559527974	-2.664791132	4.40353185	7.332395566
90	DfSL	6	0.02663663	0.677114286	-1.428148872	5.64017411	6.714074436
71	DDfL	6	0.026328567	0.700379821	-1.404883337	5.663439645	6.702441669
93	DfLPc	6	0.026161243	0.71313088	-1.392132278	5.676190704	6.696066139
79	DPcPf	6	0.0250594	0.799190877	-1.306072281	5.762250702	6.65303614
54	DcDfLPf	7	0.02335848	0.939768771	-2.393564563	5.85281225	8.196782281
63	DfLPcPf	7	0.023135291	0.958970553	-2.37436278	5.872014032	8.18718139
97	SLPf	6	0.022332941	1.0295634	-1.075699758	5.992623225	6.537849879
78	DLPf	6	0.022278074	1.034483014	-1.070780144	5.997542839	6.535390072
88	DcLPf	6	0.019942075	1.256025272	-0.849237886	6.219085096	6.424618943
98	SPcPf	6	0.019289483	1.32256884	-0.782694318	6.285628665	6.391347159
64	SLPcPf	7	0.017452414	1.522732971	-1.810600362	6.43577645	7.905300181
105	DPf	5	0.015889977	1.710311852	0.510311852	6.400581004	4.744844074
49	DLPcPf	7	0.014044312	1.957253944	-1.376079389	6.870297424	7.688039694
59	DcLPcPf	7	0.013834353	1.987379236	-1.345954097	6.900422715	7.672977049

Models comprise different combinations of diversity, dinosaur and pterosaur bearing collections and formations, stage length and Lagerstätten presence/absence that potentially explain the character completeness metric. Models are ranked in order of explanatory power according to the Akaike's second-order corrected information criterion (AICc), where a smaller value equals a superior fit. The full table can be found with Supporting Information.

Abbreviations of parameters: **D**, diversity. **Df**, Dinosaur Bearing Formations. **Dc**, Dinosaur Bearing Collections. **S**, Stage Length. **L**, Lagerstätten presence/absence. **Pf**, Pterosaur Bearing Formations. **Pc**, Pterosaur Bearing Collections.

**Table 11:** Statistical comparison of the top twenty possible explanatory models for diversity of pterosaurs through the Mesozoic.

<i>Model</i>	<i>Parameters</i>	<i>df</i>	<i>Weights</i>	<i>AICc</i>	<i>AIC</i>	<i>BIC</i>	<i>logLik</i>
119	LPf	5	0.161913896	4.054284125	2.854284125	8.744553276	3.572857938
97	SLPf	6	0.100306361	5.011955262	2.906692104	9.975015086	4.546653948
118	LPc	5	0.088667634	5.258623631	4.058623631	9.948892783	2.970688184
99	LPcPf	6	0.072214036	5.669144623	3.563881465	10.63220445	4.218059267
96	SLPc	6	0.051663081	6.338926642	4.233663484	11.30198647	3.883168258
78	CLPf	6	0.044769643	6.625352899	4.520089741	11.58841272	3.739955129
94	DfLPf	6	0.041389992	6.782335268	4.677072111	11.74539509	3.661463945
88	DcLPf	6	0.037942491	6.956270247	4.851007089	11.91933007	3.574496455
93	DfLPc	6	0.034870645	7.125122796	5.019859638	12.08818262	3.490070181
64	SLPcPf	7	0.033949556	7.178661915	3.845328581	12.09170539	5.077335709
87	DcLPc	6	0.024699875	7.81481714	5.709553982	12.77787696	3.145223009
77	CLPc	6	0.024044448	7.868605272	5.763342114	12.8316651	3.118328943
47	CSLPf	7	0.021915304	8.054043071	4.720709737	12.96708655	4.639645131
61	DfSLPf	7	0.020836498	8.155001204	4.82166787	13.06804468	4.589166065
57	DcSLPf	7	0.020757362	8.162611565	4.829278232	13.07565504	4.585360884
60	DfSLPc	7	0.016659272	8.602479664	5.269146331	13.51552314	4.365426834
49	CLPcPf	7	0.015331366	8.76861193	5.435278597	13.68165541	4.282360701
63	DfLPcPf	7	0.015171737	8.789544867	5.456211534	13.70258835	4.271894233
59	DcLPcPf	7	0.014771424	8.843024555	5.509691222	13.75606803	4.245154389
46	CSLPc	7	0.012575983	9.164835738	5.831502405	14.07787922	4.084248798

