

## Cretaceous tetrapod fossil record sampling and faunal turnover: Implications for biogeography and the rise of modern clades

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### ABSTRACT

We use newly compiled data on global occurrences of Cretaceous lepidosaurs, mammals and crocodylomorphs, and existing data on dinosaurs, to investigate faunal turnover and fossil record heterogeneity. Statistically significant relationships between many clade-specific fossil record sampling proxies within major continental areas (e.g. European mammal-bearing formations) suggest that temporal patterns of fossil record sampling intensity of the most abundant tetrapod clades are similar to each other, with a few exceptions that might reflect clade-specific facies preferences or differences in worker effort (especially in poorly-sampled regions such as Gondwana). However, the absence of strong statistical relationships between tetrapod sampling proxies from different continental areas suggests that there is no unified 'global' sampling signal for terrestrial tetrapods. The Cretaceous witnessed substantial faunal turnover and the rise of many 'advanced' clades that today dominate terrestrial faunas. Despite strong spatiotemporal heterogeneity in sampling of the Cretaceous tetrapod record, it is clear that this transition occurred in a spatiotemporally staggered fashion. Thus, it cannot be attributed to a temporally localised early Late Cretaceous (Cenomanian–Turonian) extinction event. Many advanced clades, including eutherian mammals, iguanian and gekkotan squamates, and the main cryptodiran turtle crown clades first appeared, or first attained high fossil diversities, in Asia. However, relatively poor sampling and dating of 'middle' Cretaceous terrestrial deposits means that hypotheses of Asian, rather than Laurasian, diversifications remain tentative. Differences between Gondwanan and Laurasian faunas became progressively greater during the Cretaceous, and although many Gondwanan clades survived the end-Cretaceous extinction event, these only survive to the present as relictual populations with narrow geographic ranges (e.g. monotremes and rhynchocephalians).

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### 1. Introduction

The Cretaceous Period (145.5–65.5 million years ago [Ma]) was a transitional phase in the evolution of life that saw the origins or diversifications of angiosperms (flowering plants), pollinating insects (e.g. Grimaldi, 1999; Dilcher, 2000), and a number of major extant vertebrate groups, including therian mammals (e.g. Ji et al., 2002; Luo et al., 2003, 2011), ornithuromorph birds (e.g. Zhou, 2004; Clarke et al., 2005; O'Connor et al., 2011), iguanians, gekkonomorphs, and snakes (Gardner and Cifelli, 1999; Novacek, 1999; Fara and Benton, 2000; Evans, 2003; Apesteguía and Zaher, 2006; Lloyd et al., 2008). It terminated in the

dramatic extinction of non-avian dinosaurs, alongside other 'key players' in Mesozoic ecosystems. These included other tetrapods, such as pterosaurs and most marine reptiles, as well as marine invertebrates such as ammonoid cephalopods and rudist bivalves (MacLeod et al., 1997; Bambach, 2006). Substantial research attention has focused on this extinction event, resulting in numerous palaeontological studies of terminal Cretaceous diversity (e.g. Sheehan and Fastovsky, 1992; MacLeod et al., 1997; Bambach, 2006). However, this has perhaps drawn attention away from changes in faunal composition that occurred prior to the end of the Cretaceous, many of which encompass the rise of important components of the modern fauna.

Recent studies have observed substantial faunal turnover in a diverse range of Late Cretaceous tetrapod groups, both on land, and in the marine realm. These include lepidosaurs (Evans, 1998, 2003; Nydam, 2002), dinosaurs (Coria and Salgado, 2005; Novas et al., 2005; Novas,

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2009; Upchurch et al., 2011), pterosaurs (Unwin, 2006; Butler et al., 2009, 2012a, 2012b), and ichthyosaurs (e.g. Maish and Matzke, 2000; Sander, 2000; Lingham-Soliar, 2003; Motani, 2005; Fischer et al., 2012). However, most observations have been derived by comparing relatively well-sampled 'middle' Cretaceous (Aptian–Albian/Cenomanian) and latest Cretaceous (Campanian–Maastrichtian) assemblages. The generally poor early Late Cretaceous (Cenomanian/Turonian–Santonian) terrestrial fossil record hinders characterisation of the taxonomic pattern, timing, and cause of Late Cretaceous faunal turnover (e.g. Fara and Benton, 2000; Barrett and Willis, 2001; Nydam, 2002; Fastovsky et al., 2004; Upchurch and Barrett, 2005). Nevertheless, these characterisations are central to understanding Cretaceous biogeography, the influence on vertebrates and possible ecological selectivity of a hypothesised Cenomanian/Turonian boundary extinction, and the rise of the modern biota. Crucially, this interval witnessed the decline and extinction of many ancient lineages that had crossed the Jurassic/Cretaceous boundary (145.5 Ma) more than 50 million years previously. These extinctions resulted in a substantial increase in continent-scale endemism during the Cretaceous, enforced by oceanic barriers resulting from Pangaea fragmentation that created the modern continents.

Questions regarding the influence of anthropogenic and geological sampling biases on our perception of macroevolutionary patterns and past diversity change in tetrapods have been largely restricted to examinations of global-scale palaeodiversity (e.g. Upchurch and Barrett, 2005; Fröbisch, 2008; Barrett et al., 2009; Benson et al., 2010a; Butler et al., 2011). However, the value and meaning of 'global' palaeodiversity studies have been questioned (e.g. Vermeij and Leighton, 2003; Benton et al., 2011, 2012), and regardless of the value of global studies, the necessity for confirmation via regional studies has generally been affirmed (e.g. Jackson and Johnson, 2001; Alroy, 2003). Despite this, few studies have been attempted on regional scales, and fewer still have examined and compared multiple continental areas (but see Alroy (1996, 2000) for studies of North American mammals; Benton et al. (2004), Irmis and Whiteside (2012) and Irmis et al. (2012) for tetrapods over the Permo–Triassic boundary; and Mannion and Upchurch (2011) and Upchurch et al. (2011) for Mesozoic dinosaurs). Furthermore, because most studies focus on a single taxonomic group, few quantitative data have been available to address questions of whether the fossil records of different clades (e.g. dinosaurs vs. mammals) and preservational types (e.g. macrofossil vs. microfossil) are affected by common biases, and whether these biases are driven primarily by geological factors such as rock amount, or by anthropogenic factors, such as collection bias. However, geographical, taxonomic, and preservational variations may profoundly influence hypotheses of past diversity and biogeography, so this information is central to understanding the history of Life on Earth. As a relatively well-sampled interval of geological time that has been the focus of intensive recent taxonomic interest, the Cretaceous represents an ideal case study for investigating and attempting to understand these factors.

Here, we review the evidence for Cretaceous tetrapod turnover, especially during a concentrated interval in the early Late Cretaceous (Cenomanian–Coniacian), and assemble new, stage-level palaeodiversity datasets, and clade-specific sampling proxies for major groups within higher tetrapod clades, i.e. Crocodylomorpha, Lepidosauria and Mammalia, partitioned by major continental area. We also use an existing dataset for Dinosauria (including Avialae; Mannion et al., 2012). These datasets are used to: (1) examine the impact of a possible end-Cenomanian extinction event on driving early Late Cretaceous faunal turnover in terrestrial and marine tetrapods; (2) assess the role of fossil record sampling in constraining our understanding of faunal turnover and biogeography during this important interval, and (3) investigate whether different clades, preservational types, and continental areas exhibit similar sampling biases. We also assess the possible influence of heterogeneous sampling of the Cretaceous fossil record on biogeographic hypotheses pertaining to the rise of major tetrapod taxa, including extant clades.

### 1.1. End-Cenomanian extinction event and climatic fluctuations

Nearly all studies of the end-Cenomanian extinction event concern marine taxa. By contrast, only one study has focussed on the influence of any such event on land (Eaton et al., 1997). Studies of marine invertebrates suggest a prolonged, step-wise extinction. The earliest extinctions were among dominant, reef-building, and environmentally sensitive rudist bivalves at the end of the early Cenomanian (95.9 Mya; Johnson and Kauffman, 1990). Extinction subsequently affected taxa with broader environmental tolerances, culminating 0.5–1.0 Myr before the end of the Cenomanian (94.1–94.6 Mya; Kauffman, 1995; Ogg et al., 2008). A causal link between these extinctions and rapid, contemporaneous environmental fluctuations has been suggested (e.g. Kauffman, 1995). These include: (1) a global oceanic anoxic event (OAE II; Schlanger and Jenkyns, 1976; Arthur et al., 1985) that resulted in anoxic or dysoxic (Wan et al., 2003) conditions below the marine surface mixing zone for ~880 kyrs; (2) the Cretaceous greenhouse thermal maximum, accompanied by reduced latitudinal thermal gradients (Hay, 1988, 2008); and (3) an exceptional sea level highstand (e.g. Skelton, 2003; Miller et al., 2005). Studies of local sections from around the world demonstrate high levels of extinction among benthic foraminifera (e.g. Huber et al., 1999; Wan et al., 2003) and invertebrates, especially of infaunal and most epifaunal taxa (dysoxia-resistant inoceramid bivalves are an exception) (Harries and Little, 1999). Pelagic Foraminifera show high levels of taxonomic turnover (e.g. Huber et al., 1999; Wan et al., 2003), calcareous nanoplankton (primarily coccolithophores) show a short-term, non-significant (Bown, 2005) or significant (Lloyd et al., 2012) loss of diversity, and some studies of global palaeodiversity have suggested that marine tetrapod diversity crashed after the end of the Cenomanian (Bardet, 1992, 1994; Fischer et al., 2012; but see Benson et al. (2010a) and Benson and Butler (2011) for a contradictory viewpoint). However, pelagic invertebrates such as ammonoid and belemnite cephalopods might actually have diversified through the extinction interval (Harries and Little, 1999), and Schumacher (2011) indicated a middle Turonian extinction of the macropredaceous plesiosaurian clade Pliosauridae, by competition with mosasaurid squamates, rather than by overarching environmental factors in the late Cenomanian and early Turonian.

Despite various observations suggesting a taxonomically inclusive Cenomanian/Turonian boundary extinction event, testing of this hypothesis is complicated by recent studies of both vertebrates (Benson et al., 2010a; Benson and Butler, 2011; Upchurch et al., 2011), and invertebrates (Smith et al., 2001; Smith and Benson, in press), which indicate that low Turonian species richness may be a sampling artefact, driven by a reduction in available fossiliferous rocks. This is accompanied by a major facies shift in the preserved marine fossil record, from species rich shallow water habitats in the Cenomanian, to relatively depauperate offshore habitats ('taphonomic megabias'; Gale et al., 2000; Smith et al., 2001; Smith and Benson, in press), associated with the early Turonian highstand (Miller et al., 2005). Phylogenetic ghost ranges of many taxa, including echinoids (Smith et al., 2001) and some Foraminifera (Banerjee and Boyajian, 1996), span the supposed extinction interval, indicating that a high proportion of supposed extinctions in fact represent 'pseudoextinctions'. Consequently, studies of restricted taxonomic groups (Banerjee and Boyajian, 1996), informed by accurate systematic data (Patterson and Smith, 1987, 1989; Smith et al., 2001), and studies corrected for sampling bias (Hora and Marshall, 1998; Alroy et al., 2008; Alroy, 2010a; Benson et al., 2010a; Mannion et al., 2011; Upchurch et al., 2011) have found little evidence for a substantial extinction event at the Cenomanian/Turonian boundary. Thus, it appears that the end-Cenomanian 'extinction event' might not have resulted from a crash in species diversity, but from a dramatic decline in opportunities to sample ancient biodiversity.

Although several studies of terrestrial tetrapods have examined the Early–Late Cretaceous (i.e. Albian–Cenomanian) transition in detailed regional sections (Cifelli et al., 1997, 1999; Jacobs and Winkler, 1998),

only one study focussed on the Cenomanian–Turonian transition (Eaton et al., 1997). Eaton et al. (1997) examined faunal changes in brackish, terrestrial and freshwater communities across the Cenomanian/Turonian boundary section in southwestern Utah. This showed that terrestrial (vertebrate) and brackish water families exhibited zero, or very little, extinction. In fact, metatherian mammals, and dinosaur groups that were important components in later terrestrial ecosystems, actually diversified through the Turonian (although in freshwater ecosystems, 60% of the osteichthyan and turtle families that had crossed the Jurassic/Cretaceous boundary became extinct at the end of the Cenomanian).

## 2. Materials and methods

### 2.1. Fossil record sampling proxies

Many metrics have been proposed to quantify fossil record sampling. Some, such as counts of fossil-bearing lithostratigraphic units (e.g. geological formations; Peters and Foote, 2002; Upchurch and Barrett, 2005; Barrett et al., 2009; Benson and Butler, 2011), map area of outcrop (Smith and McGowan, 2007, 2008; McGowan and Smith, 2008), and rock volume estimates or counts of continuous depositional sequences ('packages'; e.g. Peters, 2005; Peters and Heim, 2010) attempt to capture the availability of fossiliferous rock. Lithological evenness describes the range and distribution of environmental types (facies) represented (Rook et al., 2013–this issue). Others, such as counts of fossil collections, relate to the amount of collecting effort exerted by palaeontologists, and are the basis of subsampling approaches that aim to correct for uneven sampling of the available fossil record (e.g. Alroy et al., 2008; Alroy, 2010a, 2010b).

