



## SPATIOTEMPORAL SAMPLING PATTERNS IN THE 230 MILLION YEAR FOSSIL RECORD OF TERRESTRIAL CROCODYLOMORPHS AND THEIR IMPACT ON DIVERSITY

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**Abstract:** The 24 extant crocodylian species are the remnants of a once much more diverse and widespread clade. Crocodylomorpha has an approximately 230 million year evolutionary history, punctuated by a series of radiations and extinctions. However, the group's fossil record is biased. Previous studies have reconstructed temporal patterns in subsampled crocodylomorph palaeobiodiversity, but have not explicitly examined variation in spatial sampling, nor the quality of this record. We compiled a dataset of all taxonomically diagnosable non-marine crocodylomorph species (393). Based on the number of phylogenetic characters that can be scored for all published fossils of each species, we calculated a completeness value for each taxon. Mean average species completeness (56%) is largely consistent within subgroups and for different body size classes, suggesting no significant biases across the crocodylomorph tree. In general, average completeness values are highest in the Mesozoic, with an overall trend of decreasing completeness through time. Many

extant taxa are identified in the fossil record from very incomplete remains, but this might be because their provenance closely matches the species' present-day distribution, rather than through autapomorphies. Our understanding of nearly all crocodylomorph macroevolutionary 'events' is essentially driven by regional patterns, with no global sampling signal. Palaeotropical sampling is especially poor for most of the group's history. Spatiotemporal sampling bias impedes our understanding of several Mesozoic radiations, whereas molecular divergence times for Crocodylia are generally in close agreement with the fossil record. However, the latter might merely be fortuitous, i.e. divergences happened to occur during our ephemeral spatiotemporal sampling windows.

**Key words:** Crocodylomorpha, divergence times, diversity, fossil record bias, Pull of the Recent, spatiotemporal sampling.

OUR uneven sampling of the fossil record obscures and biases our reading of macroevolutionary patterns (Raup 1972). Whereas most studies have focused on understanding and ameliorating fluctuations in sampling through time (e.g. Smith & McGowan 2007; Alroy 2010), spatial bias is also an important factor, but has received relatively little attention (though see Allison & Briggs 1993; Noto 2011; Vilhena & Smith 2013; Close *et al.* 2017). If the geographical distribution of extinct taxa changes between time intervals, fluctuations in global biodiversity (both observed and subsampled) might merely be the result of shifts in spatial sampling patterns (Allison & Briggs 1993; Vilhena & Smith 2013). As such, heterogeneity in our sampling of the fossil record needs to be accounted for

on spatial scales too, with a greater focus on well-sampled regions and controlling for variation in geographical spread of the fossil record (Bush *et al.* 2004; Barnosky *et al.* 2005; Vilhena & Smith 2013; Benson *et al.* 2016; Marcot *et al.* 2016; Close *et al.* 2017).

The 24 species of living crocodylians (alligators, caimans, crocodiles and gavials) are the remnants of a once much more diverse and widespread clade. Crocodylomorpha has an approximately 230 myr evolutionary history (Brochu 2003; Irmis *et al.* 2013), punctuated by a series of radiations and extinctions (Brochu 2003; Martin *et al.* 2014; Bronzati *et al.* 2015; Pol & Leardi 2015; Mannion *et al.* 2015; Wilberg 2017) that appear to be closely tied to fluctuations in temperature

and aridity, at least in the terrestrial realm (Markwick 1998; Carvalho *et al.* 2010; Mannion *et al.* 2015). However, like most groups with a long evolutionary history, the fossil record of crocodylomorphs is biased. Previous studies have attempted to attenuate the impact of sampling biases to reconstruct temporal patterns in crocodylomorph palaeobiodiversity (Markwick 1998; Mannion *et al.* 2015; Pol & Leardi 2015; Tennant *et al.* 2016) but have not explicitly examined the effects of variation in spatial sampling.

The completeness of the fossil specimens themselves yields additional information on fossil record bias that is not captured in those diversity analyses. Several studies have tried to capture information on fossil specimen completeness via the use of coarse taphonomic classes, such as using a completeness score ranging from 0 (no elements preserved) to 4 (all elements preserved) for discrete regions of a skeleton (e.g. Fountaine *et al.* 2005; Benton 2008; Dyke *et al.* 2009; Beardmore *et al.* 2012*a, b*). A growing body of work has attempted to quantitatively estimate fossil specimen completeness, applying this to an array of Palaeozoic to early Cenozoic tetrapods (Mannion & Upchurch 2010; Brocklehurst *et al.* 2012; Walther & Fröbisch 2013; Brocklehurst & Fröbisch 2014; Cleary *et al.* 2015; Verrière *et al.* 2016; Davies *et al.* 2017; Tutin & Butler 2017; Driscoll *et al.* 2018) but this approach has never been applied to an uninterrupted time series of an extant group.

Here we present a detailed examination of the quality of the terrestrial crocodylomorph fossil record throughout the group's 230 myr evolutionary history, exploring how spatiotemporal fluctuations in sampling and specimen completeness impact upon our reading of macroevolutionary patterns.

## MATERIAL AND METHOD

A compilation of all taxonomically diagnosable species of non-marine (terrestrial + freshwater) fossil crocodylomorphs was assembled based on updates to Mannion *et al.* (2015), Tennant *et al.* (2016), information in the Paleobiology Database (<http://paleobiodb.org>) and a thorough review of the literature. Taxa were determined to be non-marine based on previous assessments in the literature (e.g. Mannion *et al.* 2015) as well as their depositional environments. Only taxa based on body fossils were included. Data on higher taxonomic level (e.g. Alligatoroidea, Notosuchia), geography (palaeocontinent, country, palaeolatitudinal range) and stratigraphy (temporal range, geological formation) were also recorded. Our dataset comprises 393 crocodylomorph species recognized in the fossil record, and is up to date as of the 4 July 2017 (Mannion *et al.* 2018*a*).

We also estimated the total length (TL) of each species as a measure of body size, primarily using formulae available in the literature to estimate TL from several parts of the skeleton. These equations are derived from linear regressions based on specimens of modern taxa. For specimens with complete skulls preserved, we used the formula from Hurlburt *et al.* (2003) that estimates TL from dorsal cranial length (DCL). For specimens with skulls that only lack the rostrum, we were able to use another formula from Hurlburt *et al.* (2003) that uses orbito-cranial dorsal length (ODCL). Also, for specimens with femora preserved, we applied the formula from Farlow *et al.* (2005) that estimates TL from femoral length (FL). Finally, for specimens lacking near-complete skulls or femora, we used other preserved elements to coarsely estimate either DCL or FL, and then applied the formulae from Hurlburt *et al.* (2003) and Farlow *et al.* (2005). When more than one specimen was available for a single species, we used the largest estimated value of TL. Similarly, when we were able to apply more than one formula to estimate TL for a species (e.g. if a skull and femur are preserved for one species) we used the largest value in our analyses. This approach enabled us to estimate TL for nearly all crocodylomorphs in our dataset (363 species). TL estimates (in metres) were log-transformed prior to correlation analyses. To test for a possible differential influence of completeness on animals of distinct size magnitudes, we also allocated taxa into four coarse size bins (categories): (A) taxa smaller than 2 m; (B) taxa between 2 and 4 m; (C) taxa between 4 and 6 m; and (D) taxa larger than 6 m.

Mannion & Upchurch (2010) devised a character completeness metric (CCM) that quantifies the amount of phylogenetic data preserved in fossil specimens. A percentage score is provided for the number of phylogenetic characters that can be scored for each taxon, based on all published specimens. We used the phylogenetic data matrix of Montefeltro *et al.* (2013), which has the greatest number of characters (484) of any published crocodylomorph morphological data matrix and samples taxa and characters from across the tree. Most characters pertain to cranial elements (393), with vertebral (31), appendicular (46), and osteodermal (14) characters providing a much smaller contribution. A similar distribution of characters is present in other crocodylomorph data matrices (e.g. Brochu & Storrs 2012). A completeness score was calculated for each species based on an extensive review of the literature and personal observations of fossil specimens (see Fig. 1 for an illustration of body regions). An element that is clearly preserved, but not visible (e.g. concealed by matrix) was regarded as complete. With regard to inapplicable characters, we 'scored' each species as to whether it had the potential to preserve that feature; for example, if one humerus was completely preserved then

all humeral characters were considered 'scorable'. The exception to this was the small number of taxa that unambiguously lack osteoderms: osteodermal characters were excluded from the CCM for these species. Inapplicable characters comprise a very small proportion of the 484 characters, and their treatment has little impact on the calculated CCM for each species.

A mean average value of crocodylomorph CCM scores and associated standard deviations was calculated for each time bin. We used two different time-binning approaches. Firstly, we used standard stratigraphic stages (though with the Quaternary counted as one interval, as some of its stages are extremely short in duration) based on the latest (2017) version of the geological time scale presented by Cohen *et al.* (2013). However, these stages display a large disparity in temporal duration, ranging from 1 myr to 19 myr in length. The ages of many crocodylomorph fossils are also poorly constrained, meaning that numerous occurrences cannot be assigned to a single stage. As such, our second binning strategy uses approximately equal-length (~9 myr) stratigraphic time bins that group together multiple stages, whilst maintaining important geological boundaries (see Mannion *et al.* 2015; Benson *et al.* 2016). In both cases, we did not exclude species that could not be assigned to a single time bin; their full stratigraphic uncertainty was used as their temporal range. Both sets of time bins are detailed in Mannion *et al.* (2018a).

