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Sharks That Pass In The Night: Using GIS to Investigate Competition in the Cretaceous Western Interior Seaway

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Abstract

One way the effects of both ecology and environment on species can be observed in the fossil record is as changes in geographic distribution and range size. The prevalence of competitive interactions and species replacements in the fossil record has long been investigated and many evolutionary perspectives, including those of Darwin, have emphasized the importance of competitive interactions that ultimately lead one species to replace another. However, evidence for such phenomena in the fossil record is not always manifest. Here we use new quantitative analytical techniques based on geographic information systems (GIS) and PaleoGIS tectonic reconstructions to consider this issue in greater detail. The abundant, well-preserved fossil marine vertebrates of the Late Cretaceous Western Interior Seaway of North America provide the component data for this study. Statistical analysis of distributional and range size changes in taxa confirms earlier ideas that the relative frequency of competitive replacement in the fossil record is limited to non-existent. It appears that typically environmental gradients played the primary role in determining species distributions, with competitive interactions playing a more minor role.

Key Words: competitive replacement, GIS, Western Interior Seaway, marine vertebrates

1. Introduction

(a) Historical Perspective

A central question in biogeography and evolution is what causes species' distributions to wax and wane through time. Traditionally, a dominant role has been ascribed to competitive interactions between species (Darwin 1859, MacArthur and Wilson 1972, Van Valen, 1987, Vermeij 1987, Jackson and McKinney 1990, Rosenzweig and McCord 1991, Sepkoski *et al.* 2000). Classic examples include the decline and replacement of brachiopods by bivalves, mammal-like reptiles by archosaurs, cyclostome bryozoans by cheilostome bryozoans, gymnosperms by angiosperms, multituberculates by rodents, and South American mammals by North American fauna; however, these cases for the most part have not been tested in detail (Benton 1987, 1996a, Rayner and Masters 1995). The theoretical importance of competition in evolution actually pre-dates Darwinian competitively driven natural selection and can be traced back to the notion of plenitude. Plenitude ascribes a fixed number of ecological niches on Earth, with rapid evolution of life to fill all available niche space. Once filled, evolution occurs in dynamic equilibrium where individual species may arise and go extinct, but patterns of global diversity remain constant (Cifelli 1981, Walker and Valentine 1984, Benton 1987, 1996b). Darwin (1859) supported this view, particularly with his famous wedge analogy, where species are akin to wedges hammered into a surface – once the surface is filled with wedges, a new wedge may only be driven in at the expense of an older wedge being driven out (Gould and Calloway 1980, Gould 1985, Benton 1996b). From this perspective, evolution occurs by a series of competitive replacements through time, species' distributions are predominantly controlled by competitive interactions with contemporaries, and interspecific competition is a primary driver of macroevolution.

An alternative perspective is where an existing species or clade is successful until an external perturbation results in its extinction and later replacement by a new taxon. For instance, a re-examination of the diversity patterns of brachiopods and bivalves by Gould and Calloway found these clades to be as "ships that pass in the night" (Longfellow, IN: Gould and Calloway 1980); a view in accord with the notion that abiotic environmental change dictates species origination and extinction patterns (Eldredge and Cracraft 1980, Vrba 1980, 1985, Cifelli 1981, Gould 1985, Masters and Rayner 1993, Benton 1996a, 2009, Barnosky 2001, Flagstad *et al.* 2001, Lieberman *et al.* 2007).

Of course these (and other) authors acknowledge that both factors likely play some role in evolution. Thus, here we test for evidence of interspecific competition on species' distributions over macroevolutionary timescales by concentrating on identification of competitive replacements in fossil taxa using GIS. GIS-based techniques are increasingly recognized as powerful tools for investigating evolutionary patterns and processes (Rode and Lieberman 2004, Stigall and Lieberman 2006, Costa *et al.* 2008, Kozak *et al.* 2008, Butler *et al.* 2010). These methods allow for quantitative measurement of distribution and range size change during specific temporal intervals. Further, GIS analyses lend themselves to statistical analysis of negative range area correlations in species pairs through time, which can be used as a proxy for evidence of competitive replacement. The focus of this analysis is a set of marine vertebrate species from the exceptionally diverse and complete record of the Late Cretaceous Western Interior Seaway of North America. This region has been the subject of palaeobiological and geological study for more than a century and has been intensely sampled. Further, palaeobiological samples can be placed in a detailed stratigraphic context.