Models comprise different combinations of completeness, dinosaur and pterosaur bearing collections and formations, stage length and Lagerstätten presence/absence that potentially explain pterosaur diversity. Models are ranked in order of explanatory power according to the Akaike's second-order corrected information criterion (AICc), where a smaller value equals a superior fit. The full table can be found with Supporting Information. Abbreviations of parameters: **C**, Completeness. **Df**, Dinosaur Bearing Formations. **Dc**, Dinosaur Bearing Collections. **S**, Stage Length. **L**, Lagerstätten presence/absence. **Pf**, Pterosaur Bearing Formations. **Pc**, Pterosaur Bearing Collections.

**Figure 1:**

Completeness and taxic diversity of pterosaurs throughout the Mesozoic. Light blue areas surrounding Character Completeness Metric represent one standard deviation around the mean.

**Figure 2:**

Sampling proxies plotted throughout the Mesozoic. **A**, Pterosaur completeness, Pterosaur Bearing Formations and Pterosaur Bearing Collections. **B**, Pterosaur completeness and Dinosaur Bearing Formations. **C**, Pterosaur completeness and Dinosaur Bearing Collections.

**Figure 3:**

Pterosaur, bird and sauropodomorph completeness plotted throughout the Mesozoic. Bird completeness is not available prior to the Tithonian.

**Figure 4:**

Plots of Lagerstätten groupings plotted throughout the Mesozoic. **A**, Overall pterosaur completeness compared with subgrouping of Lagerstätten only and Lagerstätten removed completeness. **B**, Overall pterosaur diversity compared with subgrouping of Lagerstätten only and Lagerstätten removed diversity. **C**, Lagerstätten only completeness and diversity. **D**, Lagerstätten removed completeness and diversity.

**Figure 5:**

Plots of pterosaurs found within marine and terrestrial environments for all stages of the Mesozoic. **A**, Overall pterosaur completeness compared with subgrouping of marine and terrestrial completeness. **B**, Overall pterosaur diversity compared with subgrouping of marine

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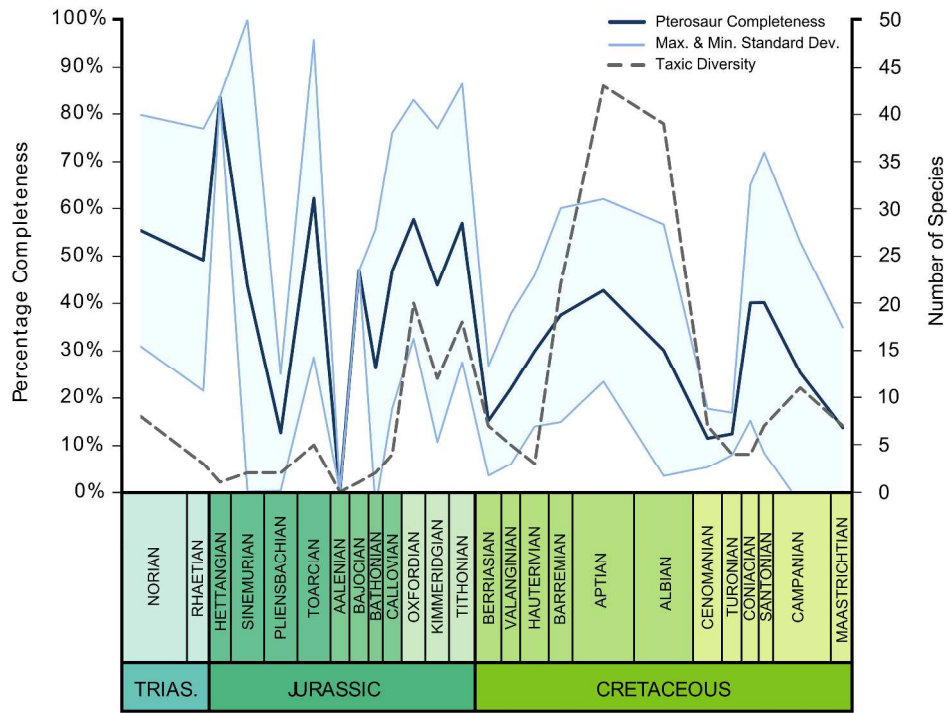
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10 **Figure 6:**