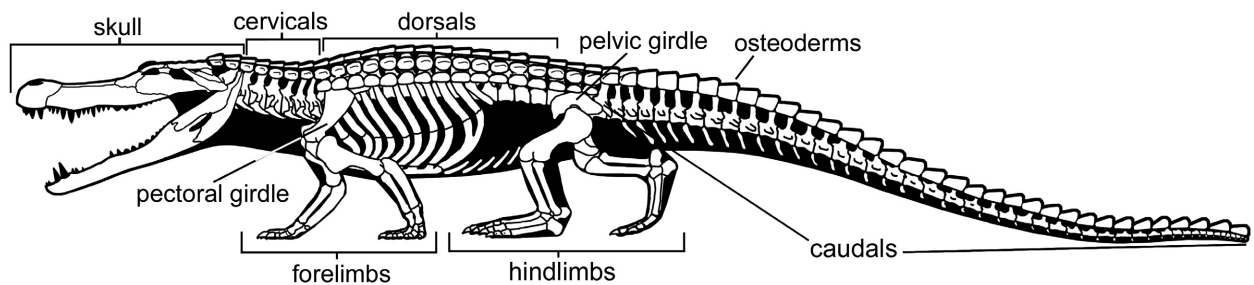
Temporal fluctuations in completeness were reconstructed at the global level for both time-binning strategies. Completeness at the palaeocontinental scale, as well as for 10° palaeolatitudinal bands, was reconstructed only for the 9 myr bins. Our palaeocontinents comprise: Africa, Asia, Australasia, Europe, India, Madagascar, North America and South America. Only one crocodylomorph species is known from Madagascar prior to the Maastrichtian: this is from the Middle Jurassic, at which time Madagascar was still connected to Africa, and thus it is considered an African species here. Otherwise, both Madagascar and India lack diagnosable crocodylomorph fossils prior to the Maastrichtian, and are therefore not grouped together as Indo-Madagascar, nor are they

incorporated with Africa, with rifting having separated these areas by the latest Cretaceous (Ali & Aitchison 2008). India is incorporated within Asia from the Eocene onwards, following their collision (Ali & Aitchison 2008). We also calculated completeness for several major taxonomic subgroups and for our four body size classes.

A species-level census of observed (= uncorrected/raw) crocodylomorph diversity through time was calculated from our dataset at global, palaeocontinental, and palaeolatitudinal scales. We also produced global, palaeocontinental and palaeolatitudinal time series of numbers of non-marine crocodylomorph-bearing collections (CBCs) as a sampling proxy (2424 collections in total), using data in the Paleobiology Database, accessed 29 May 2018 (Mannion *et al.* 2018b).

All previous equivalent studies of fossil specimen completeness have been restricted to Palaeozoic to early Cenozoic (Palaeogene) taxa (e.g. Brocklehurst *et al.* 2012; Brocklehurst & Fröbisch 2014; Cleary *et al.* 2015; Davies *et al.* 2017), meaning that we cannot undertake a comparison with other groups for the full time interval of interest. We therefore limited comparisons with existing completeness metrics to two terrestrial groups that span the Late Triassic through to end-Cretaceous (Maastrichtian): (1) sauropodomorph dinosaurs (Mannion & Upchurch 2010) with large and robust skeletal elements; and (2) pterosaurs (Dean *et al.* 2016), which are generally small-bodied, with delicate bones. In both instances, statistical comparisons with crocodylomorph completeness were made only at the stage-level, using the data presented in Dean *et al.* (2016).

Correlation tests were used to compare fluctuations in crocodylomorph completeness with other temporal and spatial series (i.e. numbers of crocodylomorph species and CBCs, completeness of sauropodomorphs and pterosaurs). All of our time series were log-transformed prior to analysis, and the effects of trend and autocorrelation were removed via generalized differencing, using a function written by Lloyd (2008). Bins with zero values were excluded from our temporal and spatial series correlation tests. Spearman's rank correlation coefficients were calculated for each pairwise comparison.



**FIG. 1.** Skeletal outline of a representative crocodylomorph (*Deinosuchus*), showing the body regions used to partition the skeleton. Illustration by Scott Hartman, used with permission.

We used ordinary least squares (OLS) regressions of the completeness scores on our body size data to test for correlation. We also performed these OLS regressions within each of our four body size categories (i.e. A–D).

All correlation analyses were performed in R version 3.4.3 (R Core Team 2017). Time series plots were produced using the R package *strap* (Bell & Lloyd 2015). The complete dataset is available in Mannion *et al.* (2018a).

*Abbreviations.* CBC, crocodylomorph-bearing collection; CCM, character completeness metric; DCL, dorsal cranial length; FL, femoral length; ODCL, orbito-cranial dorsal length; SCM, skeletal completeness metric; TL, total length.

## RESULTS

### *Global patterns in completeness and taxonomic diversity*

Just six species are known solely from postcrania, whereas 186 species are known only from cranial remains. The mean average CCM of all 393 species is 56%, with values ranging from 0.2–100% (Fig. 2). Completeness of Mesozoic species is higher on average (217 species with a mean average completeness of 60%) than that of Cenozoic species (179 species: 51%) (Fig. 2). Within the Mesozoic, the greatest average values are from Jurassic species (51 species: 72%), with notably lower values in the Late Triassic (9 species: 64%) and especially the Cretaceous (159 species: 55%). Completeness in the Palaeogene (81 species: 54%) is greater than that of the Neogene + Quaternary (99 species: 48%).

At a global level, there is no significant correlation between temporal fluctuations in crocodylomorph diversity and completeness in any of our analyses (Table 1). Whereas diversity is strongly correlated with numbers of CBCs in all of our analyses (Spearman's rho ( $r_s$ ) = 0.72–0.86), completeness and numbers of CBCs are only significantly correlated when using 9 myr bin-level analyses, after applying generalized differencing ( $r_s$  = 0.47; Table 1). Below we describe global patterns in completeness and taxonomic diversity through the last 230 myr (Figs 3, 4).

Crocodylomorph completeness is low in the first stage of the Late Triassic (Carnian), although only two valid species are known from this interval. Three times as many species are known from the Norian, which also has a substantially higher completeness value. Completeness reaches its highest percentage for the entirety of the evolutionary history of Crocodylomorpha in the Rhaetian, although this value is only based on two known species. There is a decline in completeness across the Triassic–Jurassic boundary (203 Ma), although CCM is still high for the more species-rich Hettangian–Sinemurian interval (Figs 3, 4). No diagnostic terrestrial crocodylomorph species are currently known from the last two stages of the

Early Jurassic (Pliensbachian and Toarcian) or from the first stage of the Middle Jurassic (Aalenian). Both completeness and number of species is lower in the Bajocian–Bathonian than the earliest Jurassic, but increase in the Callovian and Oxfordian. The last two stages of the Jurassic are characterized by lower completeness, but much greater numbers of species (Figs 3, 4).