We used several metrics to depict the distribution of Cretaceous terrestrial fossil record sampling and assemblage completeness in time and space. These were: (1) published measures of rock availability (western European rock outcrop area: Smith and McGowan, 2007; North American fossiliferous terrestrial units and North American sediment coverage area: Peters and Heim, 2010); and (2) counts of fossil collections and fossil-bearing formations including records of specific clades, downloaded from the Paleobiology Database (<http://paleodb.org>) on 16th January 2012, and screened manually. These data series are all available in Appendix S1.

### 2.2. Palaeodiversity data

We made a significant effort to complete entry of taxonomic and global occurrence data for Cretaceous mammals, terrestrial lepidosaurs (i.e. excluding mosasauroids and other marine squamates), and terrestrial crocodylomorphs (i.e. excluding thalattosuchians) in the Paleobiology Database. This builds on substantial previous work, especially by M. Carrano and J. Alroy (e.g. Alroy, 1996), focussed on North America. We also used an existing dataset of Mesozoic dinosaur occurrences (Butler et al., 2011; Upchurch et al., 2011; Mannion et al., 2012) to examine Cretaceous dinosaurian faunal history. Paleobiology Database data were downloaded and assigned to higher taxonomic categories chosen to reflect clades that crossed the Jurassic/Cretaceous boundary, and the rise of crown clades or other important clades, but mediated by known systematic uncertainty. For example, our taxonomic categories for terrestrial lepidosaurs include Rhychocephalia, and major squamate clades that likely crossed the Jurassic/Cretaceous boundary: Anguimorpha (other than Serpentes), Lacertiformes, 'Scincoidea', Iguania and Gekkonomorpha. They also include a category for basal taxa, either on the squamate stem lineage or at the base of one of the major squamate lineages, but for which phylogenetic consensus has not been attained. Finally, they include a category for Serpentes, an important extant clade that originated, or at least is first recorded, during the Cretaceous. Taxonomic categories for other clades are shown in Appendix S1.

All datasets were parsed into major continental areas: North America, Asia (excluding India), Europe, and Gondwana. Gondwanan sampling is sufficiently poor, and that sampling is sufficiently patchily distributed, that combining data from its constituent regions (South America, Africa, Madagascar, India, Antarctica and Australia) is pragmatic. For most regions, geographically widespread occurrences are scattered through time. However, pronounced spatiotemporal clustering is evident. In other words, a limited number of local areas have yielded most fossil occurrences within particular time bins. For example in Europe, which was an archipelago during the Cretaceous, many Early Cretaceous tetrapod fossils were collected from the United Kingdom (Berriasian Purbeck Limestone Group; Hauterivian–Aptian 'Wealden' deposits); but productive Hauterivian–Albian deposits are also present in Spain (e.g. Las Hoyas and the Galve syncline), Belgium (Barremian–Aptian deposits at Bernissart) and Italy (Albian deposits at Civita di Pietraraja). Late Cretaceous European tetrapod fossils are known from Romania (Maastrichtian Sânpetru and Densus-Ciula formations), Hungary, France and Spain.

Most North American Cretaceous tetrapod fossil occurrences are from the western half of the continent, which was located in Laramidia, a landmass west of the Western Interior seaway. By far the majority of Asian occurrences are from China and Mongolia. However, other important, predominantly microfossil, assemblages are known from the early Late Cretaceous of other Central Asian regions such as Uzbekistan and Kazakhstan (Nessov, 1997), and productive Early Cretaceous localities are present in Japan, Russia, and southeast Asia. Finally, many Gondwanan occurrences are from Patagonia in South America. However, the earliest Cretaceous Gondwanan occurrences are predominantly from Berriasian microvertebrate sites of the Anoual syncline in Morocco, and important North African Aptian–Cenomanian localities are known especially in Niger, Morocco, and Egypt. Brazilian faunas range primarily from Aptian–Maastrichtian (though the ages of Late Cretaceous Brazilian deposits are poorly constrained [see below]). Most of the records from India and Madagascar are of Maastrichtian age. Australian occurrences are restricted to the Aptian–Albian. For more details see Section 4, Appendix S1 or the Paleobiology Database (<http://paleodb.org>).

Taxon occurrences, fossil collections, and fossil-bearing formations were assigned to any stage-level bin they might intersect, following Upchurch and Barrett (2005). However, to avoid massively extended temporal ranges caused by stratigraphic uncertainty, datapoints with stratigraphic uncertainty spanning more than three stages were excluded from our data series. The most notable exclusion on this basis is the Adamantina Formation of Brazil, which has yielded numerous important tetrapod fossils. However, there is no consensus for the age of this geological unit, with some authors considering it Campanian–Maastrichtian (e.g. Gobbo-Rodrigues et al., 1999; Santucci and Bertini, 2006), whereas others have argued for a Turonian–Santonian age (e.g. Dias-Brito et al., 2001).

An important qualification must be made regarding data quality. Although every effort was made to enter data and taxonomic opinions from the published literature, not all clades have been studied equally, and the taxonomy of some clades is currently in greater flux than others. For example, far fewer publications contained data on Cretaceous crocodylomorphs (1003 publications; Paleobiology Database, downloaded 28 February 2012), lepidosaurs (940) and mammals (814) compared to dinosaurs (2825), and the relationships of many Early Cretaceous lepidosaurs are highly uncertain (e.g. Evans, 2003; Conrad, 2008). Nonetheless, many of the large-scale palaeodiversity patterns reported in the published literature, and documented in our dataset, are the subject of widespread consensus, and limited taxonomic uncertainty probably does not strongly influence our conclusions regarding the distribution of fossil record sampling in space and time.

### 2.3. Analytical methods

We use pairwise comparisons to examine whether the sampled fossil records of mammals, dinosaurs, terrestrial crocodylomorphs, and

terrestrial squamates (measured by clade-specific sampling proxies; e.g. squamate-bearing formations) were similar within continental areas (North America, Asia, Europe, Gondwana; e.g. North American squamate-bearing formations were compared to North American mammal-bearing formations), and whether the records of individual clades were similar between continental areas (e.g. Gondwanan crocodylomorph-bearing formations were compared to European crocodylomorph-bearing formations). These comparisons were made using two multiple regression techniques on log-transformed data with a start of one (i.e.  $\log(X+1)$ ). In the first, ordinary least squares (OLS) regression was used to compare the first differences of one data series with the first differences of one other data series, and of stage duration. An example of the model equation corresponding to one of our OLS regressions is:

(North American squamate-bearing formations)  
 $\sim$  (North American mammal-bearing formations) + (stage duration)

The same model equations were used in the second technique, but instead of first differencing, a first order autoregressive model fit was estimated in the context of generalised least squares regression (GLS) to capture serial correlation observed in the data. Both regression methods were implemented in R version 2.10.1 (R Development Core Team, 2009), and GLS required the package nlme version 3.1-96 (Pinheiro et al., 2009). GLS is probably more appropriate because it corrects for the amount of serial correlation actually observed in the data, but OLS of first differences is more stringent and is included for comparison because first differences are widely used in palaeontological time series comparisons.

These analyses allowed us to test whether the sampled fossil records of different clades were comparable within continents. Differences could arise from genuine geographic or facies differentiation between clades, or from incomplete and heterogeneous sampling of the available fossil record. In the latter case, our expectation was that the temporal profile of sampling of taxonomic groups should be most similar in intensively-sampled continents such as North America. These profiles could be less similar in continents with immature sampling histories, in which sampling of available outcrops is not approaching saturation. However, similar clade-specific sampling profiles might be obtained within a poorly sampled continent if fossils of all types had been collected from the same set of geological units and localities. The analyses also allowed us to test whether the sampled terrestrial tetrapod fossil records of different continents were comparable. Differences could arise from the absence of a coordinated 'global' signature (e.g. one driven by global eustatic sea level change, or some other world-wide causal mechanism) to the terrestrial tetrapod fossil record.

### 3. Results

#### 3.1. Heterogeneous spatiotemporal sampling

Sampling of Turonian–Santonian fossil ecosystems, in both the terrestrial and marine realms, is poor in North America and Europe (Figs. 1–4; Appendix S1; Fastovsky et al., 2004; Upchurch and Barrett, 2005; Smith and McGowan, 2007; Benson et al., 2010a; Peters and Heim, 2010). Counts of geological formations yielding terrestrial tetrapods, and those yielding marine animals, are both low in the middle of the Late Cretaceous (Turonian–Santonian) compared to the immediately preceding and following intervals. Counts of terrestrial tetrapod and marine animal fossil collections are also low. However, these apparently low amounts of sampling may be caused by the uneven duration of Late Cretaceous stages; those stages with the shortest duration (Turonian, Coniacian, and Santonian) are also those with the fewest fossil-bearing formations and collections. Because of the counting procedure employed here (formations and collections were counted in any stage they might intersect, even when extended temporal range reflected stratigraphic

uncertainty), formation and collection counts cannot simply be divided by stage duration, or summed between combined stages. However, this result (low counts of fossil-bearing collections and formations) remains when counts are made with early Late Cretaceous stages considered together as a single unit (i.e. Turonian–Santonian [10 Ma]; Ogg et al., 2008) (Appendix S1). In fact, zero European mammalian and lepidosaur taxa are known from this interval (Figs. 2 and 3), and all European crocodylomorphs from this time range are Santonian (from Hungary or France [with stratigraphic uncertainty]; e.g. Ősi et al., 2007).

Asia and Gondwana are relatively better-sampled in the early Late Cretaceous than North America and Europe. In Asia, crocodylomorphs and mammals are relatively well sampled over the Turonian–Santonian interval (Figs. 3 and 4). This is primarily because of important Central Asian collections (e.g. Nessov, 1997). Perhaps similarly, in South America, the Adamantina Formation of Brazil has yielded many crocodylomorph and several lepidosaur discoveries (Appendix S1). However, the age of the Adamantina Formation is uncertain (see above), and it may date from any stage of the Late Cretaceous other than the Cenomanian (Gobbo-Rodrigues et al., 1999; Dias-Brito et al., 2001; Santucci and Bertini, 2006); thus, it was excluded from our analytical datasets.

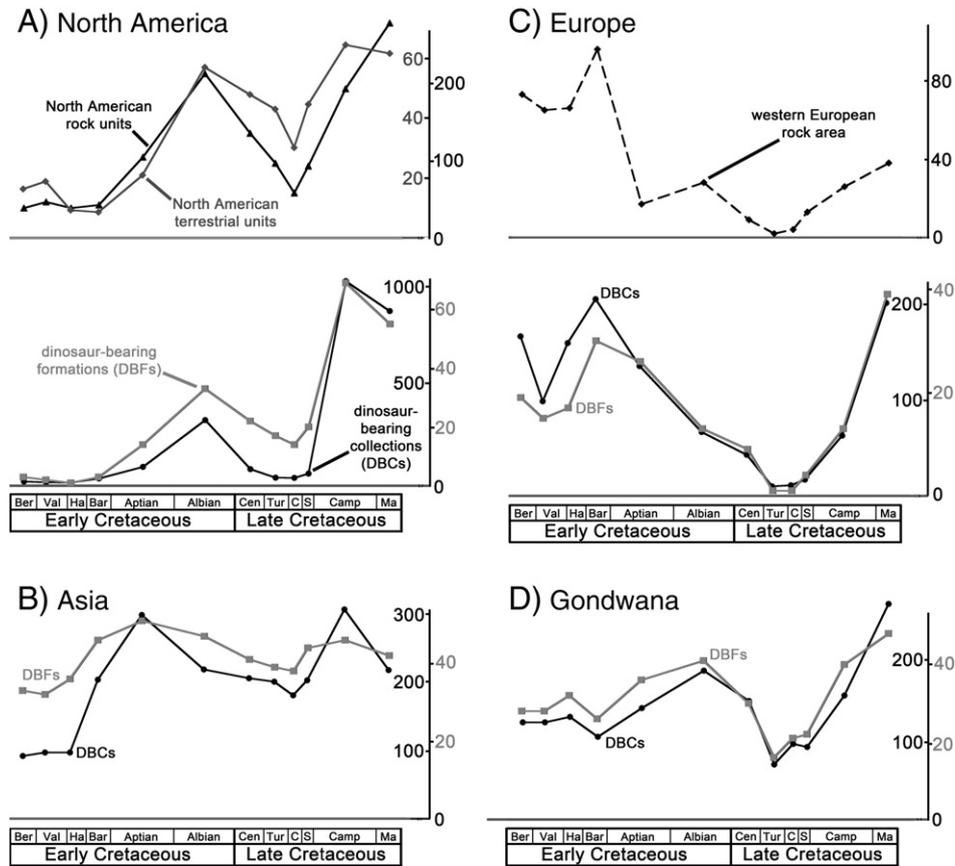
The temporal sampling profiles show other notable features. Taxonomically determinate remains of mammals, lepidosaurs and crocodylomorphs are entirely unknown from the first four stages of the North American Cretaceous (Berriasian–Barremian) (Figs. 2–4). Sampling is also very poor in the early part of the Cretaceous in Gondwana and Asia (Figs. 2–4), although rich microvertebrate faunas are known from the Anoual syncline (Berriasian) in Morocco (Sigogneau-Russell et al., 1998), and the Kuwajima Formation of the Tetori Group (Valanginian) of Japan (Isaji et al., 2005). Europe, by contrast, has a rich earliest Cretaceous record.

The Campanian–Maastrichtian record is the most intensively sampled interval for most continents and taxonomic groups examined, especially North America (Figs. 2–4). However, this effect is much less prominent in Europe, Gondwana, and Asia (and in Asia it is focussed in the Campanian), and varies among taxonomic groups. For example, crocodylomorphs may be genuinely rare in highly-arid Campanian faunas of Mongolia, which yield most Campanian Asian fossils. Thus, few crocodylomorph-bearing formations and collections are known from the Campanian of Asia (Fig. 4).

