

Spatial dimension of body size evolution in Pterosauria: Bergmann's rule does not drive Cope's rule

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ABSTRACT

Background: Little is known about the existence or validity of ecogeographical rules – spatial patterns in biological traits – over geological time scales and in extinct clades. Some have claimed that pterosaurs, a Mesozoic clade of flying reptiles, follow Cope's rule – the trend of increasing body size through time – yet no conclusive explanations for this rule have been provided and some explanations even converge with those about Bergmann's rule: the tendency of species to be larger in colder environments.

Goals: Determine whether Bergmann's rule exists in pterosaur reptiles over their evolutionary history, and discuss its potential association with Cope's rule.

Data: Previously published morphological, phylogenetic, and geographic occurrence data of Pterosauria.

Search methods: We applied cross-species and assemblage-based approaches along with phylogenetic comparative methods as well as sister-pair comparisons to evaluate the validity of Bergmann's rule in Pterosauria.

Conclusions: Pterosaurian body size did not follow Bergmann's rule during the Triassic-Jurassic. But a converse Bergmann's rule may have been present during the Cretaceous. There is no strong evidence to support an influence of Bergmann's rule in the evolution of pterosaurian body size. Therefore, Cope's rule in Pterosauria seems to be a mechanistically independent macroevolutionary pattern.

Keywords: body size, ecogeographical patterns, palaeomacroecology, wingspan.

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INTRODUCTION

Some of the most notable and intriguing, yet still unexplained biological patterns include the variation of different biodiversity aspects along geographical gradients (Lomolino *et al.*, 2006). Besides the increase in species richness from the poles to the equator, probably ‘Ecology’s oldest pattern’ (Hawkins, 2001), geographic patterns in species’ morphologies and related traits have also been widely studied to understand ecological and evolutionary processes driving biodiversity patterns (Gaston *et al.*, 2008). These so-called ecogeographical patterns describe general trends depicting the covariation between species’ traits and their position (or environmental conditions) across space (Gaston *et al.*, 2008), with some being even regarded as ‘rules’. The most widely known of such rules is Bergmann’s rule (Bergmann, 1847; Millien *et al.*, 2006), which states that within, and among, closely related endothermic vertebrate species, those living at higher latitudes, where climates are colder, are generally larger than those that live at lower latitudes in warmer environments (Olalla-Tárraga *et al.*, 2010). The negative relationship between body size and temperature, as originally described by Carl Bergmann, assumes an adaptive mechanism of heat conservation, whereby larger animals with reduced surface-to-volume ratios conserve heat better than smaller animals (Olalla-Tárraga *et al.*, 2010). Following this reasoning, climatic changes are expected to cause body size shifts across clades and their resulting spatial patterns, thus influencing body size evolution (Hunt and Roy, 2006; Gardner *et al.*, 2011).

Body size is important for almost every aspect of species’ biology (Calder, 1984; Peters, 1986), thus understanding its evolution can also help to assess the processes underlying biodiversity patterns (Benson *et al.*, 2014; Souza and Santucci, 2014). On a deep-time perspective, the tendency of clades to show an increase in body size is known as Cope’s rule (Benton, 2002). Despite its long history (Cope, 1887), the generality and mechanisms behind Cope’s rule are still a matter of debate (Alroy, 1998; Raia and Fortelius, 2014). As with other large-scale evolutionary trends, such debate revolves around two contrasting explanations: one involving passive mechanisms related to diversification and the other to active processes driven by selection (McShea, 1994). Underlying the ‘active trend’ explanation of body size evolution is the assumption that larger body sizes provide selective advantages (Hone and Benton, 2005). The benefits of being large are thought to be of particular importance during periods of climatic change, especially towards cooler environments (Lovegrove and Mowoe, 2013). Conversely, and following the same reasoning, body size evolution under climatic changes towards warmer environments would result in patterns opposite to Cope’s rule, with an overall decrease in body size (Teplitsky and Millien, 2014). Either way, the argument of climatic changes driving body size evolution conflates both Cope’s and Bergmann’s rule under the same explanation and processes across time and space (Hunt and Roy, 2006; Carotenuto *et al.*, 2015).

Despite conflation between Bergmann’s rule and Cope’s rule in explaining body size evolution, studies tackling both rules simultaneously are surprisingly lacking from the neontological and palaeontological literature (for notable recent exceptions, see Hunt and Roy, 2006; Lovegrove and Mowoe, 2013; Carotenuto *et al.*, 2015). The reasons for this shortfall may be due to the intrinsic difficulty of distinguishing between the two rules when they predict the same pattern [i.e. body size increases under climate cooling (Smith *et al.*, 2010; Carotenuto *et al.*, 2015)]. Still, probably the most important reason has been the neglect of one of the two dimensions, space or time, of body size evolution. On the one hand, the vast majority of studies investigating Cope’s rule deal with palaeontological data (Moen, 2006) and ignore the spatial dimension, thus failing to assess spatial patterns in body size (Hunt and Roy, 2006). Overlooking

the spatial dimension in palaeontological studies is common, mainly owing to the geographically fragmented nature of fossil data, regardless of the potential of spatially explicit information to provide a better understanding of evolutionary processes (Jablonski, 2009). On the other hand, studies of Bergmann's rule are often conducted over contemporary or short time scales without regard to the broader evolutionary scenario (Morales-Castilla *et al.*, 2012; Clauss *et al.*, 2013; but see Millien *et al.*, 2006 for a few examples of large-scale temporal studies). Owing to the potential interrelationships of Bergmann's rule and Cope's rule (Raia *et al.*, 2012), studies should consider both spatial and temporal dimensions to clarify their joint or separate influences in body size evolution.