(b) Geological Setting

The Late Cretaceous covers a 35 million year period between 100-65Ma. The Earth at this time was in a greenhouse climate state with little or no polar ice (Barron 1983, Huber *et al.* 2002, Spicer 2002, Everhart 2005). As a consequence of this, and higher rates of sea floor spreading, sea-level was much higher than today. In particular, central North America was covered by a shallow epicontinental sea, the Western Interior Seaway (WIS) (i.e. ≤ 600m water depth) (Hattin 1982, Kauffman and Caldwell 1993, Poulsen *et al.* 2001, Everhart 2005). The WIS represents a foreland basin formed by tectonic loading and lithospheric flexure during uplift of the Rocky Mountains to the west. This basin was inundated episodically from both boreal waters extending south from the Arctic Ocean and tropical waters extending north from the proto-Atlantic/Tethys seas (Hattin 1982, Kauffman 1984, Kauffman and Caldwell 1993, Shimada *et al.* 2006). At the end of the Early Cretaceous (late Albian, ~100Ma) a global sea-level low stand separated the northern and southern arms of the WIS for the last time until the late Maastrichtian (~65Ma). Cyclic sea-level changes are recorded in the WIS as three major transgressive/regressive events: the Greenhorn Cycle (late Cenomanian-Turonian), which included the sea-level high stand for the Late Cretaceous with eustatic sea-levels upwards of 250m higher than today; the Niobrara Cycle (late Coniacian – early Campanian); and the Claggett/Bearpaw Cycle (Campanian – Maastrichtian) (Hattin 1982, Kauffman 1984, Kauffman and Caldwell 1993).

Our understanding of the Late Cretaceous WIS is based on over one hundred years of field and laboratory work by geologists, palaeoclimatologists, and palaeobiologists. As a consequence, the tectonic, environmental, and geologic history of this area is well understood and extensively palaeobiologically sampled making it an ideal region for this type of palaeobiogeographical investigation (e.g., Hancock and Kauffman 1979, Hattin 1982, Kauffman 1984, Nicholls & Russell 1990, Glancy *et al.* 1993, Russell 1993, Schroder-Adams *et al.* 1996, Sageman *et al.* 1997, Schwimmer *et al.* 1997, Keller *et al.* 2004, Everhart 2001, 2005, Becker *et al.* 2006, Cobban *et al.* 2006, Shimada *et al.* 2006, Ufnar *et al.* 2008). However, extensive sampling does not always equate to representative sampling; consequently, we provide various tests to assess the quality of the WIS record and its use in palaeobiogeographical analyses.

2. Materials and Methods

(a) Data Collection

A temporal and geographic occurrence database was generated for ten Late Cretaceous WIS vertebrate taxa. Taxa included three genera of shark: three species of *Ptychodus* (*P. anonymus*, *P. mortoni*, and *P. whipplei*), one species of *Cretoxyrhina* (*C. mantelli*), and two species of *Squalicorax* (*S. falcatus* and *S. kaupi*); as well as two genera of mosasaur (*Platecarpus* sp., and *Tylosaurus* sp.) and one teleost genus (*Xiphactinus* sp.). The taxa included in this analysis were chosen because they are common and abundant in the WIS fossil record, persist through at least three geologic stages of the Late Cretaceous, and have been well characterized taxonomically and palaeobiologically. Further, the WIS at this time had no prominent physical barriers that might have prevented interactions between taxa.

Data on species' geographic and stratigraphic ranges were collected through examination of museum collections, fieldwork, and survey of the literature. The following museum collections were used: Natural History Museum and Biodiversity Research Center (NHM-BI, University of Kansas); Peabody Museum of Natural History (YPM, Yale University); Texas Memorial Museum (TMM, University of Texas – Austin); Sternberg Museum of Natural History (FHSM, Fort Hays State University); University of Colorado Museum (UCB, University of Colorado – Boulder); University of Nebraska State Museum (UNSM); and the Black Hills Institute (BHI, South Dakota). These museums contain important and diverse collections of WIS taxa spanning the majority of Late Cretaceous WIS geography, and taxa in these collections are well-documented geographically and stratigraphically. All museum specimens were personally examined and identification confirmed by the authors. In cases where species identifications lacked confidence, analyses were run at the generic level (e.g. *Tylosaurus*, *Platecarpus*, *Xiphactinus*). To augment information from museums, fieldwork was conducted at Late Cretaceous sites in western South Dakota and southeastern Missouri.

Resolution of geographic locality data was at the county-level and better, the standard level of resolution used in other GIS-based palaeobiogeographic analyses (e.g., Rode and Lieberman 2004, Hendricks *et al.* 2008, Maguire and Stigall 2009). However, most data represent even higher resolution at the 1 mi^2 township, range, and section. Temporal resolution was at the level of geologic stage within the Late Cretaceous and characterized by formation and member of specimen occurrence. The resulting database consists of 762 total occurrence points; the number of occurrence points per taxonomic group varies from 31 to 197 (figure 1).

(b) Range Reconstructions

Geographic locality data for each species' occurrence was georeferenced and imported into ArcGIS v.9.2 for visual representation and spatial analysis (ESRI 2006). PaleoGIS v.3.0

(Scotese 1998, Ross and Scotese 2000, Rothwell Group 2007) was then used to reconstruct the palaeogeography of each stage during the Late Cretaceous following the methods of Rode and Lieberman (2004) and Stigall and Lieberman (2006) (figure 2). This step ensures that distribution and range area reconstructions minimize estimation error due to tectonic contraction and expansion in the North American plate over the course of the Late Cretaceous.