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14 Pterodactyloidea throughout the Mesozoic.  
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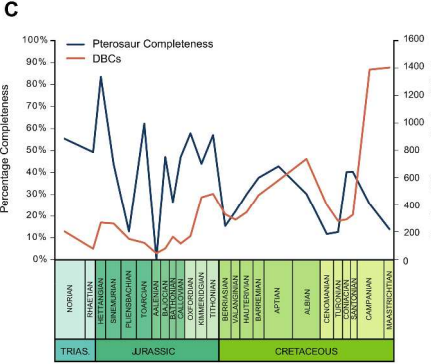
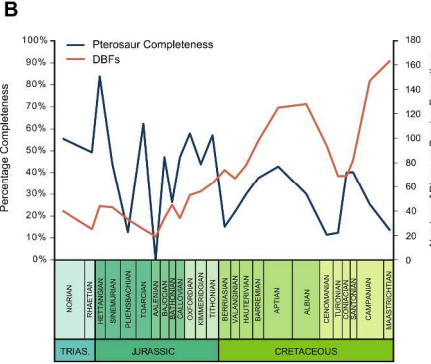
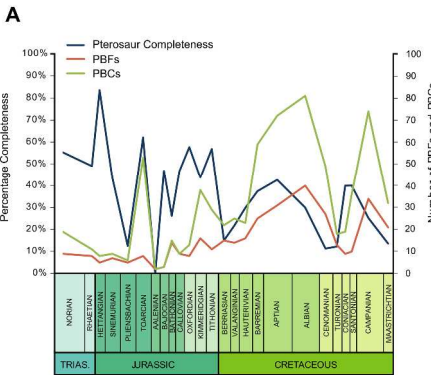
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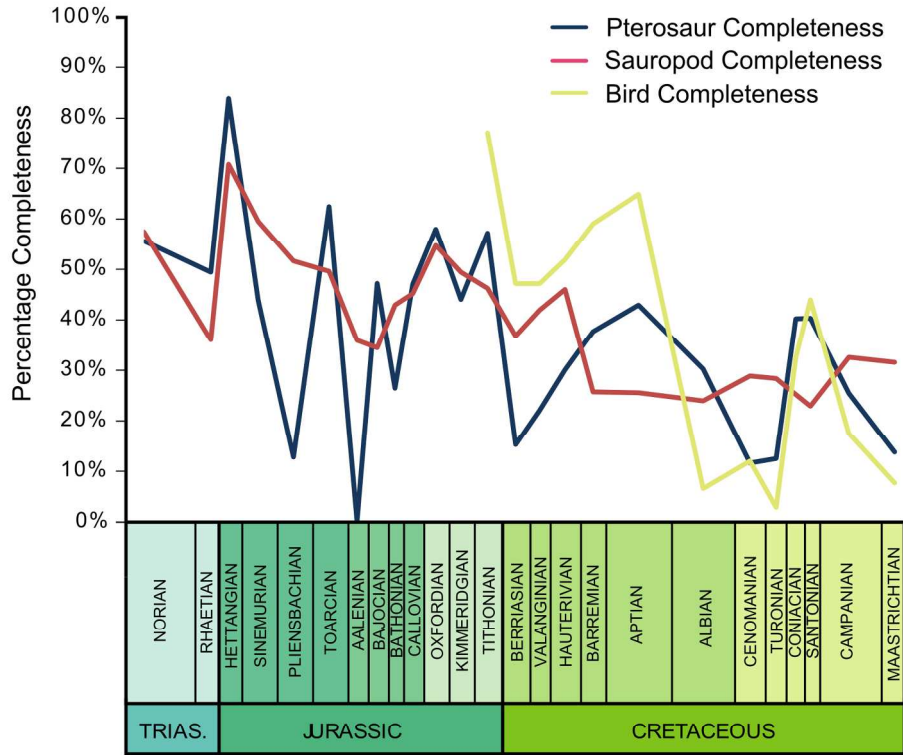
Completeness and taxic diversity of pterosaurs throughout the Mesozoic. Light blue areas surrounding Character Completeness Metric represent one standard deviation around the mean.