Our understanding of pterosaurs' body size evolution represents a good example of focusing solely on the temporal dimension while ignoring the spatial context. Indeed, biogeographical patterns of Pterosauria have received little attention (Upchurch *et al.*, 2014) and thus the spatial fabric of pterosaur evolutionary patterns is poorly documented. Pterosaurs were the first vertebrates to evolve powered flight and represented a taxonomically and ecologically diverse group of Mesozoic reptiles (Butler *et al.*, 2013). Pterosaurs are a classic example of Cope's rule owing to their distinct pattern of body size evolution throughout their long evolutionary history, ~150 million years (Myr) (Hone and Benton, 2007; Benson *et al.*, 2014). Recently, Benson *et al.* (2014) undertook a thorough evaluation of the validity of Cope's rule for pterosaurs, finding strong support for it and hypothesizing a role for intrinsic (e.g. niche differentiation and diversification) and extrinsic factors (e.g. competition with birds). These authors found two disparate phases of body size evolution in pterosaurs: one highly constrained evolution around relatively small body sizes during the Triassic and Jurassic, through the first 70 million years of their history, followed by a shift towards a consistent increase in body size for the rest of their history (~80 Myr) from the Early Cretaceous until their extinction at the Cretaceous–Palaeogene boundary (Benson *et al.*, 2014). Such a shift occurred around the Late Jurassic and Early Cretaceous (~150–130 Ma), when Pangaea was breaking up causing changes in global climate that established a latitudinal climatic pattern (Xu *et al.*, 2012).

Here, we test if such climatic changes around the Late Jurassic–Early Cretaceous transition can be associated with the shift in pterosaur body size evolution. In essence, we add the spatial dimension to study body size evolution in pterosaurs by evaluating the validity of Bergmann's rule through the two critical time periods of their evolution: Triassic/Jurassic and Cretaceous (Benson *et al.*, 2014). In doing so, we aim to identify the contribution of Bergmann's rule (size increase with latitude) to the establishment of Cope's rule in Pterosauria. More specifically, we predict an absence of Bergmann's rule (no difference in body size between high- and low-latitude species) in the Triassic/Jurassic when global climate was relatively hotter and showed no clear latitudinal gradient in temperature and pterosaur body size evolution was constrained. Conversely, we predict the presence of Bergmann's rule in the Cretaceous period when global climate became more seasonal and a latitudinal gradient in temperature was present and pterosaur body size evolved towards larger sizes. We conduct macroecological analyses to evaluate the extent to which Bergmann's rule applies to pterosaur reptiles. Accordingly, we apply cross-species, assemblage-based, and pairwise approaches while considering the phylogenetic relationship among species to assess the potential evolutionary and ecological mechanisms driving the distribution of pterosaur body sizes in a spatially explicit context. Our findings show no strong support for Bergmann's rule across all methods. Instead, we found some weak evidence for a converse Bergmann's rule (size decrease with latitude), especially under the

assemblage-based approach. We discuss the potential causes for this converse Bergmannian pattern, its independence from Cope's rule in Pterosauria, and the advantage of different macroecological methods to study ecogeographical patterns in deep-time.

MATERIALS AND METHODS

Morphological data

We obtained data of pterosaur total wingspan as well as information on the phylogenetic relationships among pterosaur species from the dataset provided by Benson *et al.* (2014), available at the DRYAD repository (doi: 10.5061/dryad.n0310). Estimates of pterosaur body mass are difficult to obtain from incomplete remains and highly variable depending on the estimation method (Witton and Naish, 2008; Prentice *et al.*, 2011). Therefore, pterosaur wingspan has been commonly used as a proxy for pterosaur body size/mass, assuming a positive correlation between wingspan and body mass, 'as the amount of lift generated by the wings must be sufficient to maintain flight' (Hone and Benton, 2007).

This dataset contains strict and less strict measurements and estimates of wingspan for 122 nominal pterosaur species, some obtained by direct calculation and others from missing data estimation based on phylogenetic regressions between forelimb elements (for details, see Benson *et al.*, 2014). For instance, to estimate missing values for the length of phalanx 4 of digit IV (IV-4; the 'wing' finger), a phylogenetic regression of observed phalanx IV-4 lengths on phalanx IV-3 lengths was performed and then used to predict the length of those missing values of phalanx IV-4 length (Benson *et al.*, 2014). Other forelimb elements used by Benson *et al.* (2014) for estimating wingspans were, in order of importance, phalanges IV-1, IV-2, II-4, I-4, and then other skeleton elements such as humerus and mandible lengths.

Phylogenetic information

Benson *et al.* (2014) also provide a strict consensus cladogram including 109 species based on the study of Andres and Myers (2013). This cladogram represents more than 70% (130–150) of currently recognized pterosaur species (Butler *et al.*, 2013). To assign ages to the species in the tree and their corresponding branch lengths, we followed the same procedure as Benson *et al.* (2014) (code available at the DRYAD repository, doi: 10.5061/dryad.n0310). First, tip ages were obtained from a uniform distribution between possible minimum and maximum ages of each species (also available in Benson and colleagues' dataset). This procedure generates a set of randomly time-scaled phylogenies based on the random assignment of first and last appearance dates within each interval to each species (Bapst, 2012). Then, these ages were used to create minimum node ages. Such time-scaled phylogenies can produce 'apparent' polytomies (zero-length branches) when a more derived species nested within a clade appears earlier in the fossil record than other species in the same clade. Forcing such zero-length branches to be some minimum length, thus pushing nodes back in time, can be used to extend them and assign a minimum branch length or MBL (Laurin, 2004). Benson *et al.* (2014) applied this procedure with two minimum lengths, 2 Ma and 1 Ma, and an additional 'equal' method based on adjusting zero-length branches by re-apportioning the time on early branches equally along later branches (Bapst, 2012). Each of these methods (MBL-2Ma, MBL-1Ma, and 'equal') was used to generate 25 phylogenies, but the use of these different phylogenies did not affect the macroevolutionary results (Benson *et al.*, 2014). However, instead

of using only one time-scaling method, we decided to work with the same three methods to consider this uncertainty in our analyses (i.e. using 75 phylogenies, 25 for each method). We followed Benson and colleagues' (2014) original R code, applying functions from the *paleotree* R package v.1.8.2 (Bapst, 2012).