Once PaleoGIS was used to reconstruct the geography of a particular stage, a ten kilometer buffer was applied to each specimen occurrence point. Buffering species' locality points helps control for any error in the translation from current geographic location to deep time georeferenced latitude and longitude. Additionally, buffering gives area to point occurrence data, enabling retention of these data in the analysis. ArcGIS was then used to construct least-fit polygons for each taxon at each temporal interval. The spatial analysis software available within this program was used to calculate area of each reconstructed range. Geographic range data for all taxa are provided in electronic supplementary material, table S1.

(c) Identifying Competition

One way competition can be observed in the fossil record is as changes in species' distribution and range size through time. Benton (1996a, b) defined "Candidate Competitive Replacements" (CCRs) as species pairs showing negatively correlated abundance and diversity patterns over time. CCRs must involve taxa with overlapping geographic and stratigraphic ranges and should also involve comparisons between taxa with similar habitat, body size, and diet. Further, all CCRs must show a distinctly "successful" taxon (the survivor) as well as a distinctly "unsuccessful" taxon, identified by range contraction and extinction within two temporal intervals after the minimum date of origin of the "successful" taxon (Benton 1996a, b).

This pattern can also be identified in the fossil record as negatively correlated geographic range area through time, which can be tested for statistical significance using nonparametric rank correlation in PAST v.2.01 (Hammer *et al.* 2001) (Spearmann's ρ and Kendall's τ, $p \leq 0.05$); these statistical analyses were corrected for multiple comparisons using the Bonferroni correction.

All taxa under investigation display geographic and stratigraphic overlap. To identify CCRs, taxa with similar inferred ecotypes were compared, as taxa within the same ecotype are most likely to have interacted competitively. The taxa in this study can be divided into two general palaeoecologies: species of *Cretoxyrhina*, *Squalicorax*, *Tylosaurus*, *Platecarpus*, and *Xiphactinus* are inferred to have been pelagic predators (e.g., Russell 1967, Williamson *et al.* 1993, Everhart 2005, Rothschild *et al.* 2005, Shimada and Cicimurri 2005, Becker 2006, Shimada *et al.* 2006; see Schwimmer *et al.* 1997 for additional discussions of *Squalicorax*); species of *Ptychodus* and *Rhinobatos* are inferred to have had a nekto-benthic, durophagous lifestyle (e.g., Stewart 1988, Williamson *et al.* 1993, Everhart 2005, 2007, Shimada *et al.* 2006; see Hamm 2008, 2010 for additional discussions of *Ptychodus*). Comparisons were also conducted by genus, as species within the same genus may be more likely to have the greatest degree of competitive overlap. Finally, an agnostic approach was used, and pairwise comparisons between all taxa were considered.

(d) Analysis of Bias

There are many phenomena that can explain why one species range might increase through time while another decreases through time. In addition to competition and other processes discussed below, an incomplete fossil record could artificially produce a pattern mirroring a CCR. Incompleteness of the fossil record is a potential source of bias in any palaeontological study. As previously mentioned, the Late Cretaceous WIS has been exhaustively studied for over a century and is well characterized both in terms of its geology and palaeontology. Further, it has not undergone significant tectonic modification since the Late Cretaceous. These may all partly serve to obviate the potential problems of an incomplete fossil record. Moreover, some areas within the WIS show exceptional preservation in the form of Konservat Lagerstätte; one of these, the Smoky Hill Chalk member of the Niobrara Formation spans three temporal intervals (Coniacian, Santonian, and Campanian stages) of this study (Schwimmer *et al.* 1997, Meyer and Milsom 2001, Bottjer 2002).

However, this does not mean that there might not be certain taphonomic factors conspiring to cloud our understanding of biogeographic patterns in these taxa over time. Because of this, three tests were used to determine if incompleteness or bias in the WIS fossil record is artifactually influencing palaeobiogeographic patterns, including those pertaining to CCRs. First, the robustness of range area reconstructions to potential outliers was tested by resampling occurrence points for each taxon. An 'n-1' jackknifing procedure was utilized to estimate the resampled mean range size and associated confidence bands for each taxon during each time interval (resampled data available in electronic supplementary material, table S1). This mean range area was then subjected to nonparametric rank correlation tests and the results were compared to those obtained using original range area calculations (tests on resampled data available in electronic supplementary material, tables S3 and S4, and discussed more fully below).

The second test compared geographic range size in each taxon to area of available Late Cretaceous sedimentary outcrop. A high percentage of overlap between the distribution of taxa and available outcrop would suggest that presence/absence of Late Cretaceous geologic record may be influencing our results. The third test aimed to identify a correlation between number of data points and geographic range size for each temporal interval. In this case, if sampling bias had an effect on our range size reconstructions, a strong positive correlation between number of data points and range size would be expected.