#### 3.2. Comparisons between tetrapod sampling and the geological record in North America and Europe

North American macrostratigraphic data (Peters and Heim, 2010) show a similar pattern to sampling of North American vertebrate fossils (Fig. 1). They indicate very few fossiliferous terrestrial units in the first four stages of the Cretaceous (Berriasian–Barremian), and also relatively few in the Turonian–Santonian. These count data are subject to the same issues of variable stage duration described for formation and collection counts (see above). However, static measures, such as the areal extent of deposits at outcrop (depositional area), should be less strongly affected by time bin duration. Three such measures are available: the depositional area of North American rock (Peters and Heim, 2010), and western European terrestrial and marine outcrop areas (Smith and McGowan, 2007) (Fig. 1). North American rock area, and western European terrestrial outcrop area exhibit minima in the Cenomanian–Santonian, and western European terrestrial area is generally lower in the Late Cretaceous than it is in the Early Cretaceous. European marine outcrop area is exceptional as it shows a Cenomanian–Santonian peak (Smith and McGowan, 2007). However, Smith et al. (2001) and Gale et al. (2001) demonstrated that the Turonian highstand allowed deep marine oceanographic conditions and an unusually depauperate deep water fauna to prevail over the preserved Turonian European shelf.

Most statistical comparisons (OLS regression of first differences, and GLS regression, both also incorporating stage duration as an explanatory



**Fig. 1.** Rock records and dinosaur fossil record sampling proxies for A, North America (rock record above; dinosaur record below), B, Asia (dinosaur record), C, Europe (rock record above; dinosaur record below), and D, Gondwana (dinosaur record).

variable) between North American macrostratigraphic data and North American clade-specific sampling proxies yield statistically significant results (Table 1). Exceptions were OLS comparisons of North American depositional area with some sampling proxies (DBC, MBF, MBC, and LBC, abbreviations explained in Table 1), and all OLS comparisons with crocodylomorph-specific sampling proxies (Table 1). One reason for the differences between depositional area and terrestrial tetrapod sampling might be that depositional area includes both terrestrial and marine deposits (Peters and Heim, 2010). It is likely that North American crocodylomorphs (which do not include 'terrestrial' [non-aquatic] basal ['protosuchian'] and notosuchian taxa) were restricted to a mesic subset of terrestrial depositional environments, and units with appropriate facies. This might explain why North American crocodylomorph-specific sampling proxies do not have a significant relationship with other measures of the North American rock record using OLS regression of first differences.

Most comparisons between western European rock outcrop area and clade-specific sampling proxies for Europe (including eastern Europe) are significant using GLS regression (Table 1). Only comparisons with DBC, LBF, and LBC are significant using OLS regression of first differences (Table 1). Comparisons here may fail because of the incorporation of eastern European data into clade-specific sampling proxies, but the absence of this data in the western European outcrop area metric. However, overall our results suggest the available fossil records of both North America and Europe are somewhat correlated with rock availability, particularly when GLS regression is used (possibly the more appropriate technique; see Section 2.3).

### 3.3. Intracontinental comparisons between taxonomic groups

Inspection of the data (Figs. 1–4), and the results of our regression analyses (Tables 2–5; Appendix S1) suggest that different clades generally

have similar sampled fossil records within a given continental area. Thus, the coefficients of most clade-specific sampling proxies were statistically significant when used (alongside stage duration) to explain other clade-specific sampling proxies from within the same continental area. OLS of first differences recovered fewer statistically significant comparisons than GLS, but suggests a similar overall pattern.

Of all the continental areas examined, the fewest statistically significant comparisons were recovered within Asia. Using OLS, significant comparisons were found between DBC and CBC, and between MBC and LBC. Both correlations suggest that within Asia, the macrovertebrate sites yielding dinosaurs and crocodylomorphs are distinct from the microvertebrate sites and Lagerstätten yielding most mammals and lepidosaurs. However, this does not seem to be the case in other continental areas (see below). GLS additionally found significant comparisons between dinosaur-bearing and crocodylomorph-bearing formations, and between dinosaur and mammal collections.

Within North America, OLS demonstrates significant comparisons between MBC and CBC, LBC and CBC, and between LBF and CBF. GLS found significant comparisons between all clade-specific sampling proxies other than DBFs and CBFs.

Within Europe, OLS recovered significant comparisons between DBC/DBFs and MBC/MBFs, between DBC/DBFs and CBC/CBFs, and between MBC/MBFs and CBC/CBFs (i.e. all comparisons not involving lepidosaurs). GLS found significant comparisons between all clade-specific sampling proxies other than those comparing lepidosaurs to crocodylomorphs.

Finally, within Gondwana OLS found significant comparisons between DBC and LBC, between DBC and CBC, and between LBC and CBC. GLS found all comparisons to be significant. The presence of fewer significant comparisons within some arguably better-sampled continents (i.e. North America, Asia) suggests that strong comparability between clade-specific sampling proxies for Cretaceous Gondwana

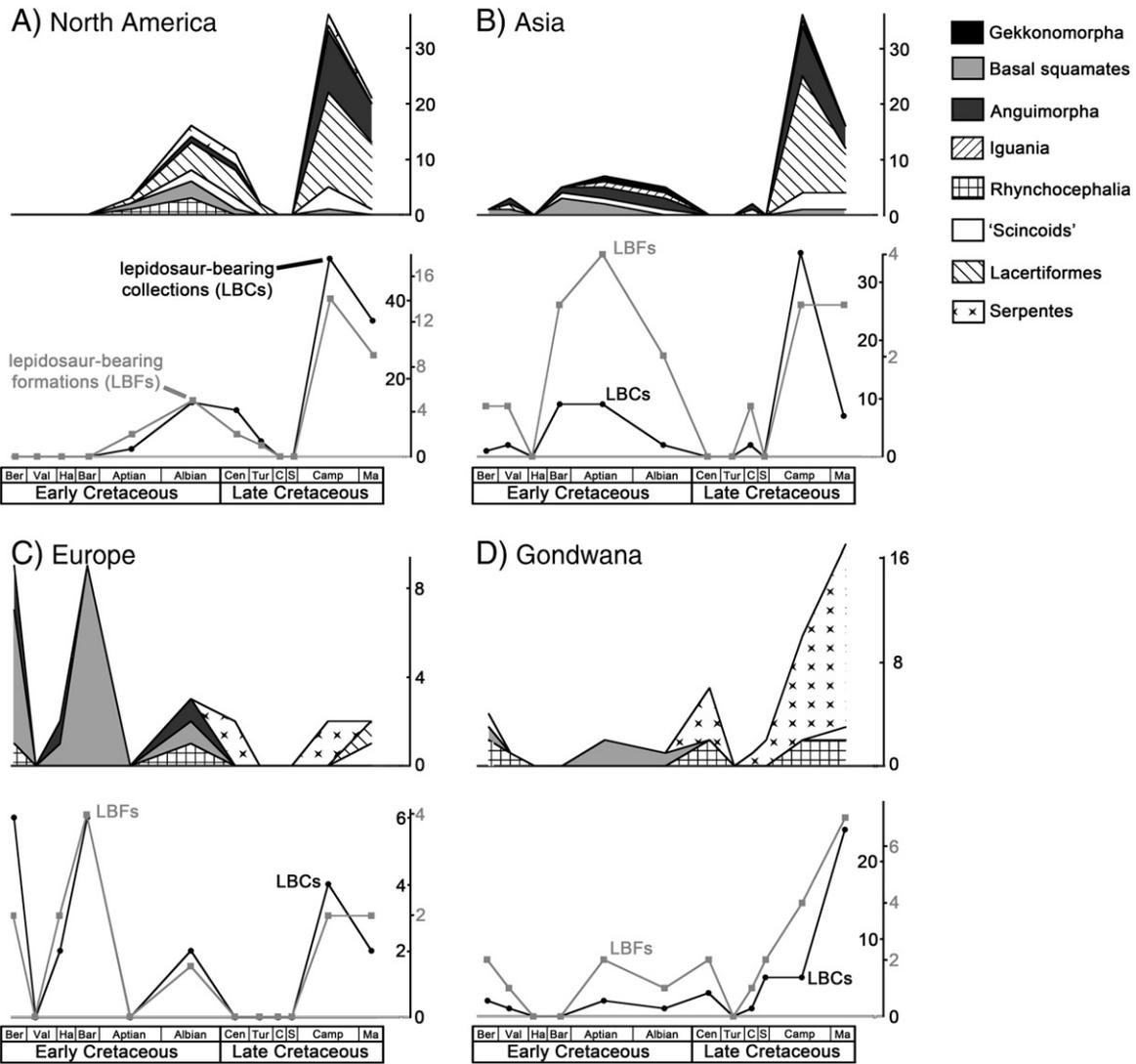


Fig. 2. Lepidosaur taxonomic abundances (above) and fossil record sampling proxies (below) for A, North America, B, Asia, C, Europe, and D, Gondwana. See key for meaning of fills.

does not arise from saturated, and thus even, sampling of the available record. In fact, it may indicate the opposite, i.e. that sparse sampling of the Gondwanan Cretaceous tetrapod record has thus far failed to reveal strong interclade geographic or facies differences evident from the records of other continents. Alternatively, most of the Gondwanan Cretaceous record may represent a more homogeneous, highly arid physical environment (Skelton, 2003; Australia is an exception to this), and contain mammals, squamates, dinosaurs, and crocodylomorphs uniformly adapted to that environment, and thus exhibiting little facies differentiation.

3.4. Intercontinental comparisons within taxonomic groups

Most comparisons of clade-specific sampling proxies between different continental areas recovered non-significant results (Appendix S1). This suggests the absence of a consistent 'global' terrestrial sampling regime (see also Upchurch et al. (2011) on dinosaurs), and is consistent with some observations of geographic heterogeneity in the marine and total rock records (McGowan and Smith, 2008; but see Peters, 2005). Comparisons between the European and Gondwanan dinosaur and mammal records were an exception; dinosaur comparisons were significant using both OLS and GLS, and mammal comparisons were only marginally non-significant (Table 6). However, the p-values associated with these significant results are generally close to the threshold for

significance (0.05) and thus may have arisen by chance, due to the large number of pairwise comparisons made during the present study, suggesting no reason to invoke a larger, causative process. Nonetheless, aspects of the gross similarity between the Cretaceous terrestrial tetrapod records of Europe and Gondwana are notable, including the abundance of earliest Cretaceous sampling (in Europe and Morocco), which is scarce elsewhere.

4. Review of Late Cretaceous faunal turnover

Compiling the data for this study resulted in many insights into the fossil records of specific Cretaceous tetrapod clades. These insights are useful in assessing the mode of Cretaceous faunal turnover, and the role of heterogeneous fossil record sampling in providing limits to our understanding of this process. Below we outline the fossil records of the major clades used in our study (lepidosaurs, mammals, crocodylomorphs and dinosaurs), before combining this information with the results from our analysis to provide a synthesis of the Cretaceous faunal transition of tetrapods, including the rise of extant clades.

4.1. Lepidosaurs

Extant lepidosaurs comprise two sister clades, Squamata and Rhynchocephalia. Rhynchocephalia are found today only in New Zealand,

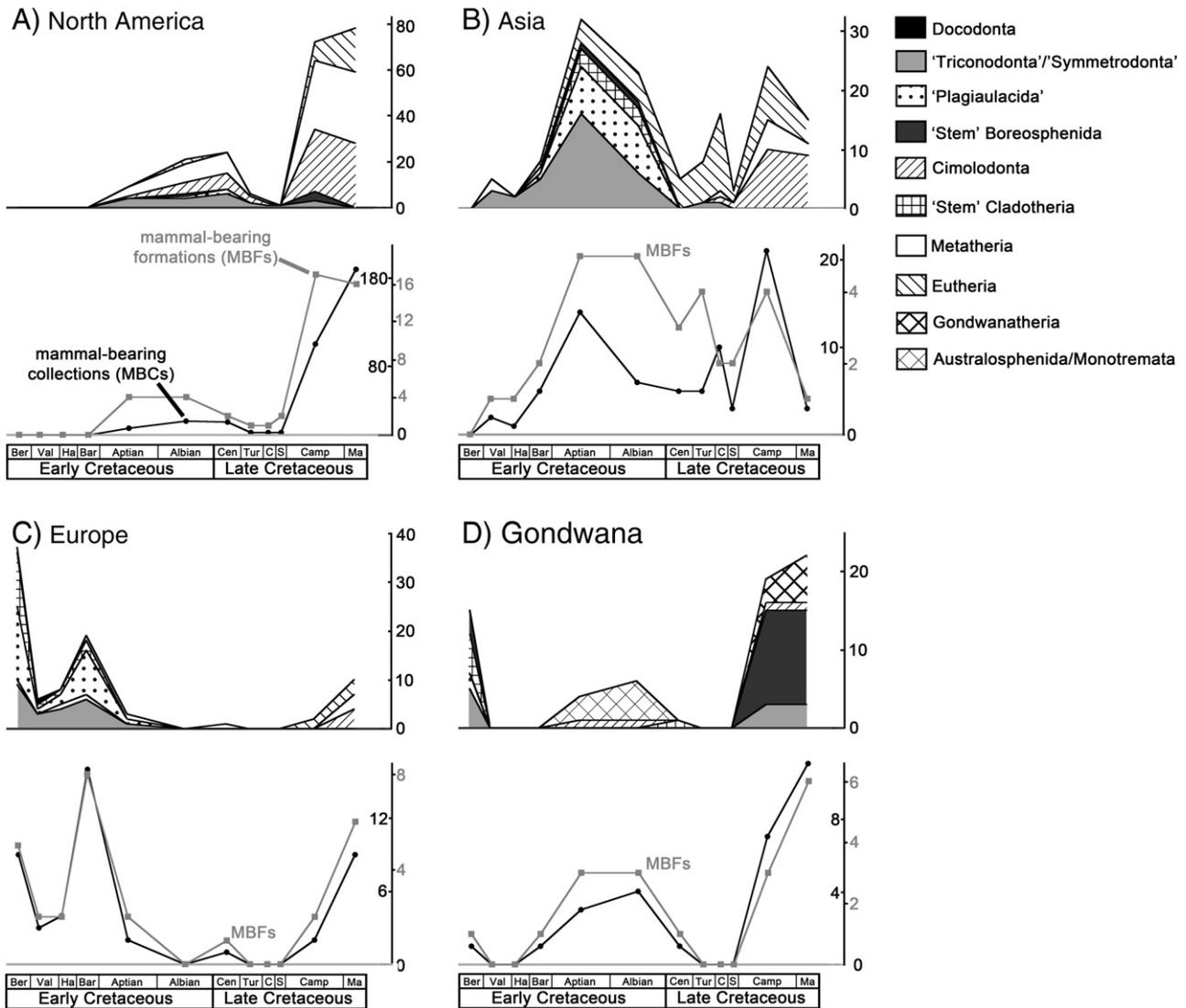


Fig. 3. Mammalian taxonomic abundances (above) and fossil record sampling proxies (below) for A, North America, B, Asia, C, Europe, and D, Gondwana. See key for meaning of fills.