Geographic occurrences

We gathered information on pterosaur fossil occurrences from the Paleobiology Database (PBDB; <http://paleobiodb.org>). The PBDB compiles palaeontological taxonomic and distributional data covering all parts of the fossil record (organisms of all geological ages) from the primary literature and institutional databases (<http://paleobiodb.org>). More specifically, the Pterosauria dataset is based mainly on data published by Barrett *et al.* (2008) and updated by Butler *et al.* (2013). We queried the PBDB for pterosaur occurrences in the Triassic, Jurassic, and Cretaceous periods by using the *pbdb_occurrences* function from the *paleobioDB* R package (Varela *et al.*, 2015). These queries returned a data frame with all the pterosaur occurrences for each time period available in the PBDB, including the site-specific palaeocoordinates for each record. We matched the species names from these queries ('matched_name' column) with those of Benson and colleagues' (2014) data and also checked for congruence with their cladogram. Finally, we selected those species that had wingspan and palaeocoordinates data and were present in the cladogram. Our final dataset comprised 86 species, with 35 species from the Triassic/Jurassic periods and 51 species from the Cretaceous.

Bergmann's rule assessment

Spatial patterns in biological traits – ecogeographical patterns – can be studied using three different approaches: intraspecific, interspecific, and assemblage-based (Gaston *et al.*, 2008). The original formulation of Bergmann's rule implied latitudinal variation in body size among closely related species, clearly an interspecific perspective. However, confusion derived from misinterpretations of Bergmann's original definition has led to a historic debate about the rule's applicability (intra- vs. inter-specifically) and the conflation of pattern and mechanism (Blackburn *et al.*, 1999; Olalla-Tárraga *et al.*, 2010). While there is a clear distinction between intra- and inter-specific approaches, the latter approach can be confused with the assemblage-based approach (Gaston *et al.*, 2008; Olalla-Tárraga *et al.*, 2010). Under the interspecific or cross-species approach, each species is treated as an observation identified by its body size value and a single spatial value (e.g. latitudinal midpoint or mean temperature of this point or across its range). Then, the covariation between body size and latitude/temperature is depicted using bivariate plots and evaluated with regression analysis (Olalla-Tárraga *et al.*, 2010). In contrast, the assemblage-based approach focuses on analysing patterns within grids overlying the study region, in which the species assemblages present in each grid-cell become the observational units thus describing the complete geographic information. In this approach, the covariation of body size and latitude is evaluated with correlations between a summary statistic for body size within assemblages (e.g. mean or median values of species within grid-cells) and the latitudinal position or environmental value of grid-cells (Olalla-Tárraga *et al.*, 2010). Importantly, both methods provide non-independent data. In the cross-species approach, species are not phylogenetically independent and thus require phylogenetic comparative methods to avoid inflated type I

error rates (Felsenstein, 1985). In the assemblage-based approach, the proximity of grid-cells can generate spatial autocorrelation that would also inflate type I error rates, thus requiring the use of spatial regression methods to avoid such problems (Beale *et al.*, 2010). This approach can also suffer from phylogenetic autocorrelation, which can now be tackled by means of phylogenetic comparative methods (Diniz-Filho *et al.*, 2007).

To comprehensively evaluate the validity of Bergmann's rule in Pterosauria, we conducted both cross-species and assemblage-based approaches at each of the two time periods of interest (Triassic/Jurassic and Cretaceous), applying phylogenetic comparative methods for both approaches. In addition, we applied pairwise comparisons between sister species (Carotenuto *et al.*, 2015).

Cross-species approach

Based on the geographic occurrences of each pterosaur species at each time period, we calculated the species' latitudinal midpoints (absolute value) and regressed these against their \log_{10} wingspan values. Definitions of species' latitudinal midpoints were dependent on the number of occurrences of each species. For species with more than four occurrences, we computed their central positions representing the actual locality that minimizes the mean distance to the other localities (Carotenuto *et al.*, 2015). For species with fewer than four but more than one occurrence, we computed the latitude halfway among all localities (i.e. mid-latitude). Finally, for species with only one occurrence, we used the locality's original palaeocoordinate. Since most species had only one occurrence, certainly an artefact of fossil sampling that underestimates species distributions, we conducted a sensitivity analysis. We generated a distribution of midpoints (100) for each species (those with one occurrence) over a latitudinal span of 10° (~1100 km) around its recorded latitude. Further analyses were done across such distributions of midpoints. We used the *aspace* (Bui *et al.*, 2012) and *letsR* (Vilela and Villalobos, 2015) R packages to obtain species midpoints. Latitudinal midpoints of pterosaur species within each time period were mapped using the GPlates software (Wright *et al.*, 2013) and its sample data for palaeoreconstructions (Seton *et al.*, 2012).

We conducted phylogenetic regressions in which both the estimation of phylogenetic signal and the regression model parameters were estimated simultaneously (Revell, 2010). That is, along with regression parameters, Pagel's λ parameter representing the phylogenetic signal in the residual error is estimated by maximum likelihood (Revell, 2010). This allowed us to estimate the relationship between pterosaur wingspan and latitudinal midpoint while considering the phylogenetic non-independence of species. We used the 75 time-scaled phylogenies (see above) to conduct the phylogenetic regressions. Phylogenetic generalized least squares (PGLS) models were fitted for each time period using the *caper* (Orme *et al.*, 2013) R package.