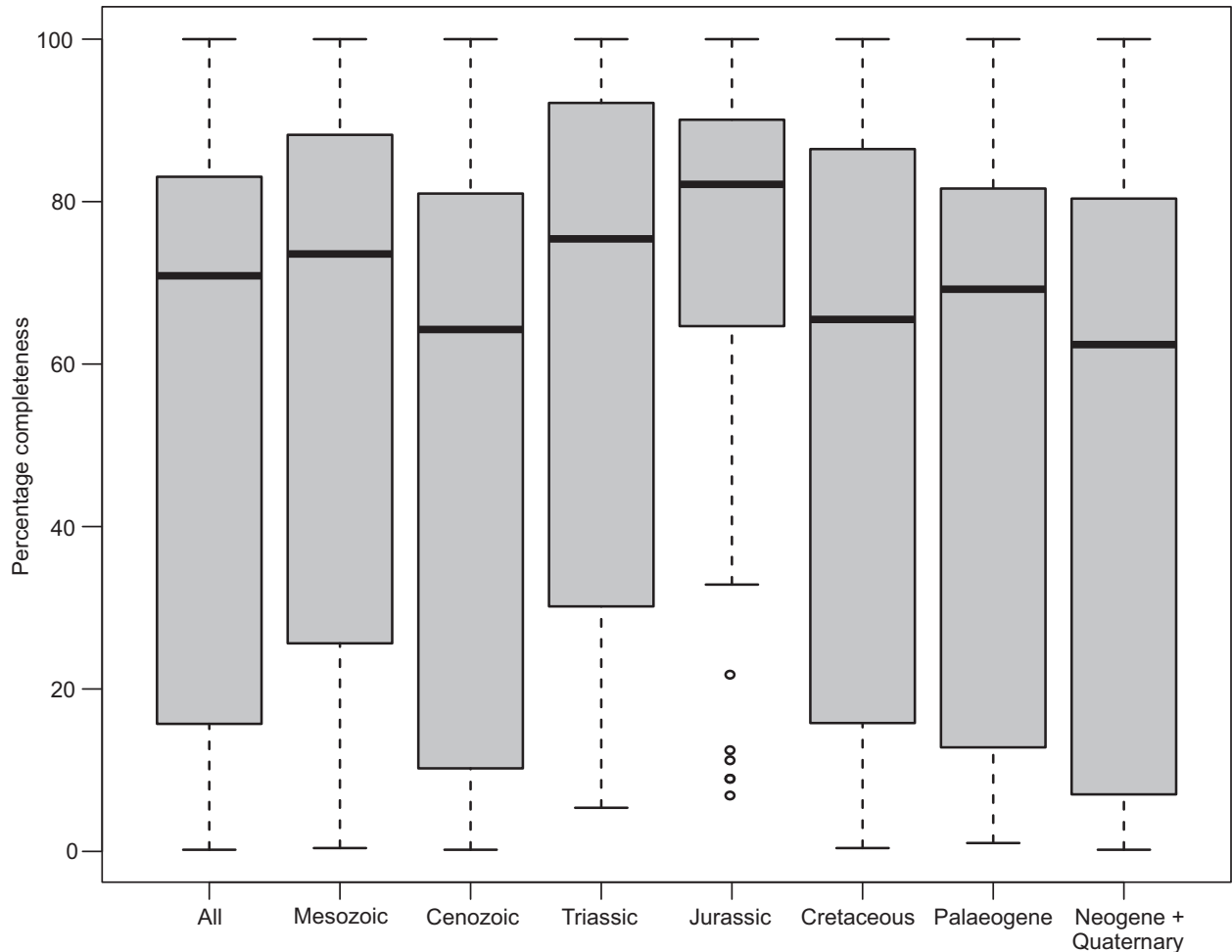
Completeness and number of species decreases slightly across the Jurassic–Cretaceous boundary (145 Ma), with species numbers declining further in the Valanginian and Hauterivian (Figs 3, 4). A much greater number of species is known from the Barremian–Albian, with slightly higher average completeness values. Although there are a similar number of species in the Cenomanian, completeness plummets in this first stage of the Late Cretaceous. Whereas the number of species declines, completeness slightly increases in subsequent stages (Turonian and Coniacian). The number of species approximately doubles in the Santonian, although there is a decrease in completeness (Figs 3, 4). Both the number of species and average completeness are considerably higher in the Campanian and Maastrichtian (note that the age of the species-rich Late Cretaceous Brazilian Adamantina Formation is poorly constrained but is here assigned to the late Campanian to early Maastrichtian interval based on recent stratigraphic work by Batezelli (2017)).

Aside from the Carnian value (see Figs 3, 4), completeness reached its nadir in the first interval (Danian) after the Cretaceous–Palaeogene boundary (66 Ma). However, completeness rebounded in the subsequent stages of the Paleocene (Selandian and Thanetian). Both the Ypresian and Lutetian have similar values, prior to a decline in the Bartonian. Completeness increases substantially in the final stage of the Eocene (Priabonian), although the number of species is unchanged from the preceding interval. Just two species are recognized from the Rupelian (early Oligocene), although their average completeness is one of the highest values. Whereas the number of species increases in the Chattian (late Oligocene), completeness drops precipitously (Figs 3, 4).

These values do not change substantially across the Palaeogene–Neogene boundary (23 Ma). Both values increase in the Burdigalian, and the number of species rises in the Langhian and Serravallian. The number of species reaches its Cenozoic acme in the Tortonian, and high values for completeness and number of species are recorded in the final stage of the Miocene (Messinian). Species counts decrease in the Pliocene. Finally, an increased number of species is recognized in the Quaternary, although completeness is reduced (Figs 3, 4).

### *Palaeocontinental sampling patterns*

The 393 crocodylomorph species have the following palaeocontinental distribution (Fig. 5): Africa (43 species



**FIG. 2.** Box-and-whisker plots showing the distribution of crocodylomorph completeness for different time intervals. The median average completeness value is shown by the horizontal black bar in each plot.

with mean average completeness of 61%), Asia (68 species: 56%), Australasia (25 species: 35%), Europe (70 species: 69%), India (one species: 15%), Madagascar (6 species: 70%), North + Central America (74 species: 57%) and South America (106 species: 48%). The spread of completeness data is relatively similar for all palaeocontinents, with the exception of Europe (Fig. 5), for which most species are known by fairly complete remains (>60%). No palaeocontinent has a continuous (i.e. uninterrupted) record throughout the evolutionary history of crocodylomorphs, and often a time interval is dominated by a single region (Figs 6, 7). There are significant positive correlations between temporal fluctuations in South American crocodylomorph completeness and both numbers of species (uncorrected time series and with generalized differencing) and CBCs (generalized differencing only) (Table 1). In contrast, there is no correlation between completeness and the numbers of species or CBCs for the other palaeocontinents with relatively complete time series (i.e. Asia, Europe and North America).

Late Triassic species are restricted to Europe, North America and South America, and only Africa (restricted to southern Africa), Asia and North America contribute to our knowledge of Early Jurassic crocodylomorph species (Figs 6, 7). Middle Jurassic–Oxfordian species are primarily restricted to Asia, with two species from South America, and just one each from North America and Africa. The Kimmeridgian–Tithonian signal reflects a slightly more global dataset, with species known from Asia, Europe, North America and South America. European and Asian species comprise most of the diversity of Berriasian–Barremian crocodylomorphs (with a small contribution from Africa and South America). The Aptian–Cenomanian record is dominated by African species (primarily from North Africa), although Asia, North America, Europe (Albian only) and South America also contribute, as does Australasia for the first time (Figs 6, 7). The Turonian–Santonian signal predominantly stems from South America and Asia, although there are additional species from Europe, and one from each of Africa and North

**TABLE 1.** Correlation test results for time series comparisons.

| Comparison                     | Raw data |                          | Generalized differencing |                         |
|--------------------------------|----------|--------------------------|--------------------------|-------------------------|
|                                | rs       | <i>p</i>                 | rs                       | <i>p</i>                |
| CCM vs TDE<br>(stage; global)  | -0.30    | 0.06                     | 0.04                     | 0.82                    |
| CCM vs TDE<br>(9 myr; global)  | -0.14    | 0.53                     | 0.34                     | 0.11                    |
| CCM vs CBCs<br>(stage; global) | -0.24    | 0.13                     | 0.04                     | 0.81                    |
| CCM vs CBCs<br>(9 myr; global) | -0.04    | 0.84                     | 0.47                     | 0.03*                   |
| TDE vs CBCs<br>(stage; global) | 0.86     | $9.06 \times 10^{-13}$ * | 0.78                     | $7.73 \times 10^{-8}$ * |
| TDE vs CBCs<br>(9 myr; global) | 0.84     | $3.26 \times 10^{-7}$ *  | 0.72                     | 0.0002*                 |
| CCM vs TDE<br>(9 myr; SAm)     | 0.55     | 0.01*                    | 0.69                     | 0.002*                  |
| CCM vs CBCs<br>(9 myr; SAm)    | 0.21     | 0.37                     | 0.50                     | 0.03*                   |

Statistical comparisons between temporal fluctuations in crocodylomorph completeness (CCM), diversity (TDE), and numbers of crocodylomorph-bearing collections (CBCs) for stage-level and 9 myr bin-level analyses. Results presented for global and South American (SAm) analyses. Spearman's rank correlation coefficients (rs) were calculated for each pairwise comparison based on the raw data and after generalized differencing.

\*Significant at alpha (*p*-value) = 0.05.

America. Campanian–Maastrichtian species are found in Asia (Campanian-only), Europe, North America, South America and Indo-Madagascar (Maastrichtian-only).

Paleocene–Eocene crocodylomorph species are known from Asia (now including India), Europe, North America and South America, with the Ypresian record supplemented by a species from Africa, and four Australasian species known throughout the Eocene (Figs 6, 7). Australasia is the principal contributor to our knowledge of Oligocene diversity, with a single species otherwise known from each of Africa, Europe and North America during this epoch (note that most of the fossil occurrences in Fig. 6I represent generically or specifically indeterminate materials). Aside from Madagascar, the Miocene record of crocodylomorph species is global. This distribution of species is retained in the Pliocene, with the exception of Europe, and Quaternary crocodylian species are known from Africa, Asia, Australasia, North America, South America and Madagascar (Figs 6, 7).