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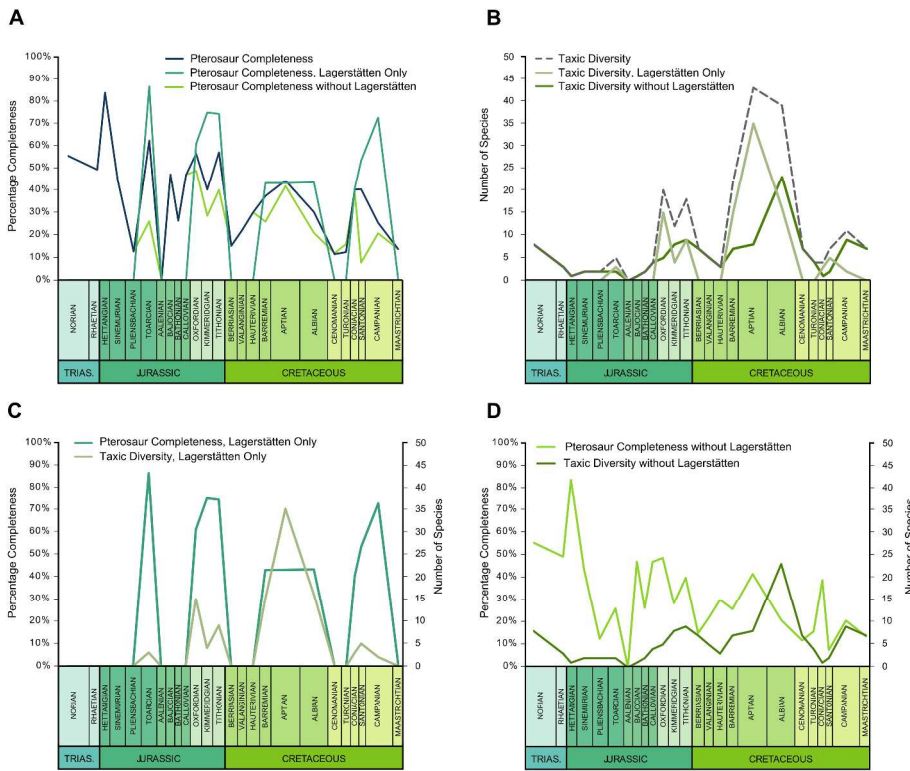


Sampling proxies plotted throughout the Mesozoic. A, Pterosaur completeness, Pterosaur Bearing Formations and Pterosaur Bearing Collections. B, Pterosaur completeness and Dinosaur Bearing Formations. C, Pterosaur completeness and Dinosaur Bearing Collections.