represented by a single genus, *Sphenodon*. However, their fossil record demonstrates a global distribution, high abundance, and diverse ecotypes, in the Triassic–Jurassic, when their diversity exceeded that of squamates (Evans, 2003; Jones et al., 2009). In contrast, extant squamates are globally distributed and taxonomically diverse, comprising ~8000 species representing several major clades within Squamata (Iguania, Gekkonomorpha, Lacertiformes, Scincoidea, Amphisbaenia, and Anguimorpha, possibly including Serpentes, which are treated separately here). Phylogenetic topology indicates that the stem lineages of most of these clades had appeared by the Middle Jurassic, and crossed the Jurassic/Cretaceous boundary (e.g. Evans, 1998; Conrad, 2008). However, this interval also saw the origin of three major groups, the snakes (Serpentes), the marine lizards (Mosasauroidea), and possibly Amphisbaenia. Snakes appeared by the late Early Cretaceous (e.g. Gardner and Cifelli, 1999), and they attained a global distribution and high ecological diversity by the early Late Cretaceous (Cenomanian; e.g. Rage and Werner, 1999), becoming especially abundant in Gondwana (Evans, 2003). Mosasauroids and other marine squamates, including some snakes (e.g. pachyophids), appeared in the Cretaceous, but are not discussed further here. The Cretaceous record of amphisbaenians is more controversial. Two central Asian taxa were initially identified as amphisbaenians, *Sineoamphisbaena* (Campanian; Wu et al., 1993) and *Hodzhakulia* (Albian; Nessov, 1985). However, *Sineoamphisbaena* has been reidentified as a gilmoretiiid lacertiform,

and *Hodzhakulia*, based on maxillary fragments, is indeterminate (Kearney, 2003).

The Cretaceous witnessed a major transition from lepidosaur assemblages dominated by clades that were abundant in the Jurassic, to 'advanced' faunas, including some extant families, in Laurasia (Evans, 1998, 2003; Nydam, 2002). 'Jurassic-type' faunas are known from the earliest Cretaceous (Berriasian) of England (Evans and Searle, 2002) and Morocco, containing squamates such as 'paramacellodids', possible early anguimorphs (e.g. 'dorsetisaurids') and rhynchocephalians (Evans and Sigogneau-Russell, 1997) (Fig. 2). There is little consensus on the relationships of many Jurassic–Early Cretaceous squamate taxa (Evans, 2003, p.524). For example, *Parviraptor* from the Middle Jurassic–Early Cretaceous of the UK might be an early anguimorph (Evans, 1994) or gekkonomorph (Conrad, 2008); and 'paramacellodids' might be stem scincoids (Evans and Chure, 1998; Reynoso and Callison, 2000) or a paraphyletic array including some basal anguimorphs (Conrad, 2008).

'Jurassic-type' faunal elements persisted until the Aptian–Albian in Europe and North America (Evans, 1998; Nydam and Cifelli, 2002), although rhynchocephalians and anguimorphs became rare, and herbivorous borioteiid lacertiformes made their first North American appearance (Fig. 2; Nydam, 2002; Nydam et al., 2007). Clear taxonomic distinctions between Gondwanan and Laurasian assemblages are not evident during this interval. However, some uncertainty exists, because

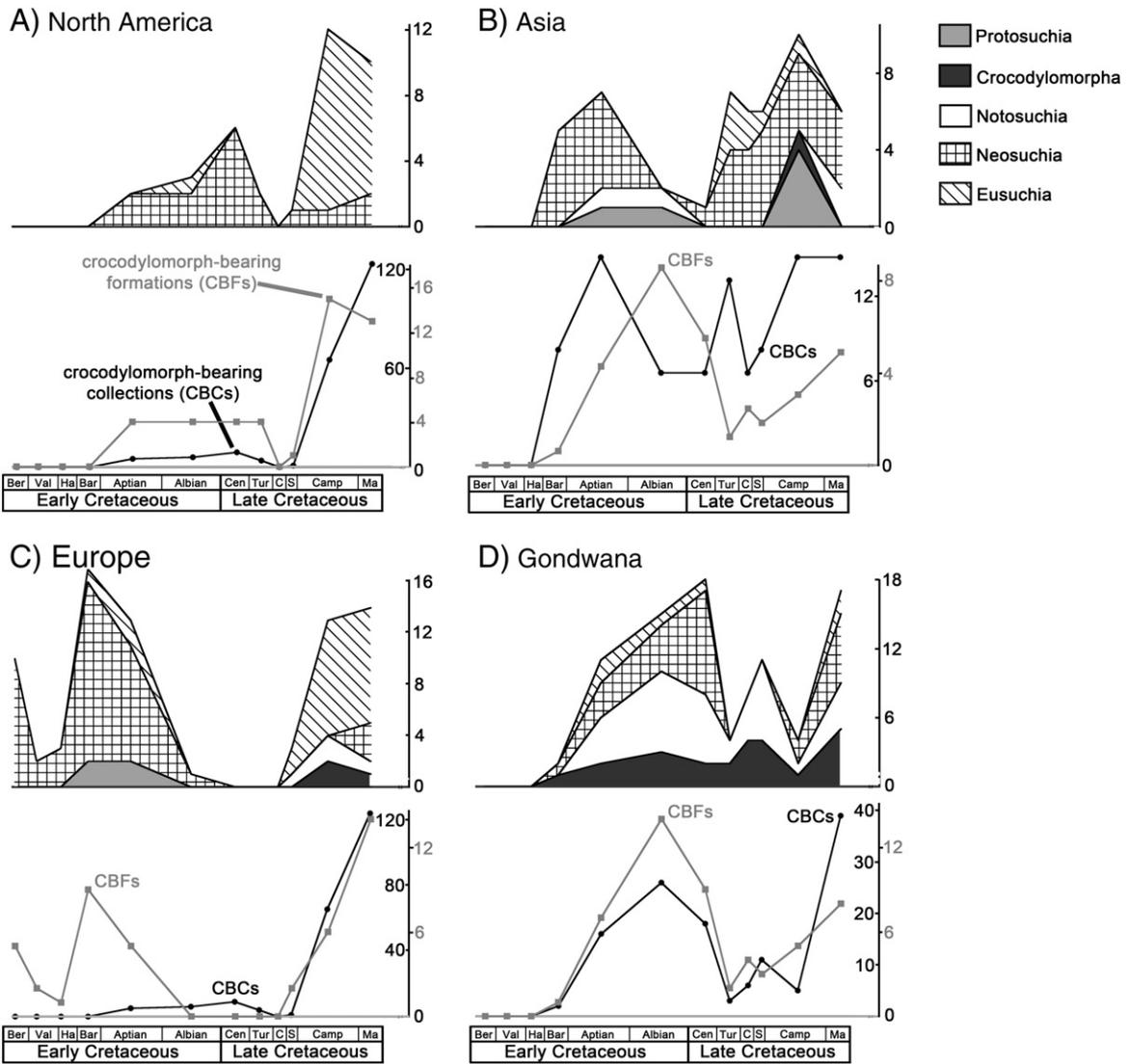


Fig. 4. Crocodylomorph taxonomic abundances (above) and fossil record sampling proxies (below) for A, North America, B, Asia, C, Europe, and D, Gondwana. See key for meaning of fills.

Gondwanan Early Cretaceous lepidosaurs are very poorly sampled. Additionally, the Early Cretaceous East Asian lepidosaur faunas might have had a more derived aspect; exceptionally well-preserved specimens from the Barremian–Aptian Yixian Formation of China suggest the absence of rhynchocephalians, but include the shinisaurid anguimorph *Dalinghosaurus* (Evans and Wang, 2005) and a long-ribbed glider, *Xianglong* (Li et al., 2007); and the Tetori Group of Japan has yielded the oldest known borioteioid *Kuwajimalla* (Valanginian; Evans and Manabe, 2008). However, the absence of North American faunas of comparable age prevents definite conclusions on the geographical origins of these clades.

Late Cretaceous lepidosaur assemblages show increasing geographic differentiation (Fig. 2), but are only sampled globally in the Campanian–Maastrichtian (sampling is particularly intense in parts of North America and Asia). European lepidosaur assemblages remain poorly-sampled, but include snakes, borioteioids of North American affinities, and putative ‘paramacellodids’ all from the Campanian–Maastrichtian of Romania (Folie and Codrea, 2005; Nydam et al., 2007) (if correctly identified, these would be the only Late Cretaceous paramacellodids, but this characterisation is weak and they are best regarded as ?scincoids). Asian and American faunas of this age also lack rhynchocephalians, and include a high proportional representation of extant squamate clades such as Platyntota, Anguinae, Iguania,

Lacertiformes (primarily the extinct borioteioids), Xenosauridae, and Xantusiidae (Nydam, 2002; Evans, 2003). In Gondwana, snakes are abundant, and rhynchocephalians remain present, sometimes at high local abundances (Fig. 2; e.g. Apesteguía and Novas, 2003; Evans, 2003; Krause et al., 2003; Jones et al., 2009). Other than snakes, Gondwanan squamates are rare, but include four taxa from Brazil: *Olindalacerta* and *Tijubina* of uncertain affinities (Aptian; e.g. Simões, 2012); and the putative iguanians *Brasiliguana* (?Turonian–Santonian; Nava and Martinelli, 2011) and *Pristiguana* (Maastrichtian; Estes and Price, 1973) from Brazil. *Brasiliguana* is based on very fragmentary material of uncertain affinities, and the type of *Pristiguana* is lost, but could represent a teioid or iguanian (S. E. E. pers. obs.).

Because the early Late Cretaceous is very poorly sampled, even in Asia and North America (Coniacian–Santonian in North America; Turonian–Santonian in Asia), aspects of the Cretaceous lepidosaur faunal transition are uncertain. However, late Early Cretaceous faunas provide some insight into the evolution of ‘advanced’ lepidosaur faunas in North America and Asia (Nydam, 2002). The Khovoor assemblage (Aptian–Albian) of Mongolia reportedly contains archaic taxa such as dorsetisaurids and ‘paramacellodids’, alongside derived elements making their first definite appearances. These derived elements (borioteioids, monsteraes, and possible scincoids and cordylids) do not appear in North America until the Mussentuchit local fauna (Albian/Cenomanian

**Table 1**  
Statistical comparisons of clade-specific sampling proxies with measures of rock availability in North America (Peters and Heim, 2010) and Europe (Smith and McGowan, 2007). Comparisons were made using multiple regression including stage duration as a non-optional explanatory variable (described in the text).  $N = 12$ .  $R^2$  is the generalized coefficient of determination described by Cox and Snell (1989; Nagelkerke, 1991).  $\Phi$  is the serial correlation coefficient at a time lag of one stage. Significant p-values are indicated by an asterisk.