#### *Palaeolatitudinal sampling patterns*

Although crocodylomorph fossils have been discovered at palaeolatitudes of 76° N (early Eocene of the Canadian

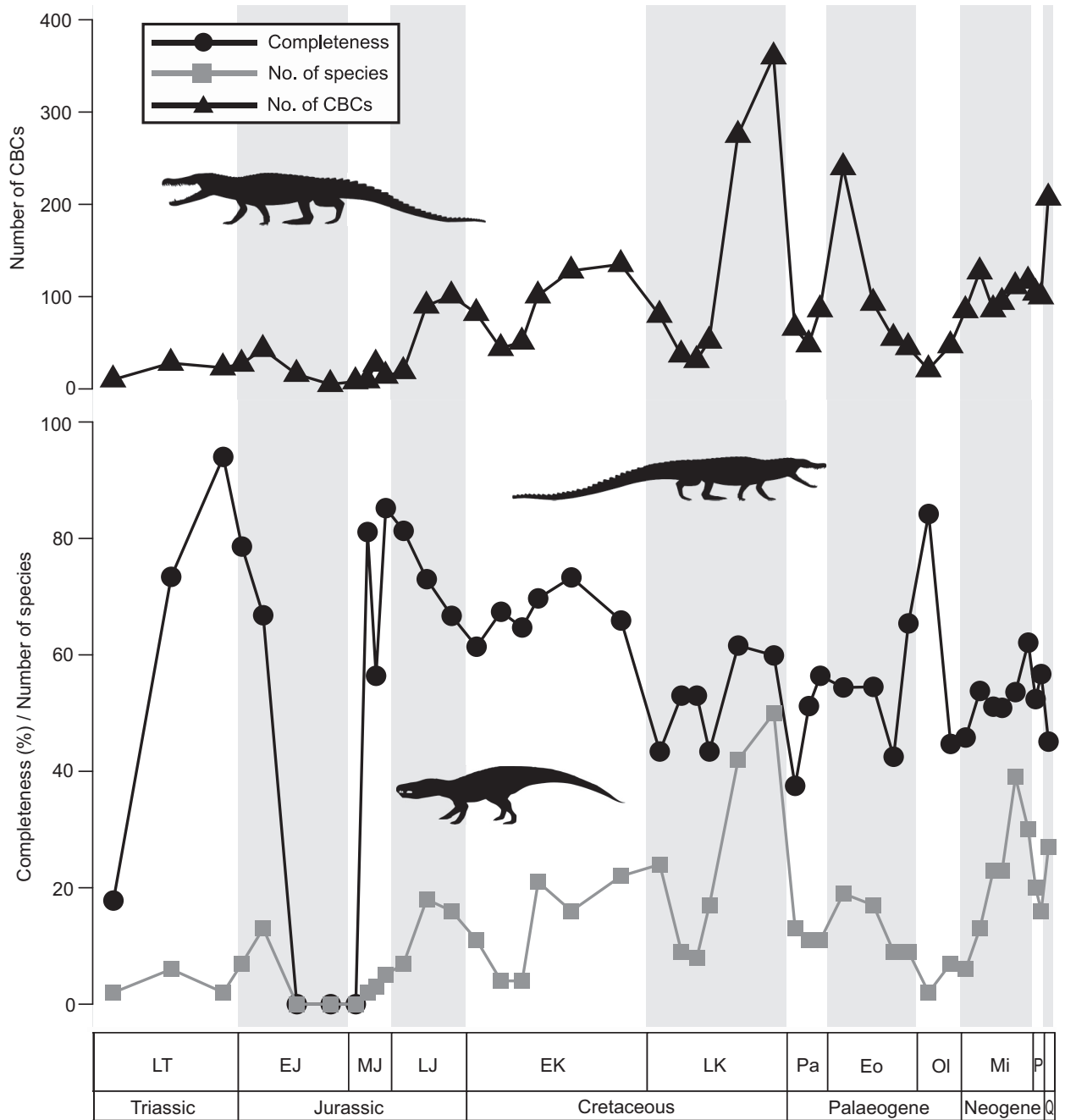
Arctic; Estes & Hutchison 1980) and 79° S (late Eocene of Antarctica; Willis & Stilwell 2000), remains that can be assigned to species are restricted to 60° palaeolatitude either side of the Equator (Fig. 8). As with the palaeocontinental data, no palaeolatitudinal belt has a continuous record throughout the evolutionary history of crocodylomorphs (Fig. 9), and for many time intervals we have little or no record of the group in the palaeotropics (a band of approximately 30° either side of the Equator) or sub-polar regions (although the latter might be a genuine absence outside of greenhouse-dominated intervals).

In general, completeness is greater in the northern hemisphere (Figs 8, 9). There are high values for 50–60° N, 40–50° N, and 20–30° N, with a moderately high value for 30–40° N, and completeness in more tropical palaeolatitudes is only slightly lower. Aside from palaeolatitudinal bins for which there is only one species, the highest completeness value for a southern hemisphere palaeolatitudinal band is 0–10° S. Completeness is also relatively high at 20–30° S, whereas values are lower at 30–40° S, 40–50° S and, especially, at 10–20° S.

There is no significant correlation between the palaeolatitudinal distribution of crocodylomorph diversity and completeness in any of our analyses (Table 2). A weak, though statistically non-significant correlation is recovered between diversity and numbers of CBCs, although only when generalized differencing is applied (Table 2). In contrast, a strong correlation between completeness and numbers of CBCs is recovered, using both the raw data and following the application of generalized differencing (Table 2). Below we describe how the palaeolatitudinal distribution of crocodylomorph completeness and taxonomic diversity varied over the last 230 myr.

Excluding the middle Miocene to Quaternary interval, for which sampling of the palaeotropics is generally good, most preceding time intervals have very low species counts (zero or one) for each of their palaeolatitudinal tropical bins (Fig. 9). With the exception of a single species from the Bathonian of Madagascar, the Late Triassic to Middle Jurassic palaeotropical record is limited to the northern hemisphere. In contrast, the palaeotropics of the Campanian–Danian (inclusive) is only represented in the southern hemisphere (Fig. 9). Notable exceptions of a palaeotropical record, based on multiple species, are restricted to: 10–20° N in the Hettangian–Sinemurian and Hauterivian–Barremian; 0–10° N in the Aptian, Albian and Cenomanian; 20–30° S in the Campanian, Maastrichtian and Selandian–Thanetian; and 0–10° N in the Aquitanian–Burdigalian (Fig. 9).

The palaeolatitudinal band spanning 30–40° N is sampled for most of crocodylomorph evolutionary history, with the exception of the Carnian, Pliensbachian–Bathonian and Ypresian, and the 40–50° N band is sampled continuously from the Callovian onwards (Fig. 9).

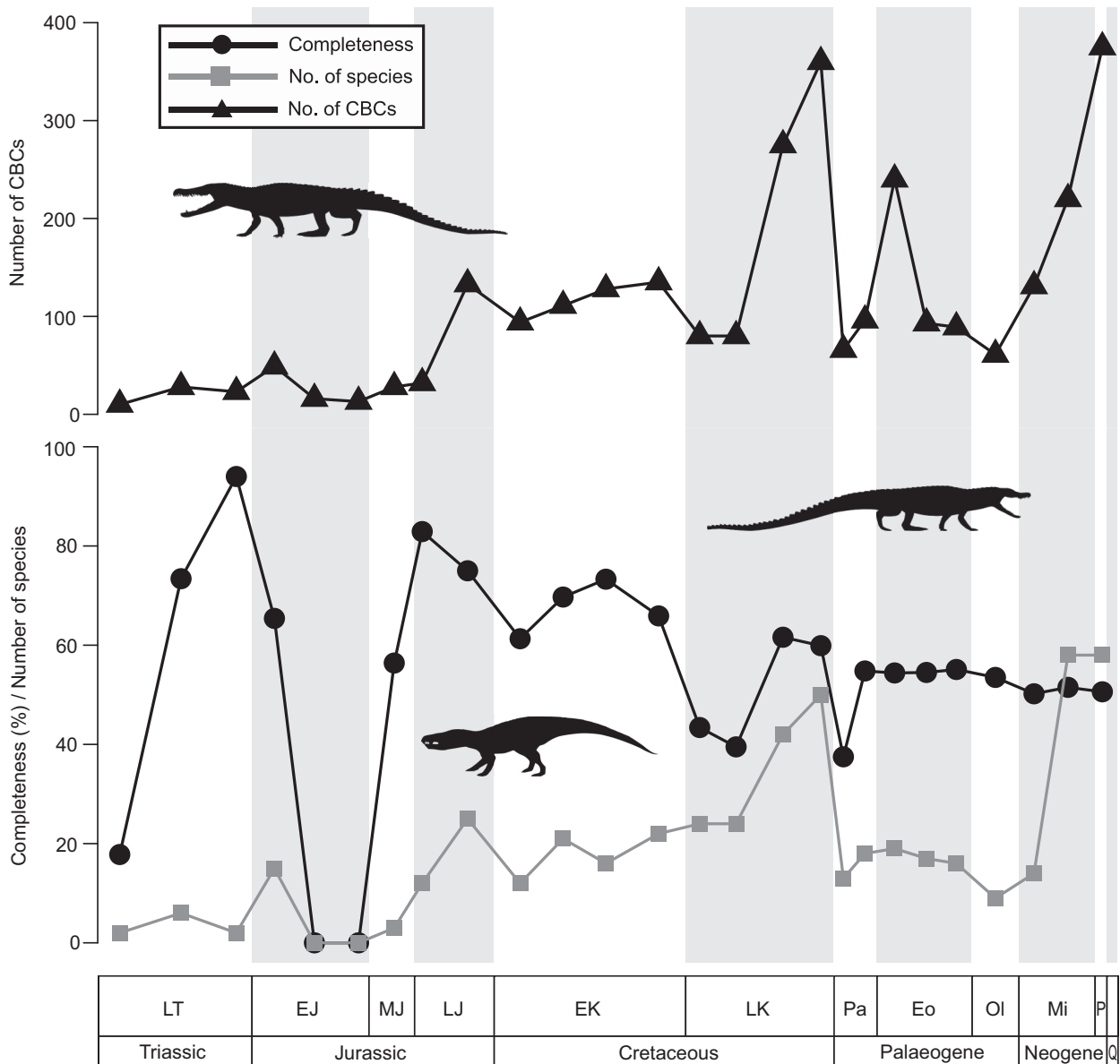


**FIG. 3.** Global patterns of crocodylomorph completeness, number of species, and number of crocodylomorph-bearing collections (CBCs) plotted through time (using stage-level time bins). Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman and Nobumichi Tamura, hosted at Phylopic (<http://phylopic.org>) where all licence information is available.