3. Results

(a) Competition in the WIS

Tables 1 and 2 show the results of intrageneric range area correlations and correlations by palaeoecotypes respectively; pairwise comparisons between all taxa are included in electronic supplementary material, table S2. All species did show changes in distribution and range size through time. The majority of the species comparisons showed no evidence of interspecific competition (e.g., figure 3). A complete set of geographic comparisons for all taxa considered is provided in the electronic supplementary material (figures S1–S43). Some taxa did generally show the basic biogeographic pattern predicted for a CCR (figure 4), however, when analyzed the pattern was not found to be statistically significant. Indeed, no statistically significant negative range area correlations were identified from intrageneric comparisons, within ecotype comparisons, or when all taxa were compared, after the Bonferroni correction was applied. For instance, consider that among the four possible intrageneric comparisons, only *Squalicorax falcatus* and *S. kaupi* is near significance using Kendall's τ ($\tau = -0.69007$, $p = 0.0518$), but the correlation is not significant after a Bonferroni correction for multiple comparisons was applied (new critical p-value of $p \leq 0.013$) (table 1). Thus, it appears that for these vertebrate taxa evidence for candidate competitive replacements in the Cretaceous WIS is negligible to non-existent.

(b) Analysis of Bias

Geographic range estimations using this palaeobiogeographic method may be susceptible to artificial inflation by widely flung single occurrence points. In order to assess the influence of these potential outliers on our range reconstructions, and thus pertaining to the identification of statistically significant CCRs, we re-ran all the pairwise comparisons using the estimated mean geographic range calculated by jackknifing (electronic supplementary material, table S3). The results are identical: before or after correcting for multiple comparisons, no statistically significant intrageneric or within ecotype CCRs were identified; when all taxa were compared, two CCRs only appeared statistically significant before the Bonferroni correction was applied: they were no longer significant after correction for multiple comparisons. Thus, the results from analysis of the original data and the resampled data are equivalent and the data appear robust to resampling. Consequently, outliers are not likely to be playing a significant role in influencing the results.

To test for the effect of available outcrop area on species distributions during the Late Cretaceous, we compared species' geographic range size with area of Late Cretaceous sedimentary record; the approximate margins of the WIS for the early, middle, and late Late Cretaceous, along with the occurrence records parsed by stage, are shown in electronic supplementary material, figure S44. Taxa were shown to occupy only 4–37% of potential habitat. Because taxa are not present in all or even the majority of available outcrop area during this time period, it is unlikely that the simple availability of Late Cretaceous sedimentary record is controlling the patterns of distribution and range size change observed in this analysis.

A correlation of number of unique geographic localities sampled with size of geographic range reconstruction for each temporal interval in this analysis is shown in table 3 (for correlation statistics using resampled means, see electronic supplementary material, table S4). The number of unique localities was used to test for sampling bias (instead of all sampled occurrences) because this reduces artificial inflation of points sampled and maximizes the potential for finding a significant correlation (thus the test is most sensitive to identifying sampling bias). None of the stages during the Late Cretaceous show significant correlations between number of data points and size of geographic range ($p >> 0.007$ using Bonferroni correction for multiple comparisons) except the Coniacian stage ($p = 0.001$) (table 3); the same is true of the resampled data (electronic supplementary material, table S4).

Many (though not all) taxa have small geographic range size during the Coniacian; it is possible that this represents a bias in collection or preservation. On the other hand, this stage is the point of origin or extinction for a number of the taxa studied (e.g., *Tylosaurus* sp., *Platecarpus* sp., *Squalicorax kaupi* originate; *Ptychodus anonymus* and *Ptychodus whipplei* go extinct). Species commonly have small geographic range size at the point of origination and extinction (particularly if speciation occurs allopatrically in small isolated populations and extinction first involves reduction to a single population). To assess the influence of this phenomenon, these taxa were removed and the correlation statistics re-run (table 3, and electronic supplementary material, table S4). Excluding taxa originating or going extinct, the number of sampled localities during the Coniacian is no longer significantly correlated with reconstructed range size in both the original and the resampled data (see table 3 and electronic supplementary material, table S4). Thus the uniquely small range size of these taxa was likely causing the suggested sampling bias during this interval.

4. Discussion

This study uses new techniques in quantitative biogeographic analysis to test for the role of competitive replacement in the fossil record. We focused on species' distributions in the abundant representatives of the vertebrate fauna from the Late Cretaceous WIS, specifically looking for two-taxon comparisons suggesting competitive replacement. No two-taxon comparisons showed any statistical evidence of significant, negative geographic range correlations. These results reiterate previous analyses indicating little evidence for competitive replacement (Benton 1996a, b). Further, this suggests that something other than interspecific competition plays the predominant role in influencing species distributions over macroevolutionary time scales. Such processes were most likely abiotic environmental changes, both climatic and tectonic, as these have been shown to have had a significant impact on species distributions and macroevolution at other times in the history of life (Lieberman and Eldredge 1996, Lieberman 2000, Barnosky 2001, Flagstad *et al.* 2001, Rode and Lieberman 2004, Stigall and Lieberman 2006, Hendricks *et al.* 2008, Benton 2009, Gates *et al.* 2010). There could, however, also be a substantial contribution from ecological factors such as food source tracking, intraspecific interactions, etc.