Assemblage-based approach

We overlaid a global 1100×1100 km equal area (Mollweide projection) grid ($\sim 10^\circ$ lat-long on the equator) on species' occurrences to create a presence-absence matrix for each time period. We chose this grid resolution to have an overall representation of the latitudinal gradient while maximizing the presence of species within grid-cells. Lower resolutions would generate too many assemblages of single species and increase the potential for spatial autocorrelation. In addition, resolutions like ours are common for global macroecological

analyses (e.g. Ceballos *et al.*, 2005; Soberón and Ceballos, 2011), producing similar patterns to those conducted at the lowest possible macroecological resolutions [e.g. 2° (Hurlbert and Jetz, 2007)]. From the presence–absence matrix of each time period, we computed the mean and median \log_{10} -wingspan values for all species present within each grid-cell. Results from mean and median wingspan values were qualitatively similar (not shown) so we retained the median values, as they are more representative of skewed distributions.

To take into account the geographic structure of phylogenetic and non-phylogenetic components of Bergmann’s rule, we applied a phylogenetic comparative framework that allows partitioning of the total variation of a trait (i.e. wingspan in this case) into a phylogenetic component (P) representing the species’ values expected by their phylogenetic relationships and a specific component (S) denoting the independent evolution of each species after speciation (Diniz-Filho *et al.*, 2007, 2009). This approach is based on a phylogenetic eigenvector regression [PVR (Diniz-Filho *et al.*, 1998)] in which orthogonal eigenvectors are extracted from a phylogenetic distance matrix describing species relatedness and then used as predictors of the trait in a linear model. The coefficient of determination of such a linear model represents the amount of trait variation explained by the selected phylogenetic eigenvectors [i.e. phylogenetic signal (Diniz-Filho *et al.*, 1998, 2007, 2009)].

To extract the phylogenetic eigenvectors, we conducted a principal coordinates analysis (PCoA) on the pterosaur phylogenetic distance matrix and then selected, sequentially, those eigenvectors that together reduced residual autocorrelation according to Moran’s *I* coefficient (Diniz-Filho *et al.*, 2012). Values estimated by a linear model of wingspan against the selected eigenvectors denote the phylogenetic component (P), whereas the residuals of this model represent the specific component (S) (Diniz-Filho *et al.*, 2009). Finally, we calculated the mean P- and S-components within each grid-cell and regressed them against their latitudinal position. We repeated this procedure for the 75 phylogenies. We did not detect spatial autocorrelation in median wingspan values across grid-cell assemblages (results not shown), thus we did not correct for this potential problem. We used the *letsR* (Vilela and Villalobos, 2015) R package to create the presence–absence matrices and calculate the grid-cell values. Such values were mapped on reconstructed shapefiles (Scotese, 2001) of 170 and 110 Ma for the Triassic/Jurassic and Cretaceous periods, respectively.

Pairwise approach

Following Carotenuto *et al.* (2015), we also tested for Bergmann’s rule at each time period by conducting pairwise comparisons. First, we selected all sister pairs (‘cherries’) on a time-scaled phylogeny (see above) and then ranked each species within each pair by their ages. Then, the youngest species ‘a’ of the pair (appearing more recently in the fossil record) was compared with its sister species ‘b’, considering that ‘b’ appeared first in the fossil record (i.e. ‘b’ older than ‘a’). We computed a \log_{10} -wingspan ratio between the sister species (‘a’/‘b’) and the difference in absolute values of their latitudinal midpoints (Carotenuto *et al.*, 2015). These variables were regressed against each other whereby a positive relationship would be indicative of Bergmann’s rule [‘new species evolve along lineages by growing larger than their respective older closest phylogenetic relative when appearing northward to them’ (Carotenuto *et al.*, 2015)]. We repeated this procedure across the 75 time-scaled phylogenies.

RESULTS

Cross-species approach

Triassic/Jurassic

We compiled data for 35 pterosaur species that lived during the Triassic/Jurassic periods. The majority of these species had occurrences in the northern hemisphere as depicted by their latitudinal midpoints (Fig. 1A), with richness peaking in central longitudes (Fig. S1, www.evolutionary-ecology.com/data/3012Appendix.pdf). No clear relationship was observed between species' \log_{10} -wingspan and (absolute) latitudinal midpoint (Fig. 2A). Phylogenetic regression models (PGLS) across the 75 time-scaled phylogenies showed an overall weak negative relationship between wingspan and midpoint (i.e. converse Bergmann's rule), with small coefficients of determination (mean $R^2 = 0.12$, $SD = 0.047$ based on phylogeny-sensitivity analyses) and slope (mean $\beta = -0.008$, $SD = 0.002$). However, the statistical significance of such models varied among the phylogenies used, with 48 and 27 trees giving significant and non-significant results, respectively, which yielded a mean P -value of 0.072 ($SD = 0.086$) across all phylogenies. The phylogenetic signal