Average completeness values based on more than two species are mostly comparable with or exceed the global average, although there are a small number of low values (i.e. 30–40° N in the Turonian–Santonian and 40–50° in the Maastrichtian and Danian). Crocodylomorph species are only sampled in the 50–60° N palaeolatitudinal band

in the Hauterivian–Barremian and Turonian–Ypresian intervals, with completeness generally high, but numbers of species mostly low (Fig. 9).

Sampling of temperate palaeolatitudes in the southern hemisphere (30–60° S) is sporadic, especially in the Late Triassic to Jurassic interval, and usually comprises two or



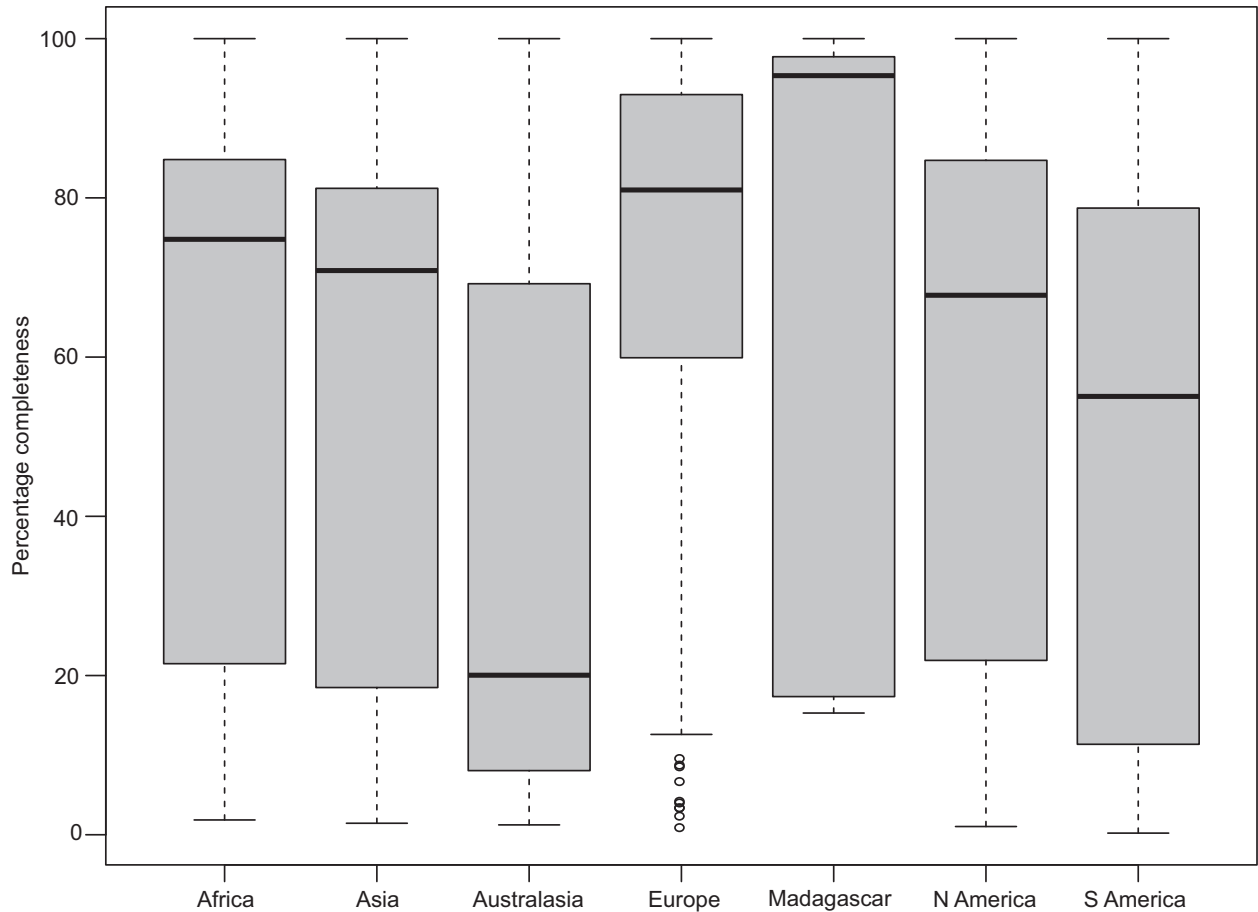
**FIG. 4.** Global patterns of crocodylomorph completeness, number of species, and number of crocodylomorph-bearing collections (CBCs) plotted through time (using ~9 myr time bins). Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman and Nobumichi Tamura (<http://phylopic.org>).

fewer species per bin (Fig. 9). Where there are more than two species, completeness values are quite variable. Whereas there is high completeness at 40–50° S in the Hettangian–Sinemurian, and at 30–40° S in the Aptian, Albian, Cenomanian and Maastrichtian, low completeness values characterize the 40–50° S band in the Turonian–Santonian, as well as the 30–40° S band in the Oligocene and Langhian–Tortonian (Fig. 9). Only one species is known from 50–60° S (Albian–Cenomanian), although it is an essentially complete skeleton (i.e. *Isisfordia duncani*; Salisbury *et al.* 2006).

#### *Body size and taxonomic variation in completeness*

In general, our regression analyses show non-significant or very weak correlations between crocodylomorph fossil completeness and body size (Fig. 10; Table 3). A significant negative correlation (i.e. negative slope) was recovered when analysing all species (with untransformed or log-transformed body size data) and species within body size category A (smaller than 2 m) indicating that smaller taxa tend to be more complete. However, in these cases, the coefficient of determination ( $R^2$ ) was very low (always





**FIG. 5.** Box-and-whisker plots showing the distribution of crocodylomorph completeness for each palaeocontinent. The median average completeness value is shown by the horizontal black bar in each plot.

smaller than 0.03), indicating that the correlation is very weak. For species within the other three size categories, no significant correlation was recovered. Comparisons between categories suggests that taxa within category C (between 4 and 6 m) are the least complete.

The mean average completeness of several well-recognized crocodylomorph subclades does not strongly deviate from the overall pattern (Fig. 11), with *Notosuchia* (72 species with mean average completeness of 54%), *Neosuchia* (256 species: 54%), *Crocodylia* (172 species: 52%), *Alligatoroidea* (73 species: 56%) and *Tomistominae* (17 species: 55%), for example, all within a few percentage points of the total average (55%), although *Tethysuchia* (10 species: 48%) and *Crocodylidae* (50 species: 49%) are slightly lower, and *Goniopholididae* (25 species: 60%) a little higher. The spread of completeness data is also relatively consistent between groups (Fig. 11), with most species represented by specimens that are approximately 15–80% complete. *Goniopholididae* is the exception to this pattern, with the majority of goniopholidid species known from specimens that are 50–80% complete (Fig. 11). Although a paraphyletic grade, non-metasuchian

crocodylomorphs (58 species) tend to preserve more complete skeletons, with an average completeness of 65% (Fig. 11).