Dependent variable	Explanatory variable	OLS of first differences			GLS (AR1 model)			
		Coefficient	R2	p-value	Coefficient	R2	p-value	$\Phi$
<i>North America</i>								
Dinosaur-bearing formations (DBFs)	Terrestrial units	0.84	0.52	0.013*	0.95	0.52	0.003*	0.97
	Rock area	0.79	0.64	0.003*		0.55		
Dinosaur-bearing collections (DBC)	Terrestrial units	1.10	0.42	0.033*	1.45	0.48	0.003*	0.74
	Rock area	0.72	0.25	0.126	0.86	0.27	0.073	1
Mammal-bearing formations (MBFs)	Terrestrial units	0.62	0.46	0.025*	0.77	0.45	0.008*	1
	Rock area	0.42	0.28	0.097	0.53	0.23	0.061	1
Mammal-bearing collections (MBC)	Terrestrial units	1.14	0.38	0.049*	1.41	0.45	0.015*	1
	Rock area	0.71	0.20	0.177	0.92	0.25	0.106	1
Lepidosaur-bearing formations (LBFs)	Terrestrial units	0.81	0.57	0.009*	0.95	0.56	0.001*	0.81
	Rock area	0.59	0.41	0.039*	0.67	0.35	0.021*	1
Lepidosaur-bearing collections (LBC)	Terrestrial units	1.42	0.38	0.047*	1.81	0.54	<0.001*	0.29
	Rock area	1.05	0.28	0.099	1.48	0.38	0.008*	0.47
Crocodylomorph-bearing formations (CBFs)	Terrestrial units	1.03	0.36	0.056	1.38	0.58	<0.001*	-0.05
	Rock area	0.69	0.22	0.151	1.07	0.33	0.004*	0.30
Crocodylomorph-bearing collections (CBC)	Terrestrial units	1.39	0.36	0.057	1.99	0.46	0.002*	0.55
	Rock area	0.76	0.14	0.261	0.95	0.23	0.161	1
<i>Europe</i>								
Dinosaur-bearing formations (DBFs)	Rock outcrop	0.59	0.40	0.394	0.67	0.53	<0.001*	-0.75
Dinosaur-bearing collections (DBC)	Rock outcrop	0.58	0.41	0.038*	0.83	0.48	<0.001*	-0.32
Mammal-bearing formations (MBFs)	Rock outcrop	0.39	0.15	0.248	0.55	0.28	0.007*	0.01
Mammal-bearing collections (MBC)	Rock outcrop	0.55	0.21	0.163	0.74	0.35	0.003*	0.05
Lepidosaur-bearing formations (LBFs)	Rock outcrop	0.64	0.41	0.036*	0.38	0.32	0.013*	-0.04
Lepidosaur-bearing collections (LBC)	Rock outcrop	0.84	0.39	0.045*	0.43	0.36	0.008*	-0.32
Crocodylomorph-bearing formations (CBFs)	Rock outcrop	0.35	0.10	0.365	0.47	0.11	0.157	0.49
Crocodylomorph-bearing collections (CBC)	Rock outcrop	0.49	0.14	0.266	0.71	0.20	0.046*	0.36

boundary) of the Cedar Mountain Formation of central Utah (Nydham, 2002). This observation led Nydam (2002) to suggest interchange between North American and Asian Cretaceous lepidosaurs in the Albian. Based on the pattern of higher taxa making their first appearances in Asia, prior to appearing in North America, Nydam (2002) also suggested two subsequent interchange events in the Turonian (Xantusiidae and Necrosauridae; Eaton et al., 1999) and Campanian (Iguania, Xenosauridae, Varanidae). However, he qualified this with a caveat regarding poor sampling of the early Late Cretaceous records of both continents.

#### 4.2. Mammals

During the Mesozoic, mammals occupied a wide range of ecological niches at body sizes <12 kg (but generally smaller ~100 g), including scansorial taxa, gliders, burrowers, beaver-tailed swimmers, and predators of small vertebrates (Luo, 2007). Cretaceous mammal

faunas document the transition from high-level taxonomic diversity in the Early Cretaceous, including many clades that first appeared in the Jurassic, to dominance of comparatively fewer clades, including the therian crown group (Eutheria + Metatheria) in the Late Cretaceous of Laurasia (Fig. 3; Kielan-Jaworowska et al., 2004). A distinctive Gondwanan fauna, rooted partially in the Middle Jurassic appearance of australotribosphenidans, developed and diversified during the Cretaceous; although many of its constituents survived into the lowermost Cenozoic (e.g. Gelfo and Pascual, 2001; Rougier et al., 2009; Goswami et al., 2011), only Monotremata are still extant. Documenting the precise timing and modality of these transitions is difficult because of poor sampling of early Late Cretaceous rocks. In fact, taxonomically-determinate remains of Turonian–Santonian age have not been collected outside of central Asia and a few North American localities (Fig. 3). Thus, although some information is available on early Late Cretaceous mammals of Laurasia, very little is known about Gondwana.

**Table 2**  
Statistical comparisons of clade-specific sampling proxies within North America. Comparisons were made using multiple regression including stage duration as a non-optional explanatory variable (described in the text).  $N = 12$ .  $R^2$  is the generalized coefficient of determination described by Cox and Snell (1989; Nagelkerke, 1991).  $\Phi$  is the serial correlation coefficient at a time lag of one stage. Significant p-values are indicated by an asterisk.

Dependent variable	Explanatory variable	OLS of first differences			GLS (AR1 model)			
		Coefficient	R2	p-value	Coefficient	R2	p-value	$\Phi$
DBFs	MBFs	0.73	0.31	0.083	0.85	0.39	0.007*	0.85
	LBFs	0.61	0.30	0.087	0.75	0.34	0.020*	0.94
	CBFs	0.29	0.17	0.223	0.38	0.14	0.104	1
DBC	MBCs	0.42	0.20	0.180	0.73	0.53	<0.001*	-0.26
	LBCs	0.43	0.32	0.075	0.51	0.29	0.030*	1
	CBCc	0.23	0.10	0.364	0.73	0.20	<0.001*	0.08
MBFs	LBFs	0.38	0.19	0.194	0.56	0.25	0.053	1
	CBFs	0.30	0.30	0.088	0.40	0.24	0.036*	1
MBCs	LBCs	0.48	0.33	0.070	0.60	0.32	0.027*	1
	CBCs	0.58	0.50	0.017*	0.99	0.50	<0.001*	0.27
LBFs	CBFs	0.41	0.39	0.045*	0.79	0.45	<0.001*	-0.13
LBCs	CBCs	0.76	0.56	0.009*	0.79	0.63	<0.001*	0.19

**Table 3**

Statistical comparisons of clade-specific sampling proxies within Europe. Comparisons were made using multiple regression including stage duration as a non-optional explanatory variable (described in the text).  $N = 12$ .  $R^2$  is the generalized coefficient of determination described by Cox and Snell (1989; Nagelkerke, 1991).  $\Phi$  is the serial correlation coefficient at a time lag of one stage. Significant p-values are indicated by an asterisk.

Dependent variable	Explanatory variable	OLS of first differences			GLS (AR1 model)			
		Coefficient	R2	p-value	Coefficient	R2	p-value	$\Phi$
DBFs	MBFs	0.65	0.44	0.028*	0.99	0.43	<0.001*	-0.17
	LBFs	0.21	0.05	0.535	0.28	0.02	0.410	0.69
	CBFs	0.54	0.40	0.041*	0.60	0.34	0.016*	0.62
DBCcs	MBCs	0.60	0.58	0.007*	0.71	0.51	0.001*	0.54
	LBCs	0.22	0.10	0.364	0.24	-0.01	0.311	0.81
	CBCc	0.47	0.43	0.033*	0.51	0.33	0.015*	0.70
MBFs	LBFs	0.44	0.18	0.204	1.16	0.29	0.003*	
	CBFs	0.70	0.60	0.006*	0.69	0.53	0.002*	0.45
MBCs	LBCs	0.46	0.26	0.116	0.61	0.22	0.054	0.44
	CBCs	0.64	0.47	0.022*	0.69	0.45	0.004*	0.35
LBFs	CBFs	0.19	0.04	0.547	0.40	0.24	0.014*	-0.30
LBCs	CBCs	0.13	0.01	0.728	0.41	0.36	0.002*	-0.63

In general, earlier Cretaceous faunas are only patchily-sampled, but seem to have been characterised by high taxonomic diversity of groups that dominated Jurassic faunas (Fig. 3): 'plagiaulacidan' multituberculates, taxa of 'triconodont' and 'symmetrodont' grades, basal cladotherians such as dryolestoids, basal boreosphenidans, and also late-surviving non-mammalian synapsids – the tritylodonts – in Japan and Russia (e.g. Isaji et al., 2005). Thus, for example, the well-sampled earliest Cretaceous (Berriasian) fauna of the UK shares genera and higher taxa with the Late Jurassic Morrison Formation of the USA (Simpson, 1928, 1929; Kielan-Jaworowska et al., 2004). Mammalian faunas from the late Early Cretaceous (Aptian–Albian) of Laurasia generally continue to exhibit a high abundance of Jurassic and earlier Cretaceous taxa, such as eutriconodontids and spalacotheriid "symmetrodonts" (Fig. 3; Kielan-Jaworowska et al., 2004).

In contrast to the high abundance of several other mammal groups, eutherians, metatherians, and cimolodontan multituberculates are relatively rare and less diverse in Jurassic and Early Cretaceous faunas (e.g. the recently described eutherian *Juramaia* from the Middle Jurassic of China; Luo et al., 2011; the metatherian *Sinodelphys* and the eutherian *Eomaia* from the Barremian of China; Ji et al., 2002; Luo et al., 2003; and the cimolodontan *Paracimexomys crossi* from the Aptian–Albian of Utah; Cifelli, 1997). As sister taxa, both Metatheria and Eutheria must have been present in the Jurassic, and thus both must have crossed the Jurassic/Cretaceous boundary. Nonetheless, both groups are rare through most of the Early Cretaceous (Fig. 3; e.g. Averianov and Skutschas, 2001; Davis and Cifelli, 2011), although a high abundance of, as yet undescribed, eutherians was reported from the Aptian–Albian Fuxin Formation of China (Kusuhashi et al., 2010). Taxonomically diverse metatherians and cimolodontans do occur from the Albian–Cenomanian boundary in North America, although only a few localities

have been sampled, and metatherians occur only at low abundances (Cifelli, 1990, 2004; Eaton, 1993, 1995). In Europe, the metatherian *Arcantiodelphys* is known from Cenomanian deposits (Vullo et al., 2009). Central Asian faunas are uniquely well-sampled from the Cenomanian–Santonian and contain abundant eutherians representing several clades, including Zhelestidae and Zalabdalestidae, alongside rarer 'symmetrodonts', cimolodontans, and metatherians from the Turonian onwards (Fig. 3; Kielan-Jaworowska and Nesson, 1992; Nesson et al., 1998; Averianov and Archibald, 2005). Based on this evidence it has been suggested that eutherians underwent their first major diversification in Asia (Kielan-Jaworowska, 1981; Archibald and Averianov, 2005), although relatively poor sampling of contemporaneous European and North American rocks renders this conclusion tentative (Fig. 3), and it has been suggested more generally that both clades have Laurasian origins (Archibald, 2003).

Later Cretaceous faunas are dominated by the stem members of the extant clades Metatheria and Eutheria, which continue to flourish to the present, as well as cimolodontan multituberculates, which are now extinct, but were diverse for the first half of the Cenozoic (e.g. Scott, 2005). These groups are overwhelmingly diverse and abundant in well-sampled Campanian–Maastrichtian faunas of North America and Asia (Fig. 3; Kielan-Jaworowska et al., 2004). Rapid increase in the dental complexity of cimolodontans in Santonian and younger rocks suggests an adaptive radiation that continued into the earliest Palaeogene, and may be linked to the rise of angiosperms (Wilson et al., 2012).

A shift from an apparently global distribution for many higher clades in the Late Jurassic and earliest Cretaceous to increasingly high levels of provincialism in the later Cretaceous is also evident (Fig. 3; Kielan-Jaworowska et al., 2004; Rich, 2008). Thus, as noted above, European and Moroccan Berriasian faunas share many common

**Table 4**

Statistical comparisons of clade-specific sampling proxies within Asia. Comparisons were made using multiple regression including stage duration as a non-optional explanatory variable (described in the text).  $N = 12$ .  $R^2$  is the generalized coefficient of determination described by Cox and Snell (1989; Nagelkerke, 1991).  $\Phi$  is the serial correlation coefficient at a time lag of one stage. Significant p-values are indicated by an asterisk.

Dependent variable	Explanatory variable	OLS of first differences			GLS (AR1 model)			
		Coefficient	R2	p-value	Coefficient	R2	p-value	$\Phi$
DBFs	MBFs	0.09	0.12	0.311	0.13	-0.08	0.103	0.58
	LBFs	0.04	0.08	0.423	0.05	-0.31	0.370	0.78
	CBFs	0.19	0.32	0.077	0.16	0.11	0.037*	0.75
DBCcs	MBCs	0.20	0.34	0.066	0.56	0.27	<0.001*	-0.81
	LBCs	0.13	0.34	0.067	0.13	0.05	0.502	0.96
	CBCc	0.38	0.79	<0.001*	0.41	0.77	<0.001*	0.01
MBFs	LBFs	0.05	0.01	0.827	0.05	-0.12	0.789	0.90
	CBFs	0.66	0.26	0.116	0.59	0.21	0.083	0.92
MBCs	LBCs	0.48	0.57	0.009*	0.49	0.41	0.005*	0.93
	CBCs	0.51	0.16	0.231	0.69	0.60	<0.001*	-0.87
LBFs	CBFs	0.71	0.10	0.361	0.21	-0.03	0.497	0.26
LBCs	CBCs	1.04	0.26	0.117	0.63	0.15	0.157	0.42

**Table 5**  
Statistical comparisons of clade-specific sampling proxies within Gondwana. Comparisons were made using multiple regression including stage duration as a non-optional explanatory variable (described in the text).  $N = 12$ .  $R^2$  is the generalized coefficient of determination described by Cox and Snell (1989; Nagelkerke, 1991).  $\Phi$  is the serial correlation coefficient at a time lag of one stage. Significant p-values are indicated by an asterisk.