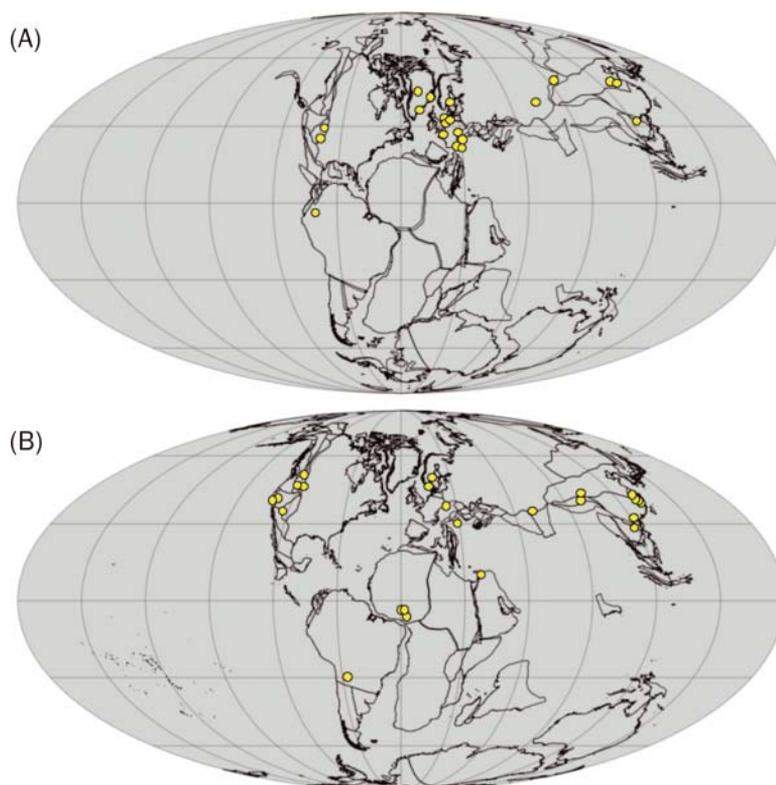


Fig. 1. Pterosaur latitudinal midpoints for species occurrences from (A) the Triassic/Jurassic (170 Ma palaeomap) and (B) Cretaceous (110 Ma palaeomap) periods. Palaeomaps were generated using GPlates.

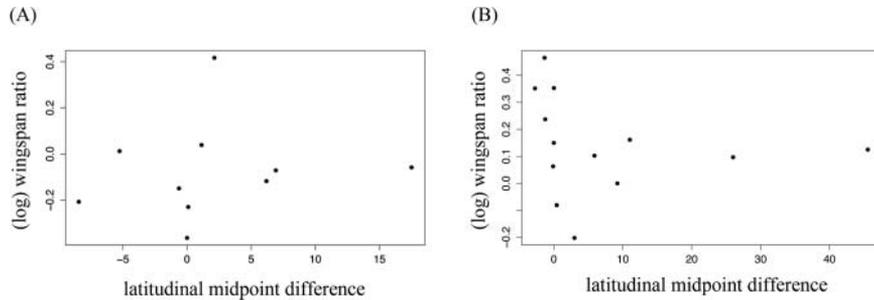


Fig. 2. Relationship between pterosaur wingspan and latitudinal midpoints of species from (A) the Triassic/Jurassic and (B) Cretaceous periods.

parameter λ , estimated using maximum-likelihood, showed high levels of phylogenetic signal across all models (mean $\lambda = 0.82$, $SD = 0.171$). Models fitted to the distribution of randomly assigned midpoints (around the recorded latitudes) showed similar results to the ones fitted to the observed midpoints (Table S1, 3012Appendix).

Cretaceous

We gathered data for 51 pterosaur species that lived during the Cretaceous period. Most of these species had occurrences in the northern hemisphere and only a few in the southern hemisphere (Fig. 1B and Fig. S2). Plotting the observed \log_{10} -wingspan and (absolute) midpoint values showed no clear relationships between these variables (Fig. 2B). As for the Triassic/Jurassic period, PGLS models showed a weak negative relationship between wingspan and midpoint (converse Bergmann's rule) with small coefficients (mean $R^2 = 0.092$, $SD = 0.017$; mean $\beta = -0.006$, $SD = 0.0005$). In this case, most phylogenies (70) produced models with significant results, with only five phylogenies producing non-significant models, resulting in a mean P -value of 0.034 ($SD = 0.013$) across phylogenies. The ML-estimated λ showed high levels of phylogenetic signal (mean $\lambda = 0.834$, $SD = 0.092$). The results of sensitivity analysis of latitudinal midpoints were similar to those using the observed midpoints (Table S1, 3012Appendix).

Assemblage-based approach

Triassic/Jurassic

Median wingspan values of pterosaur assemblages in the Triassic/Jurassic did not show clear geographical patterns (Fig. 3A). Similar results were observed for the mean S- and P-components of pterosaur wingspans across assemblages (Fig. 3B, C). Accordingly, linear models between these components and latitude did not show significant relationships either for the independent responses of species (S-component) (mean $R^2 = 0.171$, $SD = 0.018$; mean $\beta = -5.92 \times 10^{-8}$, $SD = 3.9 \times 10^{-9}$; mean P -value = 0.1, $SD = 0.018$; across the 75 used phylogenies) or the phylogenetically structured values (P-component) (mean $R^2 = 0.023$, $SD = 0.012$; mean $\beta = -1.14 \times 10^{-8}$, $SD = 3.9 \times 10^{-9}$; mean P -value = 0.581, $SD = 0.128$; across the 75 used phylogenies).