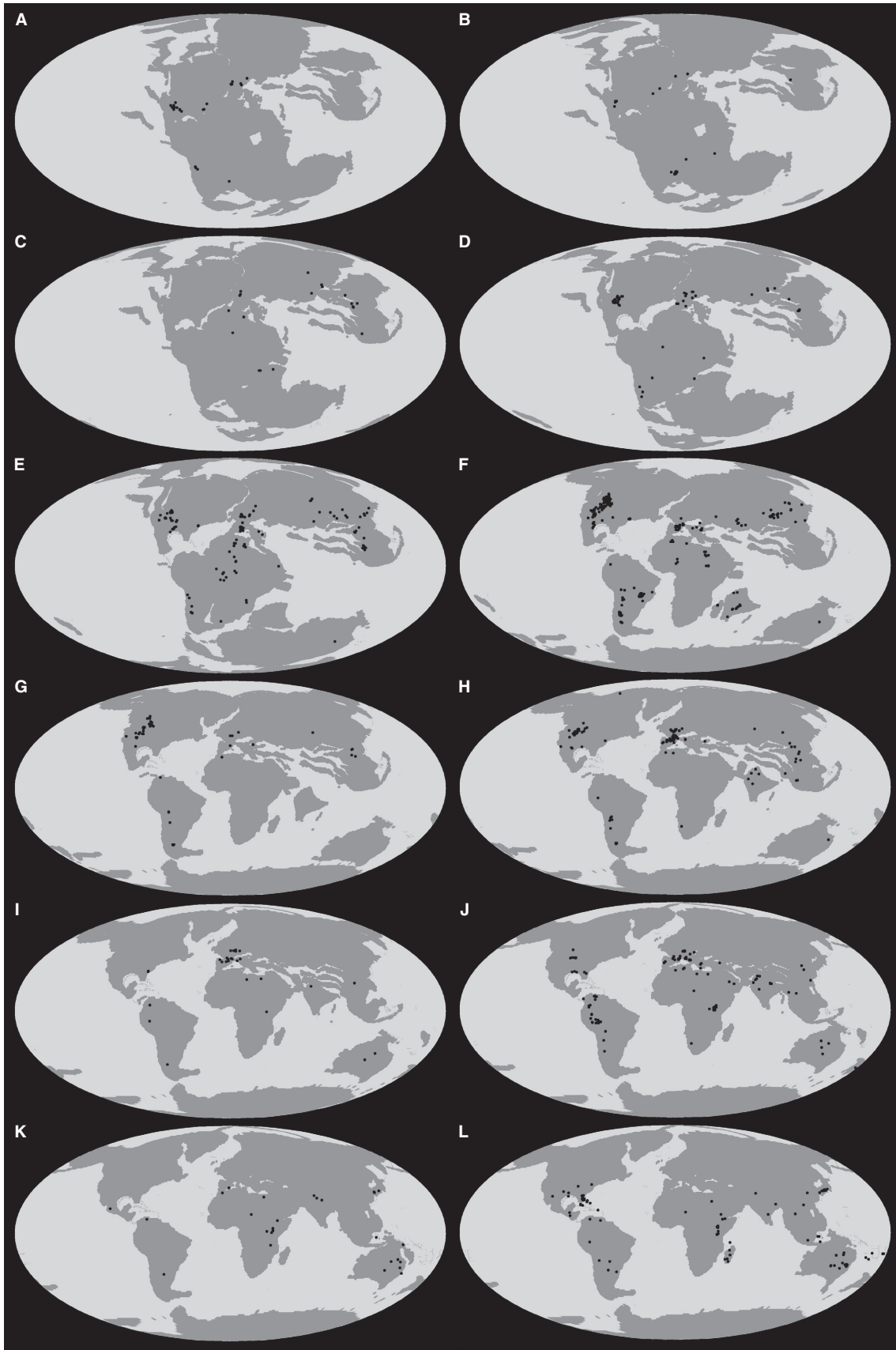
#### *Crocodylomorph completeness compared to other groups*

Moderate to strong correlations were recovered between temporal fluctuations in the raw completeness values of Mesozoic crocodylomorphs and those of sauropodomorph dinosaurs ( $r_s = 0.51$ ) and, especially, pterosaurs ( $r_s = 0.75$ ) (Table 4). However, both of these correlations disappeared when generalized differencing was applied to the time series.

## DISCUSSION

### *The completeness of the crocodylomorph fossil record*

Whereas the first two studies to use the character completeness metric (Mannion & Upchurch 2010;



Brocklehurst *et al.* 2012) examined taxonomic groups (sauropodomorph dinosaurs and Mesozoic birds) for which the skull represented approximately one-third of the total character set, analyses of other groups have all shown that the skull has a much greater character weighting for those taxa, with: (1) parareptiles = 52% (Verrière *et al.* 2016); (2) plesiosaurs = 52% (Tutin & Butler 2017); (3) pterosaurs = 59% (Dean *et al.* 2016); (4) pelycosaur = 70% (Brocklehurst & Fröbisch 2014); (5) Cretaceous–Palaeogene eutherian mammals = 73% (Davies *et al.* 2017); (6) crocodylomorphs = 81% (this study); and (7) anomodonts = 82% (Walther & Fröbisch 2013). Thus, for groups such as anomodonts and crocodylomorphs, an ‘80% complete skeleton’ might only preserve a skull. A skeletal completeness metric (SCM), in which the skeleton is divided up into percentages based on the amount of bone for each region (Mannion & Upchurch 2010), is thus likely to result in very different completeness values for groups such as crocodylomorphs, although temporal fluctuations in CCM and SCM might still be expected to correlate (see Brocklehurst & Fröbisch 2014; Verrière *et al.* 2016; Tutin & Butler 2017).

This greater weighting of the skull is largely consistent across crocodylomorph phylogenetic data sets (e.g. Brochu & Storrs 2012; Pol *et al.* 2014). Although we do not disagree that the skull is disproportionately rich in character data compared to the postcranial skeleton, we contend that this is accentuated by historical neglect of the postcrania in studies of crocodylomorph anatomy (Godoy *et al.* 2016; Martin *et al.* 2016). Although postcrania are usually listed in taxon descriptions, they are not always figured or described in detail, and this bias subsequently affects the choice of characters that end up being incorporated into phylogenetic data sets. Fortunately, this is beginning to change, with several studies generating novel postcranial characters, demonstrating their impact on resolving crocodylomorph relationships (e.g. Pol *et al.* 2012; Godoy *et al.* 2016; Martin *et al.* 2016).

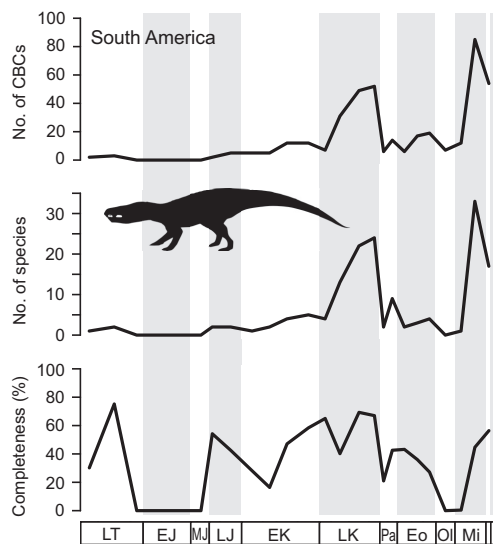
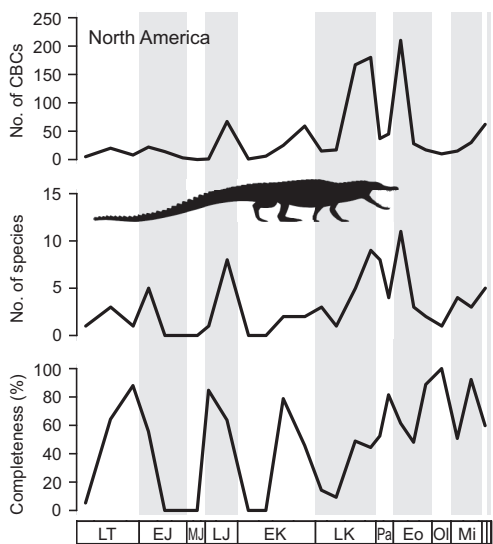
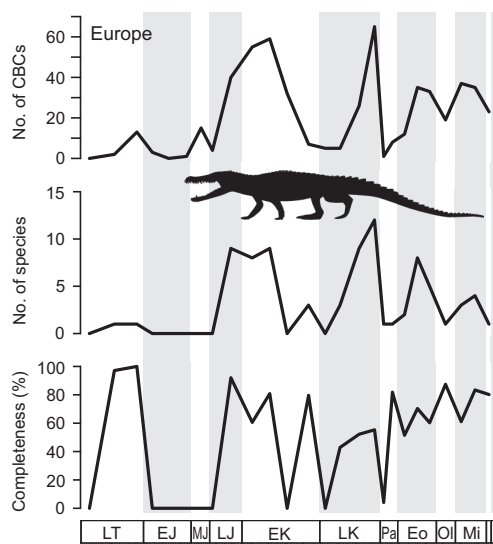
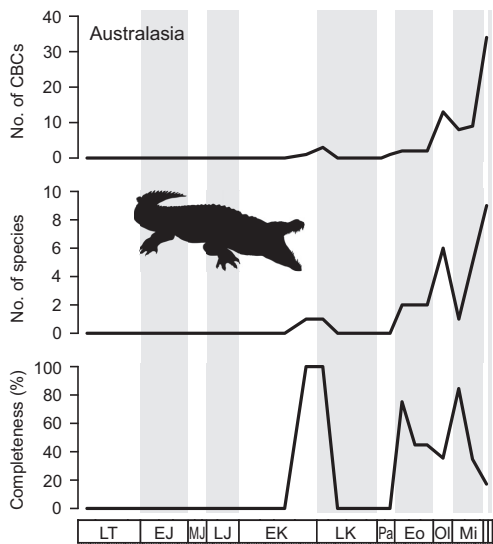
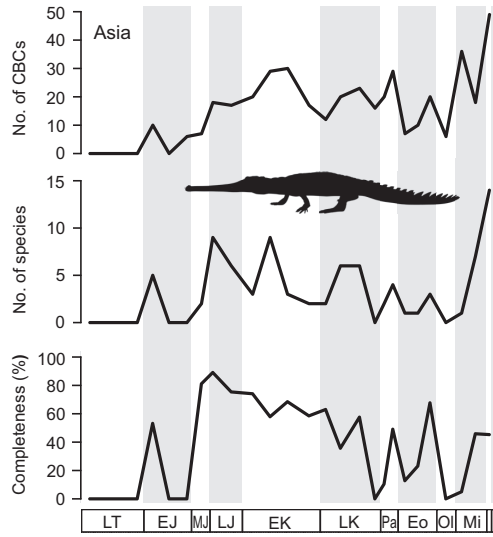
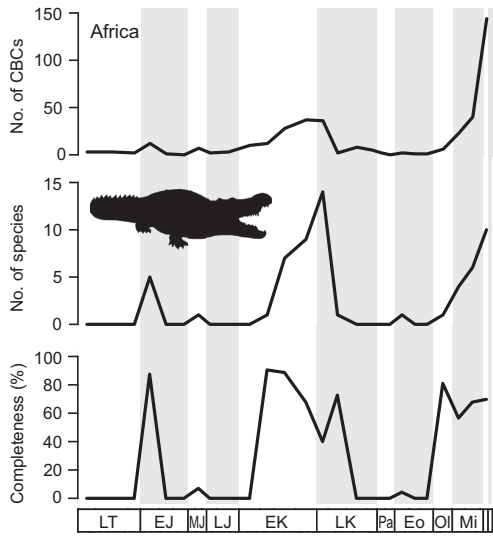
The overall consistency in average completeness across taxonomic groups suggests that depositional environment does not have any great control on non-marine crocodylomorph fossil preservation, at least at coarse levels, given that our dataset includes several semi-aquatic groups, as well as fully terrestrial notosuchians living in semi-arid climates (Carvalho *et al.* 2010). The weak negative correlation between completeness and body size might initially appear surprising, given that small-bodied individuals are likely to be most susceptible to the vagaries of