Dependent variable	Explanatory variable	OLS of first differences			GLS (AR1 model)			
		Coefficient	R2	p-value	Coefficient	R2	p-value	$\Phi$
DBFs	MBFs	0.25	0.24	0.132	0.30	0.25	0.019*	0.26
	LBFs	0.23	0.33	0.069	0.25	0.21	0.027*	0.45
	CBFs	0.25	0.36	0.054	0.24	0.15	0.033*	0.90
DBC	MBCs	0.37	0.31	0.083	0.36	0.37	0.007*	0.09
	LBCs	0.27	0.42	0.035*	0.27	0.35	0.007*	0.27
	CBCc	0.24	0.43	0.032*	0.23	0.19	0.018*	0.83
MBFs	LBFs	0.41	0.25	0.124	0.54	0.35	0.002*	-0.56
	CBFs	0.48	0.32	0.076	0.49	0.25	0.042*	0.90
MBCs	LBCs	0.30	0.22	0.156	0.62	0.44	<0.001*	-0.41
	CBCs	0.29	0.28	0.103	0.33	0.18	0.048*	0.91
LBFs	CBFs	0.65	0.35	0.059	0.60	0.25	0.044*	0.89
LBCs	CBCs	0.63	0.50	0.016*	0.62	0.42	0.008*	0.91

elements (Sigogneau-Russell and Ensom, 1998; Sigogneau-Russell, 1999), including basal boreosphenidans (Sigogneau-Russell, 1991, 1992). However metatherians and eutherians, which are especially abundant in Laurasia by the Late Cretaceous, are very rare in Gondwana. In fact, the basal eutherian (or possible euarchontan) *Deccanolestes* from the Maastrichtian of India is the only uncontentious Gondwanan eutherian or metatherian (Goswami et al., 2011), although there are disputed eutherians or metatherians described from the Cretaceous of Madagascar (Krause, 2001; Averianov et al., 2003) and Morocco (Sigogneau-Russell, 1991; Kielan-Jaworowska, 1992). Instead, Aptian–Albian Australian localities are dominated by endemic australosphenidans and monotremes (e.g. Rich et al., 1997; Kielan-Jaworowska et al., 2004), and Late Cretaceous localities in India, Madagascar, and Argentina were dominated by lineages such as meriolestid dryolestoids and the enigmatic (but possibly multituberculate) gondwanatherian clade (Fig. 3; e.g. Bonaparte, 1990; Krause et al., 1997; Gurovich and Beck, 2007; Wilson et al., 2007; Rougier et al., 2011). Cimolodontan multituberculates were also very rare in Gondwana, having been reported based on single teeth from Argentina (Kielan-Jaworowska et al., 2007; but see Gurovich and Beck, 2007) and Australia (Rich et al., 2009).

#### 4.3. Crocodylomorphs

Mesozoic crocodylomorphs occupied a wide array of terrestrial ecosystems (e.g. Carvalho et al., 2010; Martin and Delfino, 2010), with some lineages also inhabiting marginal marine (pholidosaurids/dyrosaurids), or marine (thalattosuchians, not displayed in Fig. 4) environments. They exhibited a range of body sizes, from small forms less than a metre in length (e.g. the notosuchian *Anatosuchus*; Sereno and Larsson, 2009), to giant forms up to at least 12 m and 8 metric tons in

the case of the pholidosaurid *Sarcosuchus* (Sereno et al., 2001). Cretaceous faunas record the earliest occurrences of eusuchians, the clade including all extant crocodylians, as well as basal, extinct groups such as non-eusuchian neosuchians, notosuchians, and 'protosuchians'.

Crocodyliiformes is composed of mesoeucrocodylians and an array of small bodied basal forms, including a grade of taxa often described as 'protosuchians' (Storrs and Efimov, 2000; Pol and Norell, 2004; Fiorelli and Calvo, 2007; Pol and Gasparini, 2009; Clark, 2011). Fiorelli and Calvo (2007) recovered some of these basal forms as basal mesoeucrocodylians, i.e. the clade including metasuchians (see also Andrade et al., 2011), although this has not been supported in other studies (e.g. Ortega et al., 2000; Pol and Norell, 2004; Clark, 2011). Most of these basal forms are known only from the Jurassic, but a number of lineages survived into the Cretaceous of Eurasia, with the putative shartegosuchid *Kyasuchus* known from the late Early Cretaceous of Siberia (Clark, 2011), as well as several taxa of uncertain affinities from the Early Cretaceous of China and Russia (i.e. *Edentosuchus*, *Shantungosuchus*, *Sichuanosuchus* and *Tagarosuchus*; Storrs and Efimov, 2000; Fiorelli and Calvo, 2007). The survival of basal crocodyliiforms into the latest Cretaceous is documented by the presence of *Artzosuchus* and *Zosuchus*, as well as the previously unknown gobiosuchids, in the Campanian of Mongolia (Storrs and Efimov, 2000; Pol and Norell, 2004). Lastly, one Cretaceous occurrence of basal crocodylomorph is known from outside Eurasia, *Neuquensuchus* from the Santonian of Argentina (Fiorelli and Calvo, 2007).

Trematochampsids are a poorly understood and possibly non-monophyletic group of terrestrial basal mesoeucrocodylians known from South America and Africa, whose fragmentary remains have been recovered from the Barremian through to the Maastrichtian, and which might have survived into the Eocene (Simons and Buckley, 2009). The lack of suitable outcrops in the earliest Cretaceous of Gondwana most likely masks earlier records of this group.

**Table 6**  
Selected statistical comparisons of clade-specific sampling proxies between continental areas. Only significant ( $p < 0.05$ ) or marginally non-significant ( $p < 0.10$ ) coefficients are reported here. Full results are in Appendix S1. Comparisons were made using multiple regression including stage duration as a non-optional explanatory variable (described in the text).  $N = 12$ .  $R^2$  is the generalized coefficient of determination described by Cox and Snell (1989; Nagelkerke, 1991).  $\Phi$  is the serial correlation coefficient at a time lag of one stage. Significant p-values are indicated by an asterisk.

Dependent variable	Explanatory variable	OLS of first differences			GLS (AR1 model)			
		Coefficient	R2	p-value	Coefficient	R2	p-value	$\Phi$
European DBFs	Gondwanan DBFs	2.18	0.43	0.031*	2.22	0.48	0.017*	0.71
European DBCs	Gondwanan DBCs	1.42	0.40	0.042*	1.35	0.38	0.035*	0.88
European MBFs	Asian MBFs	-0.84	0.16	0.235	-1.05	0.28	0.043*	0.26
European MBFs	Gondwanan MBFs	0.99	0.33	0.069	0.87	0.28	0.065	0.68
North American MBCs	Gondwanan MBCs	0.83	0.34	0.063	1.02	0.36	0.030*	1
European MBCs	Gondwanan MBCs	1.14	0.36	0.056	0.94	0.28	0.068	0.83
North American CBFs	Asian CBFs	0.94	0.19	0.190	1.13	0.35	0.013*	0.53
European CBCs	Asian CBCs	0.97	0.31	0.080	0.88	0.25	0.073	0.93

*Ischyrochamps*, from the Campanian–Maastrichtian of Europe (Vasse, 1995) might be a Laurasian representative of Trematochampsidae, but its affinities remain enigmatic (Martin and Delfino, 2010). The terrestrial peirosaurids are known from the Aptian–Maastrichtian of South America (Larsson and Sues, 2007; Leardi and Pol, 2009), and Larsson and Sues (2007) also recovered the African genera *Stolokrosuchus* (Aptian–Albian) and *Hamadasuchus* (Cenomanian) within this clade. However, other authors have not supported this position of *Stolokrosuchus*, instead indicating a neosuchian placement (e.g. Jouve, 2009; Andrade et al., 2011). Majungasuchids are only represented by two genera, but are known from Cenomanian–Maastrichtian terrestrial environments of northern Africa and Madagascar (Serenó and Larsson, 2009). Majungasuchids have been recovered in a variety of positions within Mesoeucrocodylia, including sister taxon relationships with Peirosauridae (Turner and Calvo, 2005; Turner, 2006) or Notosuchia (Andrade et al., 2011), and as basal neosuchians (Larsson and Sues, 2007; Serenó and Larsson, 2009).

Notosuchia is an extinct clade of small-bodied terrestrial metasuchian crocodylomorphs known from the Cretaceous of South America, Africa, China, Madagascar and Pakistan (Serenó and Larsson, 2009; Carvalho et al., 2010; Pol and Powell, 2011), as well as possibly Europe (Company et al., 2005). However, the interrelationships and composition of Notosuchia remain in flux, with the position of sebecosuchians (sebecids and baurusuchids) varying between analyses. Turner and Calvo (2005) recovered Notosuchia and Sebecosuchia as sister taxa, whereas others have found sebecosuchians to be deeply nested within Notosuchia (e.g. Ortega et al., 2000; Pol and Powell, 2011). In contrast, Larsson and Sues (2007) placed sebecids as the sister taxon to Peirosauridae (see above), outside of Notosuchia, forming a clade they named Sebecia (see also Serenó and Larsson, 2009). Although a notosuchian placement for baurusuchids now seems well supported (Serenó and Larsson, 2009; Pol and Powell, 2011), Pol and Powell (2011) demonstrated that a sister taxon relationship with peirosaurids for sebecians was only marginally suboptimal to a position within Notosuchia. Here we discuss notosuchians as a single clade for ease, but this should be treated with some caution following the above discussion. Notosuchians represent a wide range of terrestrial ecophenotypes, including hypercarnivores, omnivores, herbivores, and mammal-like forms (Young et al., 2010). The earliest putative notosuchian occurrence comes from the Berriasian of Brazil, but basal notosuchians seem to have initially diversified during the Aptian–Albian (Carvalho et al., 2010), although their apparent rarity in the earliest Cretaceous may merely reflect the poor fossil record outside of Europe for this time interval. Uruguaysuchids (*Uruguaysuchus* and the speciose *Araripesuchus*) are known from the Barremian–Cenomanian of South America and Africa, but appear to have gone extinct in South America post-Cenomanian (Soto et al., 2011). A single occurrence in the Maastrichtian of Madagascar (Turner, 2006) indicates that this clade survived at least in some parts of Gondwana during the Late Cretaceous. The presence of notosuchians on the African mainland is restricted to the Aptian–Cenomanian (O'Connor et al., 2010), although *Simosuchus* is known from the Maastrichtian of Madagascar (Buckley et al., 2000). Other notosuchians of uncertain affinities are known throughout the Turonian–Maastrichtian of South America. The sphagesaurids represent a clade of notosuchians seemingly endemic to the Bauru Basin (Turonian–Maastrichtian) of Brazil (Marinho and Carvalho, 2009; Iori and Carvalho, 2011), although in a number of analyses *Chimaerasuchus*, from the Aptian–Albian of China (Wu et al., 1995), has been recovered as the sister taxon to Sphagesauridae (e.g. Iori and Carvalho, 2011; Pol and Powell, 2011). Company et al. (2005) recovered *Doratodon*, from the Campanian of Austria and Spain, within Notosuchia. If correct, this would represent the only known Cretaceous notosuchian occurrence in Europe; however, *Doratodon* is currently only known from fragmentary material and thus its position within Notosuchia should be treated with caution. Sebecosuchians (sensu Pol and Powell, 2011) are first known from the Turonian of South America, although there is a possible earlier, but

undescribed, occurrence from the Cenomanian of Niger (Serenó et al., 2004). The group was diverse in the Late Cretaceous of South America and included the large-bodied, hypercarnivorous baurusuchids (e.g. Montefeltro et al., 2011). Outside of South America (as well as the possible African occurrence; Serenó et al., 2004), the only other Cretaceous sebecosuchian is *Pabwehshi* from the Maastrichtian of Pakistan (Wilson et al., 2001; Turner and Calvo, 2005; Pol and Powell, 2011), although Larsson and Sues (2007) recovered it as a basal sebecian. Some non-baurusuchid sebecosuchians survived the end-Cretaceous mass extinction, including spreading to Europe and North Africa by at least the Eocene, with sebecids also known from the Paleogene and early Neogene of South America (Pol and Powell, 2011). Carvalho et al. (2010) suggested that climate played a strong role in the Cretaceous distribution of notosuchians, with this group displaying a preference for arid settings that may have been the cause for their predominantly Gondwanan-restricted distribution, particularly in the Late Cretaceous. However, biogeographic analyses suggest that much of Cretaceous crocodylomorph distribution can be explained through vicariance during Gondwanan fragmentation (Turner, 2004).