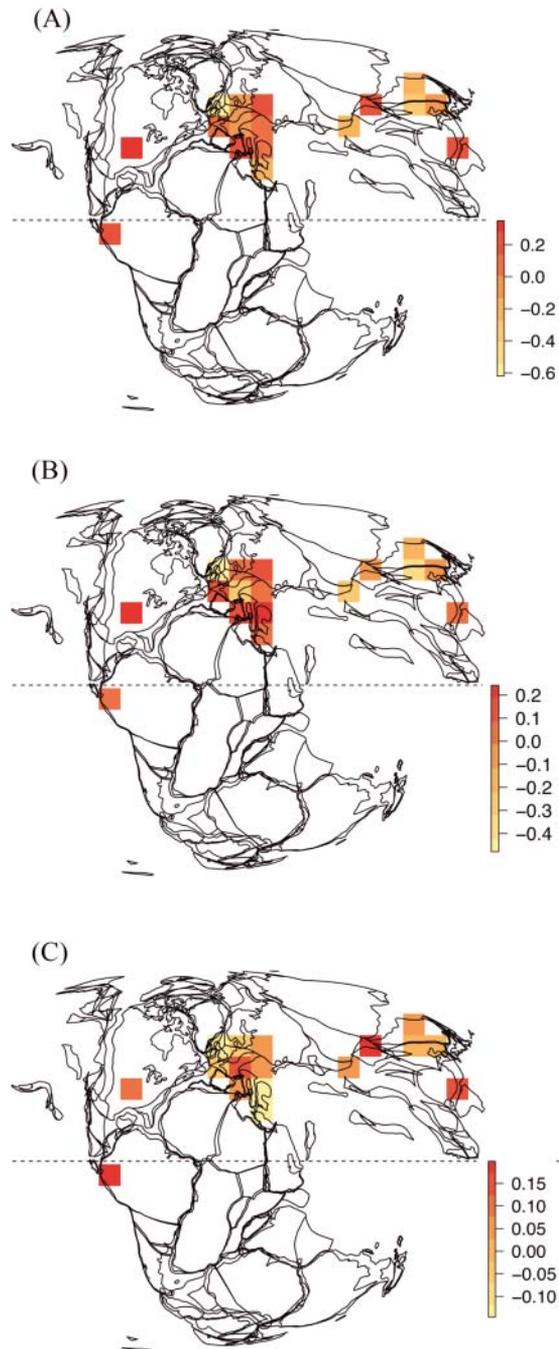


Fig. 3. Wingspan values across pterosaur assemblages for the Triassic/Jurassic period. (A) Median \log_{10} -wingspans, (B) mean specific component (S), (C) mean phylogenetic component (P). Dashed line marks the equator (0°). Maps in Mollweide projection; 170 Ma palaeoreconstruction from Scotese (2001).

Cretaceous

Median wingspan values of pterosaur assemblages in the Cretaceous also did not exhibit clear spatial patterns (Fig. 4A). The spatial patterns of mean S-component differed from the observed median wingspans (Fig. 4B), whereas the P-component showed a more similar pattern to the observed wingspans (Fig. 4C). Indeed, the pattern of the specific component (S) was the only one to show a significant negative relationship (i.e. converse Bergmann's rule) with latitude for some of the time-scaled phylogenies (11 out of 75 trees). However, mean (and SD) estimated values across the 75 phylogenies did not support an overall relationship between the S-component and latitude (mean $R^2 = 0.115$, SD = 0.067; mean $\beta = -3.269 \times 10^{-8}$, SD = 9.949×10^{-9} ; mean P -value = 0.208, SD = 0.177). No significant relationship was observed for the P-component in any of the models across the 75 phylogenies tested (mean $R^2 = 0.006$, SD = 0.01; mean $\beta = -2.313 \times 10^{-10}$, SD = 9.948×10^{-9} ; mean P -value = 0.812, SD = 0.168).

Pairwise approach

Regressions between the pairwise wingspan ratios and midpoint differences of sister species were not significant for either of the two time periods (Fig. S3). All models across the 75 time-scaled phylogenies showed no tendency for younger sister species to have larger wingspan when they appeared northward to their older sister species. Non-significant results were observed for the Triassic/Jurassic (mean $R^2 = 0.042$, SD = 0.069; mean $\beta = 0.003$, SD = 0.002; mean P -value = 0.665, SD = 0.237); similar results were found for the Cretaceous period (mean $R^2 = 0.022$, SD = 0.032; mean $\beta = 6.68 \times 10^{-5}$, SD = 0.002; mean P -value = 0.698, SD = 0.209).

DISCUSSION

Pterosaurs characterize an important component of vertebrate evolutionary history, as the first vertebrates to evolve powered flight (Hone and Benton, 2007). Compared with birds, the current dominant flying vertebrates, pterosaurs had higher body size disparity, ranging from starling-sized flapping fliers (such as some pterodactyls) up to sizes larger than any known bird, with wingspans of up to 11–12 m (in *Quetzalcoatlus*). Such great pterosaur disparity has stimulated heated debate about their functional (e.g. could these glider-sized animals really fly?) and evolutionary (e.g. why and how did pterosaurs evolve such body size?) causes and consequences. Indeed, pterosaurs have attracted much attention owing to their particular history of body size evolution. Pterosaurs are commonly cited as an example of Cope's rule, showing an increase in body size through time (Benson *et al.*, 2014). Such a pattern of body size evolution could be associated with environmental changes throughout Earth's history, which warrants consideration of the spatial and environmental settings of such evolution (Hunt and Roy, 2006; Raia *et al.*, 2012; Carotenuto *et al.*, 2015). Therefore, we included the spatial dimension here to evaluate if Cope's rule in Pterosauria can be associated with Bergmann's rule (size increase with latitude) as a response to climatic changes from the Jurassic to the Cretaceous periods. Our findings do not support an influence of Bergmann's rule in the evolution of pterosaur body size, suggesting that Cope's rule in Pterosauria is a mechanistically independent macroevolutionary pattern.

According to Bergmann's rule, we expect larger pterosaur species to live in colder regions compared with smaller pterosaurs in warmer regions. We did not find such a relationship