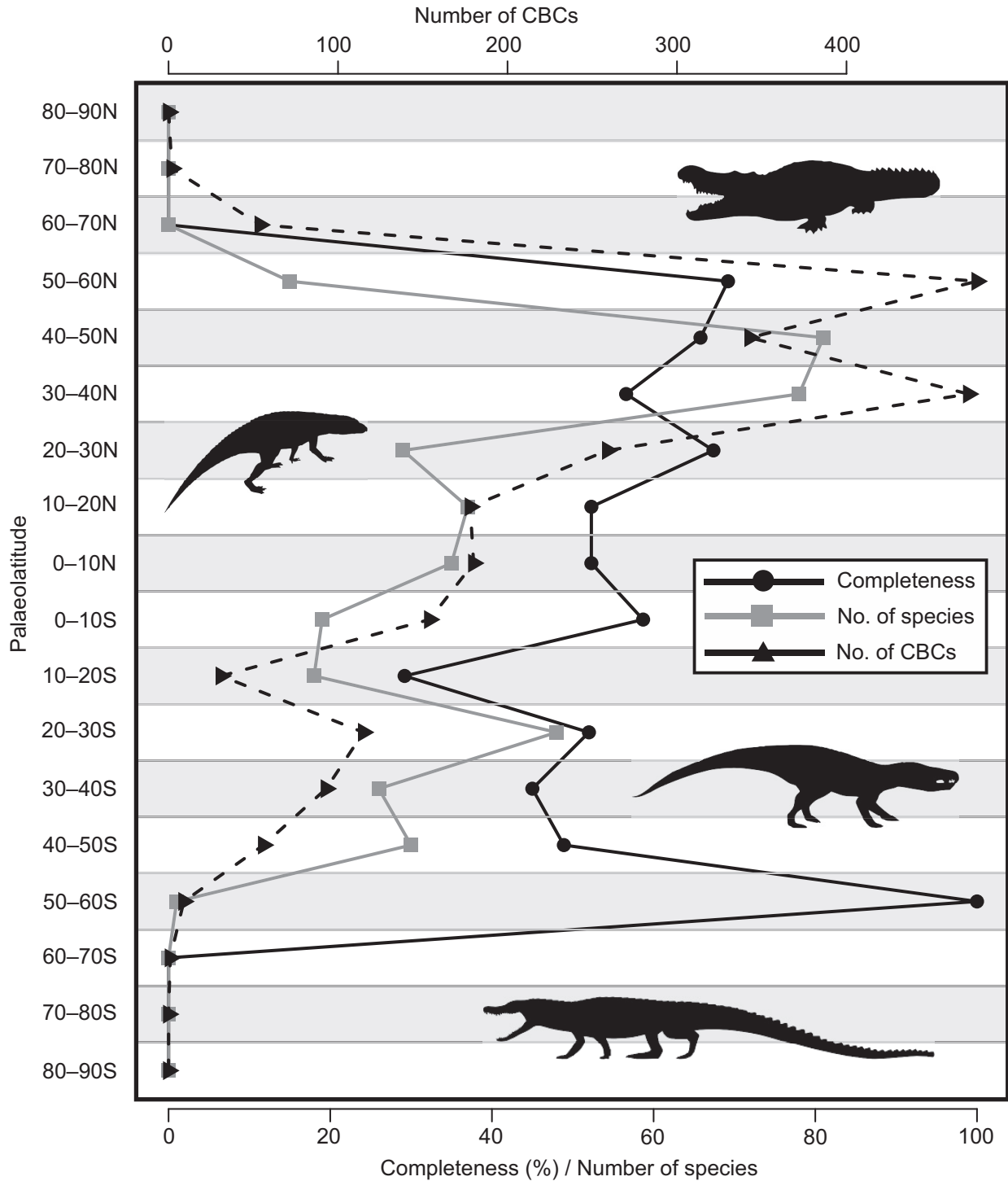
preservation (e.g. Hill & Behrensmeyer 1984; Brand *et al.* 2003). Lagerstätten probably account for the high completeness of some of the very smallest species, but given that this general pattern can be observed within size classes (albeit statistically non-significantly) it is probable that this does not drive the overall trend. One possibility pertains to the nature of the crocodylomorph skeleton. In contrast to the delicate bones that comprise the skeletons of primarily small-bodied tetrapod groups such as lepidosaurs and lissamphibians, as well as the light skeletons of birds and pterosaurs, the skeletal elements of crocodylomorphs tend to be fairly robust, especially those of the skull. Given that the skull comprises most of the character information for crocodylomorphs, this might explain why even small-bodied taxa tend to have relatively ‘complete’ (i.e.  $\geq 80\%$ ) skeletons. There might also be an upper limit of body size for good fossil preservation (Cleary *et al.* 2015); for example, Mannion & Upchurch (2010) demonstrated that the largest species of sauropodomorph dinosaurs tend to be known from less complete remains than their smaller-bodied relatives. However, a bias against the completeness of small-bodied species was recovered in studies of ichthyosaurs (Cleary *et al.* 2015; Beardmore 2017) and some dinosaur groups (Brown *et al.* 2013). Given that average completeness through time of crocodylomorphs correlates with neither pterosaurs nor sauropodomorphs, it seems that perhaps neither group is a suitable analogue.

#### *Spatiotemporal bias pervades the crocodylomorph fossil record*

Although fossil completeness does not appear to be a primary driver of observed crocodylomorph diversity, there are a number of time intervals in which the two covary (Figs 3, 4). Both decline across the Jurassic–Cretaceous boundary, 145 Ma (see below), but the most notable instance occurs at the K/Pg boundary, 66 Ma. A substantial decline in completeness, from 60% (Maastrichtian) to 38% (Danian), coincides with a taxonomic diversity crash from 50 to 13 species. Given that a sampling standardization approach reveals little change in overall standing diversity for crocodylomorphs across this mass extinction (Mannion *et al.* 2015), we might regard low average specimen completeness as a confounding factor in our ability to identify species in the Danian. However, we caveat this interpretation by noting that, whereas the Maastrichtian