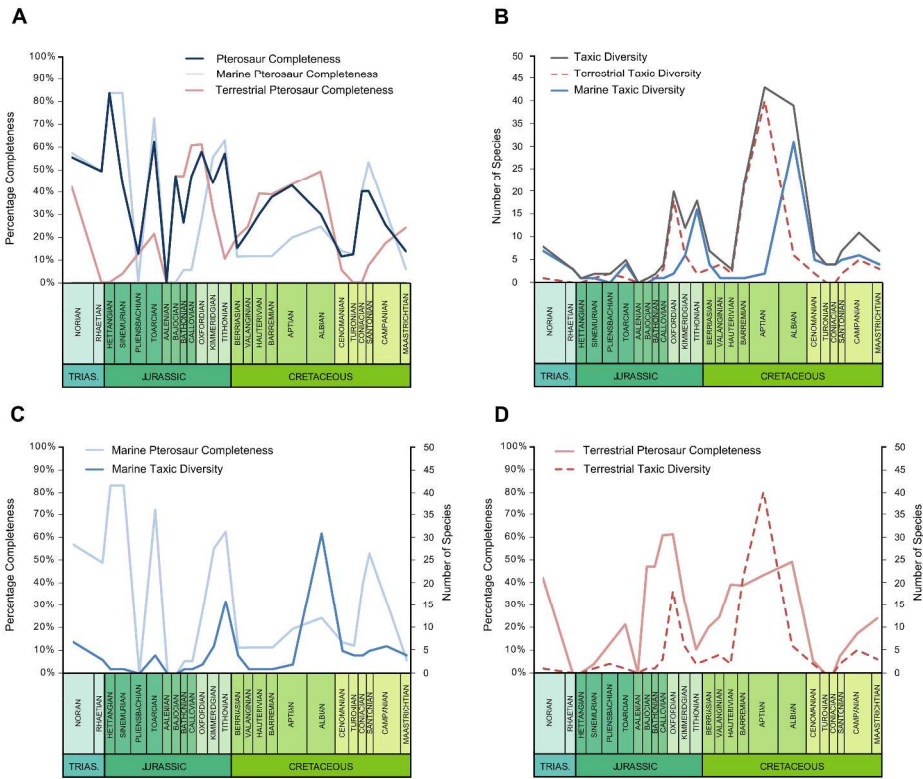
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Pterosaur, bird and sauropodomorph completeness plotted throughout the Mesozoic. Bird completeness is not available prior to the Tithonian.