It is worth noting that competitive replacement may be more prevalent among species that are rare and/or geographically restricted. Such cases are difficult to identify in the fossil record, and thus by necessity our study focused on more abundant and potentially more "successful" taxa from the outset. As a consequence, even though we attempted to maximize recovery of CCRs by using broad definitions of palaeoecological similarity, our estimate of the frequency of CCRs is most surely an underestimate. Nonetheless, it is based on quantitative and detailed investigation of these groups, and thus the best estimate possible at present.

Moreover, while we believe that our analysis includes real species using a phylogenetic species concept, it is impossible to exclude the possibility that some of these species actually represent ecomorphs within a single lineage. If this were the case, then instead of identifying cases of competitive replacement between species, our analysis would be testing for intraspecific interactions occurring between co-occurring ecomorphs. The apparent non-prevalence of competitive replacement within potentially adaptive lineages then might suggest that ecomorph evolution also may not be strongly influenced by these types of competitive interactions.

Ultimately, this study provides little evidence that CCRs play a defining role in shaping species' distributions at the macroevolutionary scale. The driving force is instead likely to be abiotic environmental factors, such as climate and sea-level changes, that determine species distribution and range size. Other ecological factors may have been important as well, but interspecific competition does not appear to have had a major affect on macroevolutionary patterns of species in the fossil record (Vrba 1980, Nicholls & Russell 1990, Barnosky 2001, Flagstad *et al.* 2001, Benton 2009, Gates *et al.* 2010, Venditti et al. 2010).

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Figure and Table Captions

Figure 1. Data points showing occurrence records of Late Cretaceous marine vertebrate specimens analyzed in this study. *Xiphactinus* sp. (pink), *Platecarpus* sp. (dark green), *Tylosaurus* sp. (dark blue), *Squalicorax kaupi* (orange), *Squalicorax falcatus* (red), *Rhinobatos incertus* (light green), *Ptychodus whipplei* (white), *Ptychodus mortoni* (dark gray), *Ptychodus anonymus* (light gray), *Cretoxyrhina mantelli* (yellow). Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure 2. Example of PaleoGIS (Rothwell Group 2007) plate tectonic reconstruction. Distribution of *Cretoxyrhina mantelli* (yellow), *Tylosaurus* sp. (blue). Present day outcrop of Late Cretaceous sediments is also shown (brown). (a) PaleoGIS present day tectonic configuration. (b) PaleoGIS Coniacian reconstruction (~87Ma).

Figure 3. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for the majority of two-taxon comparisons in this study. *Tylosaurus* sp. (blue) and *Platecarpus* sp. (dark green) distributions are shown during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. These taxa do not show a statistically significant negative range area correlation through time and thus are not identified as CCRs. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure 4. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the general predicted geographic pattern of a CCR, although the negative relationship in range size is not statistically significant. *Squalicorax falcatus* (red), and *S. kaupi* (orange) distributions are shown during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. *S. falcatus* shows stable, though dynamic, range size until the origination of *S. kaupi* in the Coniacian (c). After this time, *S. falcatus* experiences sequential decrease in range size resulting in extinction at the end Campanian (e). This example

illustrates a negative relationship between the range area of two ecologically similar species within the same genus, and thus could represent a competitive replacement of *S. falcatus* by *S. kaupi*. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Table 1. Intrageneric range area correlations. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.013$ for statistical significance.

Table 2. Range area correlations among species with similar palaeoecology. (a) Inferred large, pelagic (circular vertebral centra suggesting fusiform-body) predators; (b) inferred large, nekto-benthic durophagous lifestyle. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.002$ for statistical significance.

Table 3. Correlation results between number of unique geographic localities sampled and reconstructed geographic range size for each stage during the Late Cretaceous. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.007$ for statistical significance. Coniacian* represents correlation between number of unique geographic localities and reconstructed range size after removing taxa that either originate or go extinct during this stage.

Electronic Supplementary Figure and Table Captions

Figure S1. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Squalicorax falcatus* (red) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S2. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Squalicorax kaupi* (red) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S3. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Platecarpus* sp. (dark green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S4. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Tylosaurus* sp. (blue) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S5. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S6. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S7. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S8. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late

Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S9. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S10. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Platecarpus* sp. (dark green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S11. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Tylosaurus* sp. (blue) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S12. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S13. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S14. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S15. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S16. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S17. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Platecarpus* sp. (dark green) during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S18. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Tylosaurus* sp. (blue) during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S19. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S20. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S21. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Turonian, (b) Coniacian, (c) Santonian, (d) Campanian, (e) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S22. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S23. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S24. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Platecarpus* sp. (dark green) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S25. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Platecarpus* sp. (dark green) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S26. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Platecarpus* sp. (dark green) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Turonian, (b) Coniacian, (c) Santonian, (d) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S27. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Platecarpus* sp. (dark green) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S28. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Platecarpus* sp. (dark green) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S29. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S30. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S31. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Turonian, (b) Coniacian, (c) Santonian, (d) Campanian, (e) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S32. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S33. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S34. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S35. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S36. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S37. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S38. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus anonymus* (grey) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S39. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus anonymus* (grey) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S40. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus anonymus* (grey) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S41. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus mortoni* (black) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late

Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S42. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus mortoni* (black) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S43. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus whipplei* (white) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Figure S44. PaleoGIS (Rothwell Group 2007) reconstructions showing the approximate boundaries of the WIS and occurrence records during the Late Cretaceous stages: (a) Cenomanian, (b) Coniacian, (c) Maastrichtian. Boundaries of seaway provided with assistance of Richard Mackenzie and Peg Yacobucci. Note that boundaries represent average sea-level at any stage, not necessarily high-stand. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Table S1. PaleoGIS range area reconstuctions for each taxon during each stage of the Late Cretaceous. S = range area (km), S* = estimated mean range area calculated by jackknifing (km), SE = standard error, L1 and L2 = 95% confidence bands on S*.

Table S2. Correlation results for range area analysis of all pairwise comparisons. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.001$ for statistical significance.

Table S3. Correlation results for range area analysis of all pairwise comparisons using resampled mean range estimated by jackknifing procedure. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.001$ for statistical significance.

Table S4. Correlation results between number of unique geographic localities sampled and reconstructed geographic range size for each stage during the Late Cretaceous using resampled mean range estimated by jackknifing procedure. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.007$ for statistical significance. Coniacian* represents the correlation between number of unique geographic localities and reconstructed range size after removing taxa that either originate or go extinct during this stage.

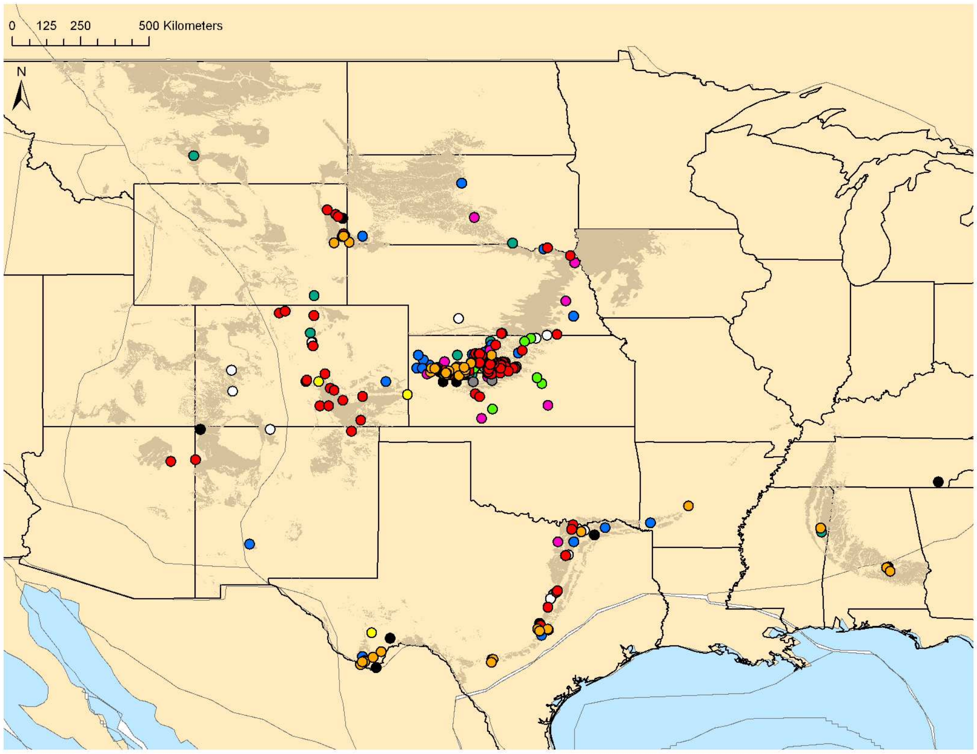

Figure 1. Data points showing occurrence records of Late Cretaceous marine vertebrate specimens analyzed in this study. Xiphactinus sp. (pink), Platecarpus sp. (dark green), Tylosaurus sp. (dark blue), Squalicorax kaupi (orange), Squalicorax falcatus (red), Rhinobatos incertus (light green), Ptychodus whipplei (white), Ptychodus mortoni (dark gray), Ptychodus anonymus (light gray), Cretoxyrhina mantelli (yellow). Present day outcrop of Late Cretaceous sediments is also shown (brown).
279x215mm (300 x 300 DPI)