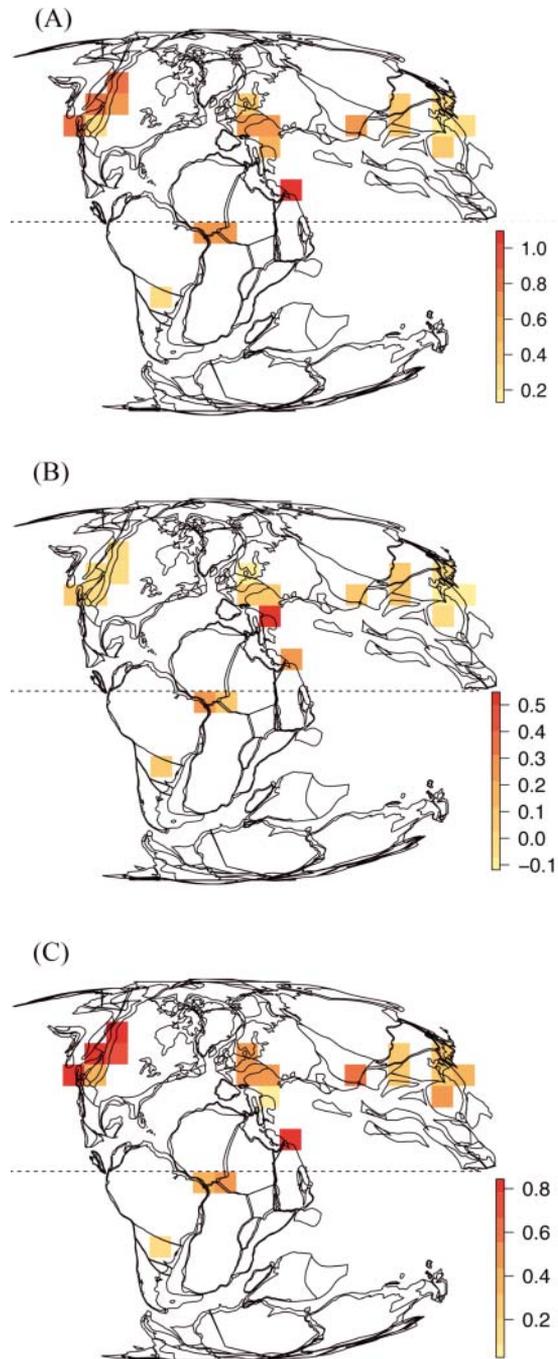


Fig. 4. Wingspan values across pterosaur assemblages for the Cretaceous period. (A) Median \log_{10} -wingspans, (B) mean specific component (S), (C) mean phylogenetic component (P). Dashed line marks the equator (0°). Maps in Mollweide projection; 110 Ma palaeoreconstruction from Scotese (2001).

for the pterosaur fauna of the Triassic/Jurassic period. Except for some cases in the cross-species approach, all three methods we applied did not support a significant relationship between wingspan and latitudinal positions of pterosaur species. In fact, this lack of relationship between wingspan and latitude is what we expected for Triassic and Jurassic pterosaurs given the climatic conditions across the globe in these time periods. During the Triassic, a widespread Pangaeian arid region with a very low climatic gradient characterized the globe, with some warm, humid conditions towards the poles (Xu *et al.*, 2012). Then, during the Jurassic period, conditions remained mostly arid within interior Pangaea with tropical/subtropical conditions at coastal regions and warm, humid climates towards the poles (Xu *et al.*, 2012). By that time, pterosaurs are thought to have achieved a global distribution (Upchurch *et al.*, 2014). Therefore, given the absence of a strong climatic gradient across latitude, pterosaur species may not have been subject to selective pressures favouring body size gradients to cope with varying climatic conditions. Indeed, focusing on the specific, phylogenetically independent component (S) of the assemblage-based approach showed no significant spatial gradient of adaptive responses of pterosaur species (Fig. 3B).

During the Triassic and the Jurassic, pterosaur body size evolution did not follow a directional trend (Cope's rule), being constrained around small sizes (Benson *et al.*, 2014). These time periods were characterized by pterosaurs belonging to the paraphyletic suborder Rhamphorhynchoidea, relatively small and long-tailed pterosaurs (Hone and Benton, 2005). Along with a more or less stable arid and humid global climate with no significant changes, the constrained body size evolution of Triassic/Jurassic pterosaurs agrees with the absence of Bergmann's and Cope's rule (Jablonski, 1997). Similar to the S-component, the spatial structure of the wingspan phylogenetic component (P) showed no clear patterns (Fig. 3C), suggesting that pterosaur body size evolution did not vary consistently across space, which is in line with a global distribution and a lack of response to palaeogeographic events (Upchurch *et al.*, 2014). Moreover, looking deeper into sister species confirms the absence of Bergmann's rule in the Triassic/Jurassic during which younger pterosaur species appearing at higher latitudes were no larger than their older sister species at lower latitudes. Thus, most of our evidence and that of others (Benson *et al.*, 2014) supports the view that pterosaur body size was not spatially and temporally structured during the Triassic and Jurassic periods.

The Cretaceous period represented a distinct phase of pterosaur body size evolution. From the beginning of this period and until their extinction at its end, pterosaurs showed a sustained directional body size evolution (Benson *et al.*, 2014). This second phase was characterized by the monophyletic order Pterodactyloidea, relatively large and short-tailed pterosaurs (Hone and Benton, 2007). Benson *et al.* (2014) proposed two non-mutually exclusive hypotheses for this pterosaur evolutionary shift from the Triassic/Jurassic to the Cretaceous period: one related to intrinsic features such as morphological changes favouring diversification and colonization of new niches, and another related to extrinsic factors, mainly competition with birds that radiated at the Early Cretaceous. An additional extrinsic factor that could have influenced the pterosaur evolutionary shift was the abiotic environment, such as temperature, as shown for mammals (Smith *et al.*, 1995; Carotenuto *et al.*, 2015) and bivalves (Hunt and Roy, 2006). Global climate changed significantly from the Jurassic to the Cretaceous (Gröcke *et al.*, 2003), with the reappearance of a latitudinal climatic belt pattern characterized by tropical/subtropical humid and arid belts as well as warm and cool temperate belts around the equator (Xu *et al.*, 2012). In fact, recent studies suggest a well-established equator-to-pole temperature gradient in this time period, especially in the late Cretaceous, supported by both climate models and geological data (Upchurch *et al.*, 2015). However, we found ambiguous

evidence that such changes may have influenced the spatial variation in pterosaur body size. While the pairwise comparisons did not support Bergmann's rule, the cross-species and assemblage-based approaches instead suggested a converse Bergmann's rule in Cretaceous pterosaurs.