Neosuchia represents the other main clade of metasuchians and includes all extant crocodylians (i.e. derived eusuchians). Extinct neosuchian clades include goniopholids and atoposaurids, as well as the marine/marginal pholidosaurids and dyrosaurids (not discussed here). The semi-aquatic goniopholids represent the oldest known neosuchian fossils, dating back to the Early Jurassic of North America (Tykoski et al., 2002). Goniopholid diversification in the Middle–Late Jurassic, spreading into Europe and Asia, and crossed the Jurassic/Cretaceous boundary relatively unscathed, remaining diverse throughout the earliest Cretaceous (Andrade et al., 2011). However, their post-Aptian record is sparse, with no known occurrences from Europe, and only putative goniopholids, such as *Denazinosuchus* from the Campanian of North America (Andrade et al., 2011) and dubious referrals based on fragmentary remains from the Santonian–Campanian of Eurasia (Storrs and Efimov, 2000). Goniopholid occurrences suggesting a Late Cretaceous dispersal into South America have been refuted (Andrade et al., 2011). Two other semi-aquatic neosuchian clades, Elosuchidae and Stomatosuchidae, are currently only known from the Aptian to the Cenomanian of Africa (Lapparent de Broin, 2002; Serenó and Larsson, 2009). Small-bodied terrestrial atoposaurids are known from the late Middle Jurassic to Early Cretaceous of Laurasia and Africa (Martin et al., 2010), but were seemingly in decline by the Albian–Cenomanian. *Theriosuchus sympietodon*, from the Maastrichtian of Romania, along with indeterminate material from the Campanian–Maastrichtian of France and Portugal, represent the only post-Cenomanian atoposaurid occurrences, indicating a long ghost lineage (Martin et al., 2010), and a possible end-Cenomanian extinction outside of Europe. The earliest neosuchian eusuchian, *Hylaeochamps*, is known from the late Barremian–early Aptian of the Isle of Wight, United Kingdom (Clark and Norell, 1992). Additional hylaeochampsids are known from the Santonian–Maastrichtian of Europe, as well as in the Albian of North America (Ösi et al., 2007; Buscalioni et al., 2011; Brochu et al., 2012). Other basal eusuchians, or taxa closely related to this radiation, are known throughout the remainder of the middle Cretaceous and into the Santonian, e.g. *Bernissartia* in Europe, *Isifordia* in Australia and *Shamosuchus* in Asia (Salisbury et al., 2006; Pol et al., 2009; Martin and Delfino, 2010), but it was only towards the latest Cretaceous (Campanian–Maastrichtian) and into the Paleogene that crocodylians (i.e. alligatoroids, crocodyloids and gavialoids) truly began to diversify, with definite occurrences known from Europe, North America and Africa (e.g. Brochu, 2003; Jouve et al., 2008; Martin and Delfino, 2010). The affinities of several putative crocodylians from the Turonian–Campanian of Asia remain uncertain (Storrs and Efimov, 2000; Martin and Delfino, 2010). In Europe and North America, eusuchians seem to have replaced other crocodylomorphs in the Late Cretaceous, but this transition did not occur elsewhere (Salisbury et al., 2006; Martin and Delfino, 2010).

#### 4.4. Herbivorous dinosaurs (*Ornithischia* and *Sauropoda*)

Sauropods, the dominant large-bodied herbivores of the Jurassic, include only two lineages that crossed the Jurassic/Cretaceous boundary: Diplodocoidea and Macronaria (Upchurch and Barrett, 2005; Mannion et al., 2011). Diplodocoids are conspicuously absent from well-sampled Campanian–Maastrichtian dinosaur faunas, and make their last appearance in the Coniacian (the rebbachisaurid *Cathartesaura anaerobica*; Gallina and Apesteguía, 2005), whereas lithostrotian titanosauriforms appear to have radiated in the mid-Cretaceous (Aptian: Coria and Salgado, 2005; Lloyd et al., 2008; Mannion et al., 2011). Northern hemisphere Cretaceous dinosaur faunas have often been characterised as ornithischian-dominated (Bonaparte, 1986; Bonaparte and Kielan-Jaworowska, 1987). However, although ornithischians are diverse throughout the Cretaceous of the northern continents, much of this diversity occurs at small body sizes (femoral length <400 mm), and large- and medium-bodied ornithischian diversity (i.e. Hadrosauoidea, Ceratopsidae, Ankylosauria, some basal ornithopods) only slightly exceeds that of sauropods in the ‘middle’ Cretaceous of North America, and the Campanian–Maastrichtian faunas of Asia and Europe. It is only in the Campanian–Maastrichtian faunas of North America that medium–large bodied ornithischian diversity is overwhelmingly greater than that of sauropods, and possibly also in earlier (Turonian–Santonian) faunas, which are very poorly sampled. Furthermore, some of the apparent decline in sauropod diversity in North America may be partly related to an environmental sampling bias, due to under-representation of the inland facies preferred by titanosaurs in the North American Late Cretaceous record (Mannion and Upchurch, 2011).

In all three northern continents, large-bodied ornithischians (femoral length >800 mm) are substantially less diverse than sauropods for most of the Cretaceous. A radiation of medium- and large-bodied ornithischians is evident in the fossil record of the Campanian and Maastrichtian of the northern hemisphere, and is driven by the diversification of Hadrosauoidea in Asia and North America (and, to a lesser extent, in South America and Europe), and Ceratopsidae in North America. Coincident with these radiations is the Campanian–Maastrichtian diversification of mostly small-bodied pachycephalosaurs, primarily within North America, and the extinction of most non-hadrosauroid iguanodontians, with the exception of rhabdodontids within Europe (e.g. Osi et al., 2012). Among armoured (thyreophoran) ornithischians, stegosaurs declined dramatically after the Jurassic, apparently becoming extinct prior to, or at, the end of the Early Cretaceous. By contrast, ankylosaurs radiated from the earliest Cretaceous onwards, possibly replacing stegosaurs ecologically.

Basal ceratopsians (Middle–Late Jurassic, *Yinlong*, Xu et al., 2006; diverse by the Aptian–Albian and surviving until the end of the Cretaceous), possible ceratopsids (Turonian, *Turanoceratops*, Sues and Averianov, 2009; but this is controversial: Farke et al., 2009), and the major diversification within Hadrosauoidea (Prieto-Márquez, 2010) make their first appearances in Asia. However, poor sampling of contemporaneous North American rocks dilutes the significance of this observation.

The situation in Gondwana is highly distinct. Earliest Cretaceous faunas are poorly documented (Berriasian–Hauterivian of South Africa), with only the stegosaur *Paranodon* known. The situation changes in the late Early Cretaceous, in which sauropods make up almost all of Gondwanan herbivorous dinosaur diversity. It has been suggested that ornithopod dinosaurs became extinct in Africa after the Cenomanian (Lamanna et al., 2004), although this may be due to very sparse sampling of post-Cenomanian Mesozoic rocks in Africa (Lamanna et al., 2004). Finally, a latitudinal signal, in which sauropods were generally more diverse at low latitudes, and ornithischians at higher latitudes was observed by Mannion et al. (2012), and some of the exceptionally high Gondwanan sauropod diversity may be explained by the relatively low palaeotemperate latitudes of preserved Gondwanan faunas. This is consistent with the greater abundances of small–medium ornithopod and

ankylosaurian ornithichians at higher latitudes in Early Cretaceous Australia and Antarctica (Rich and Vickers-Rich, 1999; Novas et al., 2002; Barrett et al., 2010).

#### 4.5. Carnivorous dinosaurs (*non-avian theropods*)

Early Cretaceous theropod faunas are well known from North America, Asia, and Europe, and contain carcharodontosaurian allosauroids (Benson et al., 2010b; Carrano et al., 2012), and spinosaurid megalosauroids (Allain et al., 2012; Carrano et al., 2012), alongside smaller taxa, almost all of which are coelurosaurs (e.g. Weishampel et al., 2004). Coelurosaurs are abundant where taphonomic conditions favour the preservation of small individuals, especially in the Jehol Biota of China (Zhou and Wang, 2010), and represent a high diversity of clades in all three Laurasian regions, including dromaeosaurids (Turner et al., 2012), oviraptorosaurs (Ji et al., 1998; Makovicky and Sues, 1998), therizinosauroids (Xu et al., 1999; Kirkland et al., 2005), tyrannosauroids (Hutt et al., 2001; Xu et al., 2004) and ornithomimosaurs (Pérez-Moreno et al., 1994; Ji et al., 2003). These groups are highly abundant and diverse in the well-known Late Cretaceous faunas of North America and Asia (e.g. Weishampel et al., 2004). Rare abelisauroid ceratosaur remains are also known from the Early Cretaceous of Europe, including *Genusaurus*, from the Albian of France (Accarie et al., 1995; Carrano and Sampson, 2008).

Fewer Gondwanan Early Cretaceous theropods are known, but also include carcharodontosaurians and spinosaurids (e.g. Sues et al., 2002; Novas et al., 2005). Most Early Cretaceous Gondwana theropods are from Patagonia, which has produced a fauna containing abundant small- and large-bodied abelisauroids, but few coelurosaurs (primarily unenlagiine dromaeosaurids, which are unknown from Laurasia: Makovicky et al., 2005; Novas, 2009). This suggests a strong distinction between the Early Cretaceous theropod faunas of Laurasia and Gondwana (e.g. Bonaparte, 1986; Novas, 2009), which may have emerged as early as the Middle Jurassic (Pol and Rauhut, 2012), and persisted into the Late Cretaceous (Bonaparte and Kielan-Jaworowska, 1987). However, these abelisauroid-rich theropod faunas represent a palaeotropical, and otherwise warm, arid biome that was widespread in Jurassic–Cretaceous Gondwana, but restricted for most of that interval in Laurasia (Skelton, 2003). Although few Cretaceous theropods are known from cool, higher palaeolatitudes in Gondwana, those that are suggest Early Cretaceous faunas richer in coelurosaurs, and thus more similar to the taxonomic composition of Early Cretaceous Laurasian faunas: the ornithomimosaur *Nqwebasaurus* is known from the Berriasian of South Africa (Choiniere et al., 2012), and abundant, but isolated, bones from the Aptian–Albian of southern Australia provide evidence of a high taxonomic diversity of coelurosaurs, including tyrannosauroids (Benson et al., 2011; but see Herne et al., 2011), ornithomimosaurs, and maniraptorans (Benson et al., 2012). However, unlike in other Gondwanan regions, ceratosaurs are rare in this Australian fauna (Fitzgerald et al., 2012). This is consistent with an essentially global distribution of most theropod clades in the Early Cretaceous and early Late Cretaceous, overprinted by the signal of local climatic variation, with clearer distinctions between northern and southern continents only emerging in the latest Cretaceous (Campanian–Maastrichtian).

A major transition in Cretaceous theropod evolution was the extinction of Allosauoidea and Megalosauoidea, clades that filled the colossal predator niche from the Middle Jurassic, spanning at least 75 Ma, from the Bajocian (170 Mya; Ogg et al., 2008; Wu et al., 2009; Benson, 2010). Until recently, both clades had their last record in the Cenomanian (Holtz et al., 2004) and were thought to have been replaced ecologically by tyrannosauroids in Laurasia and abelisauroids in Gondwana at approximately this time. However, younger spinosaurids are now known from teeth from the ?Turonian–?Maastrichtian Adamantina Formation of Brazil (Candeiro et al., 2004) and Santonian Majiacun Formation of China (Hone et al., 2010). New discoveries and reassessments indicate the last records of Laurasian allosauroids to be Turonian or

younger (Brusatte et al., 2009; Benson et al., 2010b), and the last Gondwanan carcharodontosaurians also persisted for longer than previously recognised, documented by *Aerosteon* (Santonian) and the small-bodied taxon *Orkoraptor* (?Maastrichtian) (Novas et al., 2008; Benson et al., 2010b). However, giganotosaurine carcharodontosaurians, the giant, apex predators of late Early Cretaceous ecosystems of South America (Novas et al., 2005), which possessed a distinctive, recognisable dental morphology (e.g. Stromer, 1931) are absent in the Neuquén Basin of Patagonia following the Turonian (Coria and Salgado, 2005; Novas, 2009), suggesting at least local extinction of a subset of carcharodontosaurian diversity at this time (possible carcharodontosaurid teeth from the Campanian–Maastrichtian of Brazil (Canderio et al., 2006) and Argentina (Martinelli and Forasiepi, 2004) may represent abelisaurids (Canale et al., 2009)).

Campanian–Maastrichtian faunas of both hemispheres are well-sampled and indicate the absence of both carcharodontosaurians and spinosaurids at large body sizes, and attainment of large body sizes among tyrannosauroids in the Northern hemisphere. Pre-Campanian tyrannosauroids attained only medium body sizes (femoral length <800 mm; *Sinotyrannus* and *Yutyrannus* from the Barremian of China are possible exceptions (Ji et al., 2009; Xu et al., 2012)) suggesting that the incumbency of allosauroids and megalosauroids as large-bodied predators prevented tyrannosauroids from becoming successful at large body sizes in Turonian and older ecosystems of the Northern hemisphere (Brusatte et al., 2009).

#### 4.6. Birds (avian theropods)

Birds (avian theropods) make their earliest fossil appearance in the Late Jurassic of Europe, known from *Archaeopteryx lithographica*. However, well-preserved bird skeletons are first known in high abundances from the Barremian–Aptian Jehol Biota of China (e.g. Zhou and Wang, 2010) and Barremian Las Hoyas locality of Spain (e.g. Sanz et al., 1996). These represent a high ecological diversity of primitive long-tailed birds and confuscusornithids, alongside both ornithuromorphs (a large clade including extant birds) and enantiornithes (a major radiation of Mesozoic birds that became extinct at the end of the Cretaceous) (O'Connor et al., 2011). Late Cretaceous avian faunas were dominated by enantiornithes and ornithuromorphs (Longrich et al., 2011; O'Connor et al., 2011), although rare long-tailed birds may still have been present (O'Connor et al., 2011). A peak in sample-size corrected avian diversity in the early Late Cretaceous (Coniacian–Santonian) (Brocklehurst et al., 2012), coincides with radiations of aquatic ornithuromorphs (e.g. Hesperornithiformes) perhaps driven by the Turonian sea level highstand (high diversities of other shallow marine tetrapod groups also occurred at this time; Benson and Butler, 2011). The avian crown group is represented in the latest Cretaceous by the anatoid *Vegavis* from the Maastrichtian of Antarctica (Clarke et al., 2005), and the relatively incomplete fossil record of Late Cretaceous birds raises the possibility that other clades from within the crown group await discovery (Brocklehurst et al., 2012).