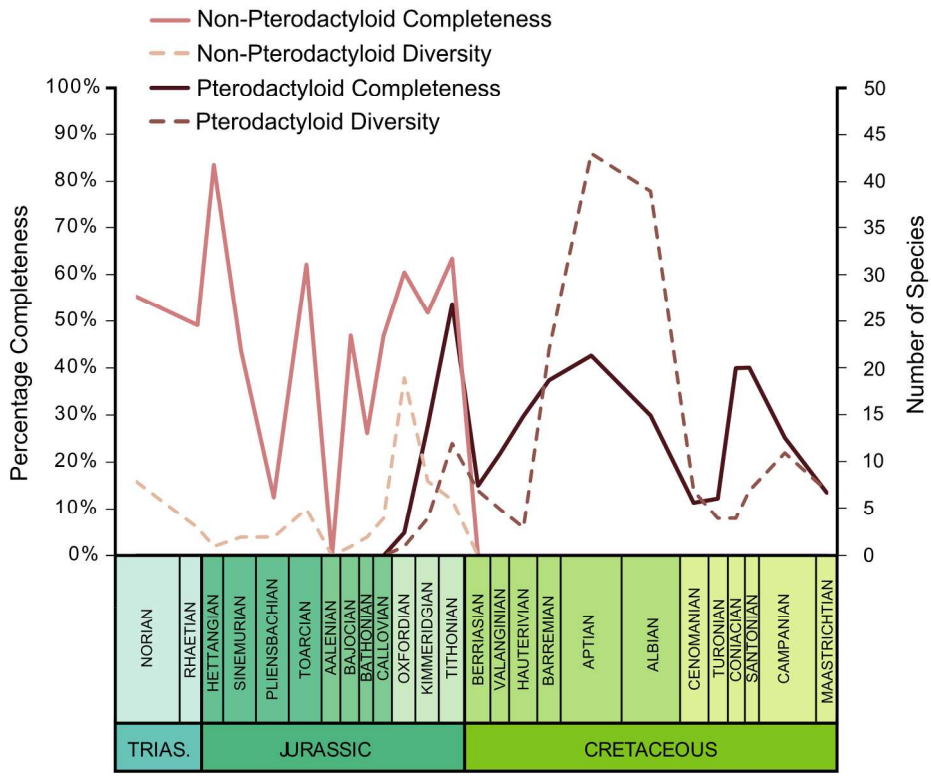


Plots of Lagerstätten groupings plotted throughout the Mesozoic. A, Overall pterosaur completeness compared with subgrouping of Lagerstätten only and Lagerstätten removed completeness. B, Overall pterosaur diversity compared with subgrouping of Lagerstätten only and Lagerstätten removed diversity. C, Lagerstätten only completeness and diversity. D, Lagerstätten removed completeness and diversity.

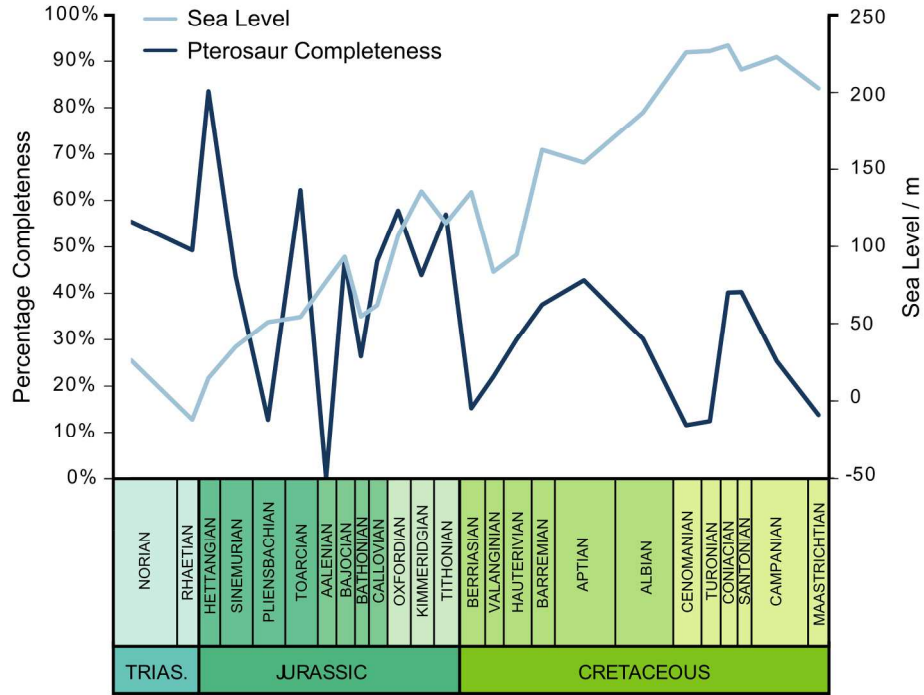


Plots of pterosaurs found within marine and terrestrial environments for all stages of the Mesozoic. A, Overall pterosaur completeness compared with subgrouping of marine and terrestrial completeness. B, Overall pterosaur diversity compared with subgrouping of marine and terrestrial diversity. C, Marine completeness and diversity. D, Terrestrial completeness and diversity.

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Plots showing completeness and diversity in subgrouping of Pterodactyloidea and non-Pterodactyloidea throughout the Mesozoic.



Comparison between global sea level (Butler et al. 2013, after Haq et al. 1987) and pterosaur completeness for the Mesozoic.