Given the global climate changes and the widespread distribution of Pterosauria, we expected Bergmann's rule to apply for Cretaceous pterosaurs. Instead, we found some evidence for a reversed Bergmann pattern with larger body sizes at lower latitudes and smaller body sizes at higher latitudes. This converse Bergmann's rule is a prediction of the heat balance hypothesis (Olalla-Tárraga and Rodríguez, 2007) for thermoconforming ectotherms. In contrast to thermoregulating ectotherms, where the heat balance hypothesis predicts the same outcome as Bergmann's rule for endotherms, thermoconforming ectotherms would tend to be smaller in colder regions to increase heating rates and remain active for longer time periods under low environmental temperatures (Meiri *et al.*, 2007; Olalla-Tárraga and Rodríguez, 2007). Pterosaurs have long been seen as endothermic because of their fossilized covering of hairs/feathers, interpreted as an insulating layer since first discovered around 1840. In addition, based on bone histology, respiratory anatomy, and high growth rates and activity levels, pterosaurs are thought to have been true endotherms, although this remains controversial (Pontzer *et al.*, 2009; Clarke and Pörtner, 2010). How, then, could we explain a potential converse Bergmann's rule in pterosaurs? The main feature of pterosaur body size is their wingspan, ranging from 3 to 10 m in the latest pterosaurs (Benson *et al.*, 2014). Such large wings significantly increase surface-to-volume ratios, as suggested for bats (Storz *et al.*, 2001; de Barros *et al.*, 2014). Increasing surface-to-volume ratios (here associated with longer wingspans) could have been advantageous for pterosaurs at lower latitudes, conferring better heat dissipation capacity in warmer and humid environments. The significant geographical pattern of the specific component (S) supports this possibility, implying adaptive responses of species across space (Fig. 4B). In addition, this same possibility may have favoured extreme sizes under an increase in thermals that could be used for soaring (Hone and Benton, 2007).

Our findings are not decisive on the validity of Bergmann's rule, traditional or converse, in the evolutionary history of Pterosauria. As in most palaeontological studies, findings are affected by data quality, sampling biases, and availability (Hunt and Roy, 2006; Butler *et al.*, 2012). Our study focused on an ecogeographical pattern relating body size and temperature, with the former being informed by fossil data and the latter by the geographical location (i.e. latitude) of such data. Regarding the actual fossil data, the pterosaur fossil record we used seems to be sufficiently adequate to inform biological patterns (Dyke *et al.*, 2009), as evidenced by several studies confirming the late peak in pterosaurian diversity and disparity (Dyke *et al.*, 2009; Prentice *et al.*, 2011; Butler *et al.*, 2012, 2013). In contrast, owing to the lack of detailed temperature data (i.e. spatially explicit) for the fossil localities in the studied time periods, we used latitude as a proxy for temperature assuming a relationship between a latitudinal gradient and a climate gradient. This assumption is fundamental for interpreting our findings. Indeed, if no relationship between temperature and latitude were present, there would be no reason to expect a Bergmannian pattern. Actually, our lack of strong support for Bergmann's rule in pterosaurian history, particularly during the Cretaceous, may be due to the absence of a temperature–latitude relationship in that period. However, evidence from palaeoclimatological studies suggests that such a relationship was indeed well established by the Cretaceous period (Upchurch *et al.*, 2015), whereas shallower or non-existing temperature gradients were present before that [e.g. Triassic and Jurassic periods (Eldrett *et al.*,

2009)]. This evidence supports our assumption of a relationship between temperature and latitude, especially in the Cretaceous, thus guiding our expectation of a Bergmannian pattern of pterosaur body size in that period.

Another issue when studying fossil phenotypic patterns is determining the importance of evolutionary and ecological mechanisms (Hunt and Roy, 2006). We addressed this issue in our assemblage-based approach combined with phylogenetic eigenvector regression (Diniz-Filho *et al.*, 2007), which allowed us to test the potential adaptive responses of Cretaceous pterosaurs to temperature (with latitude taken as a proxy). However, our findings were not further supported by the more stringent method of sister pair comparisons. Finally, discrepancies among our results within the same method (and probably among methods) may result from the different phylogenies used. We followed Benson *et al.* (2014) in time-scaling the original cladogram of Andres and Myers (2013). These authors reported congruent results among these phylogenies, which could have persuaded us to use only one time-scaling method. This would certainly have biased our results and precluded our consideration of phylogenetic uncertainty. Recent claims have highlighted the effect of time-scaling methods on the fidelity of tree-based analyses, calling for caution and consideration of biases (Bapst, 2014). Although outside the scope of our study, such considerations warrant their inclusion when testing for ecogeographical patterns and their evolutionary causes.

CONCLUSIONS

Here we applied a macroecological approach to evaluate the influence of Bergmann's rule in determining Cope's rule in Pterosauria following the proposed climatic explanations for both rules (Hunt and Roy, 2006; Carotenuto *et al.*, 2015). Overall, our results do not support Bergmann's rule along the evolutionary history of Pterosauria. Therefore, we conclude that pterosaur body size evolution seems to have only one dimension: time. Nevertheless, our findings should not be viewed as definitive since additional information on pterosaur data, especially distributional data, could confirm or dismiss our weak evidence for a converse Bergmann's rule during the Cretaceous period. Insights into the potential ecogeographical patterns of pterosaurs may help inform other aspects of pterosaur evolution such as metabolic physiology and biogeographical history, and contribute to the general understanding of biological responses to climate gradients and changes over time. We encourage the application of macroecological approaches to palaeontological data to overcome the final frontier of considering the spatial dimension in deep-time studies as well as to foster our comprehension of the mechanisms behind broad-scale spatial and temporal patterns of biodiversity.

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