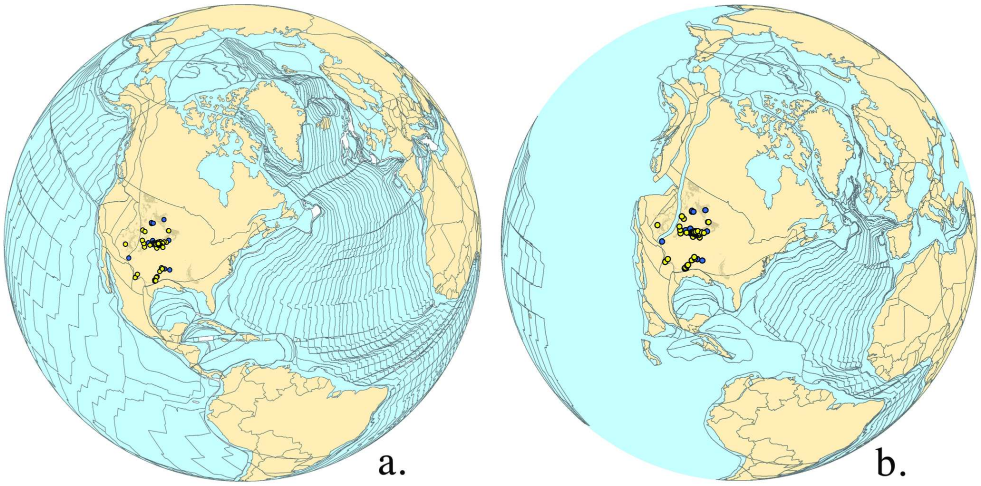

Figure 2. Example of PaleoGIS (Rothwell Group 2007) plate tectonic reconstruction. Distribution of Cretoxyrhina mantelli (yellow), Tylosaurus sp. (blue). Present day outcrop of Late Cretaceous sediments is also shown (brown). (a) PaleoGIS present day tectonic configuration. (b) PaleoGIS Coniacian reconstruction (~87Ma).
177x87mm (300 x 300 DPI)

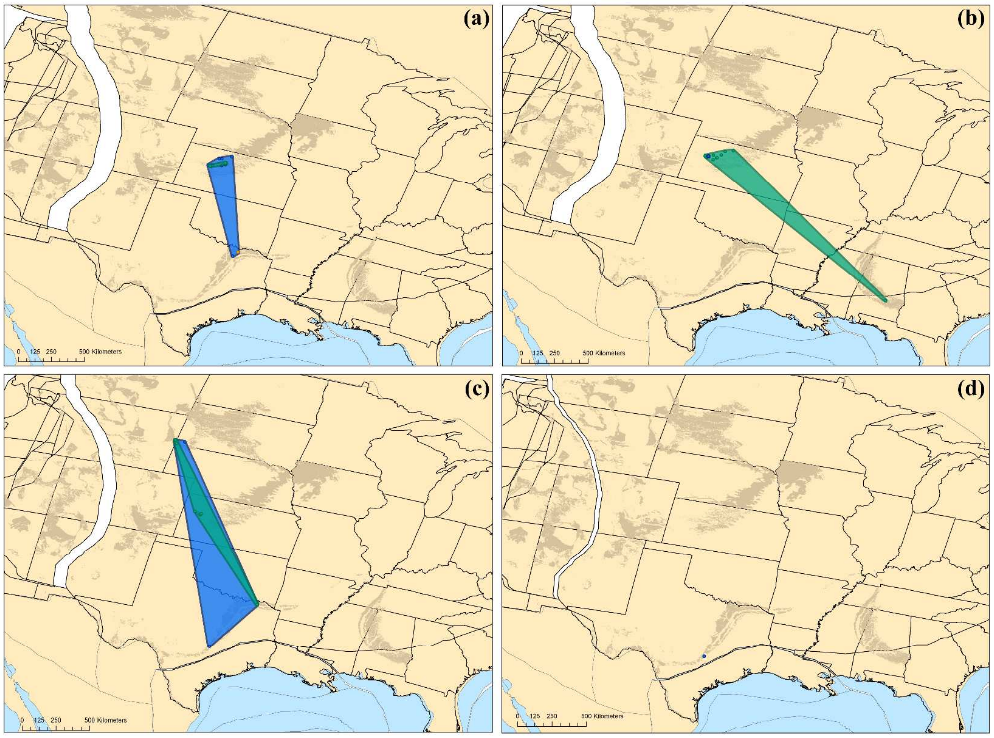

Figure 3. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for the majority of two-taxon comparisons in this study. Tylosaurus sp. (blue) and Platecarpus sp. (dark green) distributions are shown during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. These taxa do not show a statistically significant negative range area correlation through time and thus are not identified as CCRs. Present day outcrop of Late Cretaceous sediments is also shown (brown).
278x206mm (300 x 300 DPI)