## 5. Discussion

### 5.1. Absence of a globally synchronous Cretaceous tetrapod fossil record

The absence of intercontinental statistically significant correlations between sampling proxies for the tetrapod clades examined here demonstrates the absence of a globally synchronous tetrapod fossil record. This suggests that factors other than eustatic sea level change, such as tectonic uplift, erosion, modern day exposure and outcrop accessibility, and perhaps also anthropogenic factors, contribute to the availability and sampling of the terrestrial fossil record (Butler et al., 2011). McGowan and Smith (2008) also demonstrated that the Phanerozoic marine and total rock records for a number of different continental areas (map outcrop area of western Europe,

Australia, Chile; and North American rock volume data from Peters (2005)) showed substantial differences to one another. Moreover, this view was supported by Upchurch et al. (2011), who reported few correlations between various regional dinosaur fossil record sampling metrics such as DBFs and DBCs. However, Peters (2005) suggested that the North American Phanerozoic rock record exhibited substantial global signal. This awaits further testing, but does not invalidate our observation that the Cretaceous tetrapod fossil records of different continents have been sampled in a spatiotemporally heterogeneous fashion.

Correlations between North American terrestrial rock record data (terrestrial units; Table 1) and sampling proxies for dinosaurs, mammals and lepidosaurs suggest that sampling of the North American tetrapod record has been controlled by rock availability. Good rock record measures for the other areas examined in our study (e.g. Asia, Gondwana) are not currently available, so we cannot confirm whether this relationship occurs outside of the intensively sampled North American land-mass. Relationships between western European rock outcrop area and tetrapod sampling proxies are weaker (Table 1), and mostly obtained by GLS regression, but not OLS regression. However, these weaker relationships provide only limited information because, in this instance, the rock record measure does not contain information from the whole continental area (i.e. it excludes eastern Europe). Furthermore, it is possible that the lack of extensive arid areas in western Europe, which decouples exposed rock availability from map outcrop area, also causes the relationship between rock and fossil record proxies to break down.

### 5.2. Common sampling signals across tetrapod clades and preservational types

In general, sampling proxies for the different clades examined here are statistically related within each continental area, especially in Europe using OLS regression of first differences, and in Europe, North America, and Gondwana using GLS regression (Tables 2–5). This suggests that sampling of each clade from available rock is saturated in Europe, and possibly other regions. However, an alternative possibility, especially for statistically significant comparisons within poorly sampled areas such as Gondwana, is that sampling of all four clades has been executed in a relatively homogeneous fashion. Some differences between clade-specific sampling proxies are observed. For example, in Europe, lepidosaur sampling proxies do not correlate with those for other taxa. This might reflect either different facies preferences, or differences in study and reporting of each fossil group. There is little evidence that the records of groups commonly found as microvertebrate remains (i.e. mammals and lepidosaurs) have more similar fossil records to each other than those of macrofossil groups (i.e. dinosaurs and crocodylomorphs); this pattern is only found in one of our studied areas, Asia. This suggests that anthropogenic biases (e.g. study intensity) and facies preferences are generally more important in determining clade-specific fossil record sampling than is preservational mode. Paucity of statistically significant interclade comparisons in Asia may arise from the enormous areal extent of this continent, combined with its geographically heterogeneous palaeoenvironments.

### 5.3. Late Cretaceous rise of extant clades

Our data confirm that substantial faunal turnover among tetrapods occurred during the early Late Cretaceous (Cenomanian–Santonian). Quantitative estimates of taxonomic turnover rates are highly prone to sampling biases (e.g. Fara and Benton, 2000; Alroy, 2008) and are not attempted here. Currently, the tempo, geography, and taxonomic pattern of replacements are poorly resolved, especially in Gondwana (although South American dinosaurs are an exception to this; Coria and Salgado, 2005; Novas, 2009). Terrestrial faunas from the critical Turonian–Santonian interval, especially in North America and Europe, are poorly sampled. Many clades are represented only by sporadic occurrences and exhibit substantial range gaps. As a consequence of

these impediments to quantitative study, we provide only qualitative discussions of Cretaceous faunal turnover.

During the early Late Cretaceous, archaic clades were progressively replaced by derived elements that constitute the modern fauna, including several squamate clades (e.g. snakes, iguanians; Evans, 1998, 2003; Nydam, 2002), metatherian and eutherian mammals (e.g. Cifelli, 2004; Archibald and Averianov, 2005), cryptodiran turtles (Hirayama et al., 2000), and eusuchian crocodylomorphs (Martin and Delfino, 2010). These clades were exceptionally rare, or remain unknown, prior to the late Early Cretaceous, and first attained high diversity only by the latest Cretaceous (Campanian–Maastrichtian). Although the critical early Late Cretaceous interval documenting this faunal transition is poorly-sampled globally, portions of it are preserved in North America and South America, and substantially more is known in central Asia (e.g. Nessov, 1997). These provide no evidence for near-simultaneous extinction of 'archaic' clades (Figs. 2–4) such as triconodont and symmetrodont mammals, 'basal' squamate lineages, Laurasian rhynchocephalians, diplodocoid sauropods, or megalosauroid and allosauroid theropods. Thus, the rise of these extant clades cannot be attributed to radiation following a single, geologically-rapid mass extinction event such as a possible Cenomanian/Turonian event. Instead, extinctions were temporally and geographically staggered, and display interesting geographic patterns (see below).

#### 5.4. Biogeographic implications of geographical sampling heterogeneity

A recurrent observation in discussions of biogeography in many Cretaceous tetrapod groups has been the transition from an apparently cosmopolitan global fauna in the Jurassic, to a more regionalised set of faunas displaying higher levels of endemism through the Cretaceous (dinosaurs: e.g. Sereno, 1997, 1999; Barrett et al., 2011; Benson et al., 2012; mammals: Kielan-Jaworowska et al., 2004; Rich, 2008; lepidosaurs: Nydam, 2002; Evans, 2003) or as early as the Late Jurassic in terrestrial turtles (Hirayama et al., 2000). It is undeniable that well-sampled late Cretaceous faunas were highly regionalised and distinctive (e.g. Bonaparte, 1986; Bonaparte and Kielan-Jaworowska, 1987). However, at present, Early Cretaceous faunas are poorly sampled (Figs. 1–4). In particular, data from the first three stages of the Cretaceous (Berriasian–Hauterivian) are very poorly known, and geographically restricted (primarily from Europe, Morocco and Japan). Thus, potentially high levels of earliest Cretaceous cosmopolitanism are difficult to distinguish from an alternative hypothesis, in which an exclusive biogeographic connection was present between Europe and Gondwana, which may have driven vicariant evolution, resulting in similar faunal compositions (Ezcurra and Agnolin, 2012).

Slightly younger faunas, such as the Barremian–Aptian Jehol Biota Lagerstätten of China, suggest a more distinctive Asian fauna lacking rhynchocephalians, and including 'advanced' clades such as metatherian and eutherian mammals as rare components (Zhou et al., 2003; Zhou and Wang, 2010). However, the special preservational environment, and cool temperate climatic regime of the Jehol Biota (Amiot et al., 2011), may provide an equally good explanation of faunal differences as does endemism driven by continental fragmentation. For example, the absence of crocodylomorphs, which are generally thought to be sensitive climatic indicators (Markwick, 1998); and the presence of choristoderes, including a form considered ecologically analogous to some crocodylomorphs (the 'gavial-like' *Ikechosaurus*) may reflect tolerance for lower temperatures in choristoderes (Lehman and Barnes, 2010; Amiot et al., 2011).

Interesting biogeographic 'signals' are evident in the pattern of Late Cretaceous faunal replacement. Most clades that dominate extant faunas make their first appearances, or first appear at high abundances and diversities, in Asia. These include the major clades of cryptodiran turtles (Hirayama et al., 2000), the squamate clades Iguania and Gekkota (Evans, 1998, 2003; Nydam, 2002), and eutherian mammals (e.g. Archibald and Averianov, 2005). The Barremian–Aptian Jehol

Biota and earlier Lagerstätten deposits in China yielded many of these first appearances, leading some previous authors to propose Asia as a centre of origin for several groups (Zhou, 2006; Zhou and Wang, 2010). Our data suggest that this may not simply be an effect of the presence of exceptional Lagerstätten, because Aptian–Albian and Late Cretaceous appearances in central Asia also support this general pattern (e.g. Nessov, 1997; Gao and Norell, 2000; Hirayama et al., 2000; Archibald and Averianov, 2005). If this pattern is real, and does not reflect sampling bias, then it is an important observation, and is consistent with Asia's possible role as a 'staging area' for the invasion of higher level mammal groups such as rodents, lagmorphs and perissodactyls and artiodactyls into North America during the Palaeogene (Beard, 1998, 2002; Novacek, 1999). However, a key difficulty regarding the Cretaceous data is establishing whether these Asian first appearances and apparent diversifications are genuine, or reflect a Laurasian origin, masked by relatively poor 'middle' Cretaceous sampling of North America and Europe. At least one important extant clade, Metatheria, is known to have first attained high diversities in another Laurasian area: North America (Cifelli, 2004).

Biogeographic work based on molecular phylogenies initially suggested a Gondwanan origin for the eutherian crown clade Placentalia (e.g. Hedges et al., 1996; reviewed by Hunter and Janis, 2006a). However, subsequent appraisals including data on the geographic occurrence of fossil taxa support an Asian or Laurasian origin, with subsequent dispersals to Gondwana (Hunter and Janis, 2006a, 2009b; Goswami et al., 2011). Molecular phylogenies provide a more complex picture of the geographic origins of the squamate groups considered here. A Laurasian origin has been proposed for Anguimorpha (Macey et al., 1999; Vidal and Hedges, 2005), with neoanguimorphs (sensu Vidal and Hedges, 2009: anguoids, xenosaurs, helodermatids) having a North American ancestry, and paleoanguimorphs (sensu Vidal and Hedges, 2009: varanids, shinisauroids, lanthanotids) being of Asian origin (Vidal and Hedges, 2009; Vidal et al., 2012). In contrast, a Gondwanan origin has been suggested for snakes (Vidal and Hedges, 2009) and iguanians (Macey et al., 2000; Acrodonta: Okajima and Kumazawa, 2010), and the crown group of teiids may have South American origins, although Cretaceous fossils may indicate that the stem lineage originated in North America (Giugliano et al., 2007). A possible Gondwanan origin of Iguania conflicts with fossil data as it currently stands. However, in light of the exceptionally poor Cretaceous Gondwanan record of squamates (other than snakes), further progress on this issue awaits future discoveries.

In support of the observation of Laurasian, or possibly Asian, origins of most important extant tetrapod clades, few of these clades have any definite Gondwanan Cretaceous representatives (the Indian eutherian *Deccanolestes* is an exception; e.g. Goswami et al., 2011). However, for most clades, many fewer Gondwanan tetrapod fossil localities and formations have been sampled. Thus, it remains possible that perceptions on the geographic locations of tetrapod radiations in the Cretaceous will be changed by future discoveries. However, we note that previous Cretaceous, and older, records of putative Gondwanan eutherians (Rich et al., 1997), and squamate clades such as Teiidae and Iguania (Estes and Price, 1973; Bonfim-Júnior and Marques, 1997; Datta and Ray, 2006), have mostly been reassigned to non-extant clades (Simões, 2012), or reidentified as recent rather than palaeontological specimens (*Tikiguania*; Hutchinson et al., 2012). Furthermore, as sampling of Gondwanan Cretaceous tetrapod fossils has improved in recent years, increasingly distinct southern clades have been identified, especially from Late Cretaceous deposits (e.g. Novas, 2009; Rougier et al., 2011). Although some Gondwanan clades survived the end-Cretaceous mass extinction event, few survive to the present day. Those that do, monotreme mammals and rhynchocephalian lepidosaurs, form relictual populations of highly reduced diversity and specialised ecology. One possible exception are snakes, which were diverse and abundant in the Late Cretaceous of Gondwana (e.g. Evans, 2003; Krause et al., 2003), but rare in Laurasia. However, snakes may have existed at low diversities in Cretaceous Laurasia;

one of the oldest terrestrial snakes, *Coniophis*, is from the Albian–Cenomanian boundary of Utah (Gardner and Cifelli, 1999).

## 6. Conclusions

We used data on the distribution of higher taxa among lepidosaurs, mammals, crocodylomorphs and dinosaurs, and on Cretaceous tetrapod fossil record sampling to address several critical questions relating to apparent macroevolutionary patterns in the fossil record: (1) Is there a common 'global' temporal sampling signal, or do different continents have idiosyncratic records?; (2) Are local records controlled by measures of rock availability (in North America and Europe)?; (3) Do different taxonomic groups and preservational modes have similar patterns of fossil record sampling within major continental areas?; and (4) What is the observed pattern of Cretaceous faunal turnover, and how much of it can be attributed to spatiotemporally heterogeneous fossil record sampling?

We conclude that different continental areas have distinct temporal patterns of tetrapod fossil record sampling, and that these are controlled by rock availability. Differences in the pattern of fossil record sampling occur between major tetrapod groups within continental areas, but these do not reflect preservational mode (i.e. microfossil vs. macrofossil) and likely arise instead from a combination of anthropogenic study bias and clade-specific facies preferences. Finally, although many modern groups (e.g. eutherian mammals; squamate clades; major cryptodiran clades) have their first fossil occurrences, or first occurrences at high diversity in the early Late Cretaceous of Asia, poor sampling of contemporaneous rocks in North America and Europe means that we cannot exclude wider Laurasian origins for these clades.

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## Appendix A. Supplementary data

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