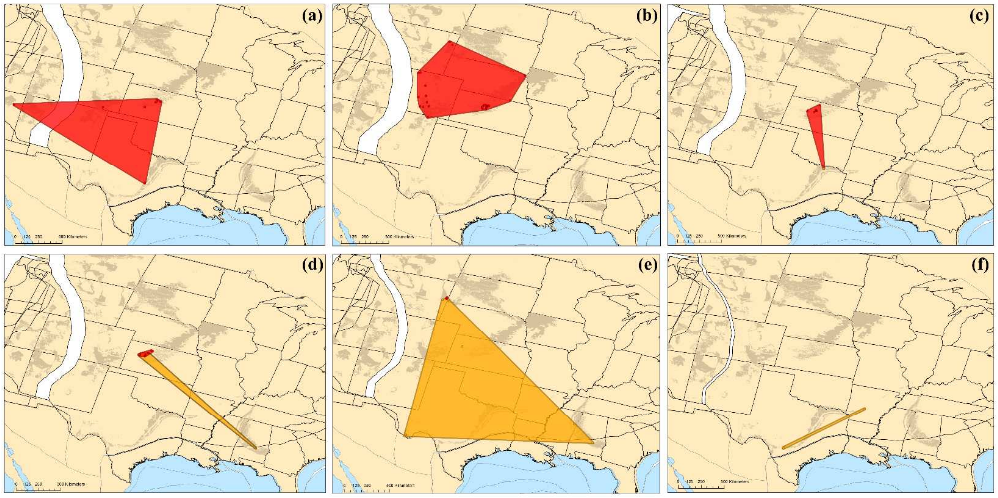

Figure 4. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the general predicted geographic pattern of a CCR, although the negative relationship in range size is not statistically significant. Squalicorax falcatus (red), and S. kaupi (orange) distributions are shown during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. S. falcatus shows stable, though dynamic, range size until the origination of S. kaupi in the Coniacian (c). After this time, S. falcatus experiences sequential decrease in range size resulting in extinction at the end Campanian (e). This example illustrates a negative relationship between the range area of two ecologically similar species within the same genus, and thus could represent a competitive replacement of S. falcatus by S. kaupi. Present day outcrop of Late Cretaceous sediments is also shown (brown).
277x138mm (300 x 300 DPI)

Table 1.

Taxon A	**Taxon B**	**Spearman's ρ**	**p-value**	**Kendall's τ**	**p-value**
Squalicorax falcatus	*Squalicorax kaupi*	-0.812	0.072	-0.690	0.052
Ptychodus anonymus	*Ptychodus mortoni*	-0.185	0.742	-0.077	0.828
Ptychodus anonymus	*Ptychodus whipplei*	0.936	0.025	0.833	0.019
Ptychodus mortoni	*Ptychodus whipplei*	0.092	0.883	0.077	0.828

Table 2.

Taxon A	Taxon B	Spearman's ρ	p-value	Kendall's τ	p-value
(a) Inferred pelagic, predatory taxa					
Cretoxyrhina mantelli	*Squalicorax falcatus*	0.928	0.022	0.828	0.020
Cretoxyrhina mantelli	*Squalicorax kaupi*	-0.882	0.036	-0.786	0.027
Cretoxyrhina mantelli	*Tylosaurus* sp.	-0.765	0.097	-0.643	0.070
Cretoxyrhina mantelli	*Platecarpus* sp.	-0.431	0.392	-0.386	0.277
Cretoxyrhina mantelli	*Xiphactinus* sp.	0.174	0.733	0.138	0.697
Squalicorax falcatus	*Squalicorax kaupi*	-0.812	0.072	-0.690	0.052
Squalicorax falcatus	*Tylosaurus* sp.	-0.696	0.144	-0.552	0.120
Squalicorax falcatus	*Platecarpus* sp.	-0.334	0.533	-0.298	0.401
Squalicorax falcatus	*Xiphactinus* sp.	0.371	0.419	0.333	0.348
Squalicorax kaupi	*Tylosaurus* sp.	0.765	0.097	0.571	0.107
Squalicorax kaupi	*Platecarpus* sp.	0.770	0.108	0.617	0.082
Squalicorax kaupi	*Xiphactinus* sp.	0.058	0.933	0.000	1.000
Platecarpus sp.	*Tylosaurus* sp.	0.524	0.283	0.463	0.192
Platecarpus sp.	*Xiphactinus* sp.	0.152	0.833	0.149	0.674
Tylosaurus sp.	*Xiphactinus* sp.	-0.058	0.933	-0.138	0.697
(b) inferred nekto-benthic, durophagus taxa					
Ptychodus anonymus	*Ptychodus mortoni*	-0.185	0.7417	-0.0772	0.828
Ptychodus anonymus	*Ptychodus whipplei*	0.936	0.0250	0.8333	0.019
Ptychodus anonymus	*Rhinobatos incertus*	0.880	0.0500	0.7454	0.036
Ptychodus mortoni	*Ptychodus whipplei*	0.092	0.8833	0.0772	0.828
Ptychodus mortoni	*Rhinobatos incertus*	-0.058	0.9333	0.0000	1.000
Ptychodus whipplei	*Rhinobatos incertus*	0.7860	0.1167	0.5963	0.093

Table 3.

Stage	Spearman's ρ	p-value	Kendall's τ	p-value
Cenomanian	0.886	0.016	0.733	0.039
Turonian	0.775	0.049	0.683	0.031
Coniacian	0.905	0.001	0.805	0.001
Coniacian*	0.700	0.2333	0.600	0.142
Santonian	0.551	0.163	0.743	0.101
Campanian	0.764	0.056	0.651	0.040
Maastrichtian	0.886	0.667	0.817	0.201
Total (combined)	0.733	0.020	0.556	0.025