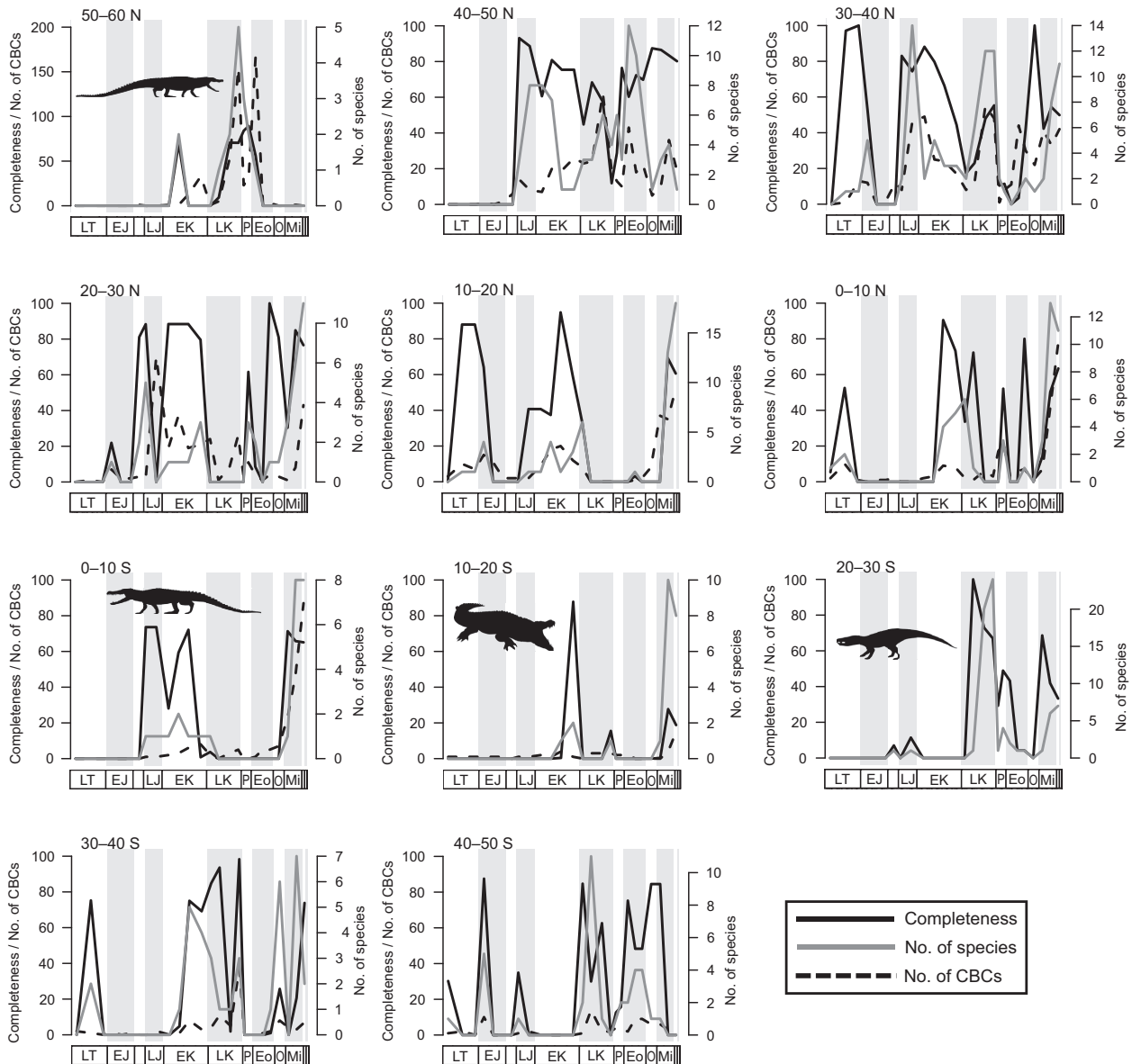
**FIG. 6.** Global palaeogeographical reconstructions showing the distribution of non-marine crocodylomorph fossil occurrences through time for the: A, Late Triassic (plate reconstruction age = 220 Ma); B, Early Jurassic (200 Ma); C, Middle Jurassic (170 Ma); D, Late Jurassic (150 Ma); E, Early Cretaceous (120 Ma); F, Late Cretaceous (80 Ma); G, Paleocene (60 Ma); H, Eocene (45 Ma); I, Oligocene (30 Ma); J, Miocene (15 Ma); K, Pliocene (4 Ma); L, Quaternary (1 Ma). Global palaeogeographical reconstructions from Fossilworks (<http://fossilworks.org/>) (Alroy 2013)) based on data in the Paleobiology Database (<https://paleobiodb.org/>) (Mannion *et al.* 2018b).





**FIG. 8.** Crocodylomorph completeness, number of crocodylomorph species, and number of crocodylomorph-bearing collections plotted through space, using 10° palaeolatitudinal bands. Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman and Nobumichi Tamura (<http://phylopic.org>).

**FIG. 7.** Palaeocontinental patterns of crocodylomorph completeness, number of species, and number of crocodylomorph-bearing collections (CBCs) plotted through time (using ~9 myr time bins) for: Africa; Asia; Australasia; Europe; North America; and South America. Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman and Nobumichi Tamura (<http://phylopic.org>).



**FIG. 9.** Palaeolatitudinal patterns of crocodylomorph completeness, number of species, and number of crocodylomorph-bearing collections (CBCs) plotted through time (using ~9 myr time bins) for: 50–60° N; 40–50° N; 30–40° N; 20–30° N; 10–20° N; 0–10° N; 0–10° S; 10–20° S; 20–30° S; 30–40° S; 40–50° S. Silhouettes of representative crocodylomorphs from selected palaeolatitudinal regions are modified from illustrations by Evan Boucher, Scott Hartman and Nobumichi Tamura (<http://phylopic.org>).

record comprises a high number of species from several palaeocontinents, 8 of the 13 Danian species are from North America, and completeness actually increases across the K/Pg boundary on that palaeocontinent. As such, although poor levels of completeness might contribute to low observed (i.e. uncorrected) diversity in the Danian, the reduction in our spatial sample appears to be the primary control (see below). This interpretation is also supported by the subsequent parallel increase in diversity, completeness, and geographical spread of fossil localities in the middle–late Paleocene (Figs 4, 7).

As documented above, no palaeocontinent or palaeolatitudinal band has a continuous fossil record throughout the evolutionary history of crocodylomorphs, and often a time interval is dominated by a single geographical region (Figs 5–8). Consequently, there is no meaningful concept of global terrestrial palaeobiodiversity, with our understanding of nearly all diversification and extinction ‘events’ essentially driven by regional patterns. This is well illustrated by diversity patterns across the J/K boundary: whereas there is a semi-cosmopolitan Late Jurassic record, the earliest Cretaceous signal predominantly comes from

**TABLE 2.** Correlation test results for palaeolatitudinal data series comparisons.

| Comparison           | Raw data |         | Generalized differencing |       |
|----------------------|----------|---------|--------------------------|-------|
|                      | rs       | p       | rs                       | p     |
| Completeness vs TDE  | 0.04     | 0.90    | 0.19                     | 0.61  |
| Completeness vs CBCs | 0.88     | 0.0004* | 0.77                     | 0.01* |
| TDE vs CBCs          | 0.25     | 0.45    | 0.56                     | 0.10  |

Statistical comparisons between the palaeolatitudinal distribution of crocodylomorph completeness, diversity (TDE), and numbers of crocodylomorph-bearing collections (CBCs) for 10° palaeolatitudinal bands. Spearman's rank correlation coefficients (rs) were calculated for each pairwise comparison based on the raw data and after generalized differencing.

\*Significant at alpha ( $p$ -value) = 0.05.

Europe (Tennant *et al.* 2016). Is the documented diversity decline across the J/K boundary a global event, or was it restricted to Europe? A similar problem is apparent across the K/Pg boundary (see above), as well as at hypothesized times of a number of evolutionary radiations (see below).

A poor, often entirely absent, fossil record characterizes the palaeotropics for much of pre-Neogene crocodylomorph evolutionary history (Markwick 1998; Brochu & Storrs 2012; Scheyer *et al.* 2013; Mannion *et al.* 2015; Salas-Gismondi *et al.* 2015). Although it remains possible that the palaeotropics were too hot to sustain crocodylomorph diversity during some time intervals, this seems unlikely given that there is a fossil record during the Late Triassic, early Late Cretaceous and late Paleocene, all of which represent warmer intervals (Sellwood & Valdes 2006; Zachos *et al.* 2008). Also, if 'taphonomic control taxa' (i.e. taxa with an approximately similar preservation potential as crocodylomorphs; *sensu* Bottjer & Jablonski 1988) are present, then we might infer that the absence of crocodylomorphs in this area is genuine (Markwick 1994; Matsumoto & Evans 2010). However, an examination of the distribution of the fossil record of Mesozoic dinosaurs, for example, indicates that there are no palaeotropical regions that yield abundant dinosaur, but not crocodylomorph, remains (e.g. Mannion *et al.* 2012). As such, this scarcity of crocodylomorph fossil remains is best explained as an artefact, resulting from a palaeotropical bias.

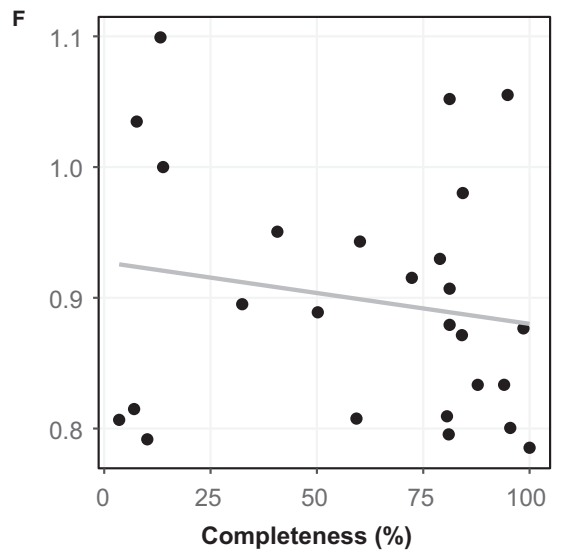
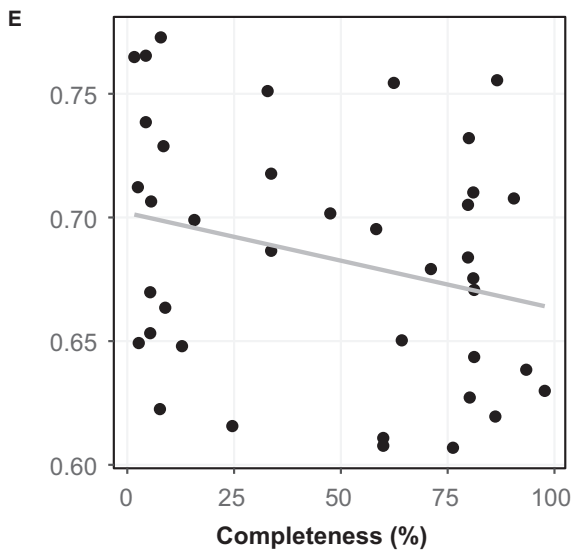
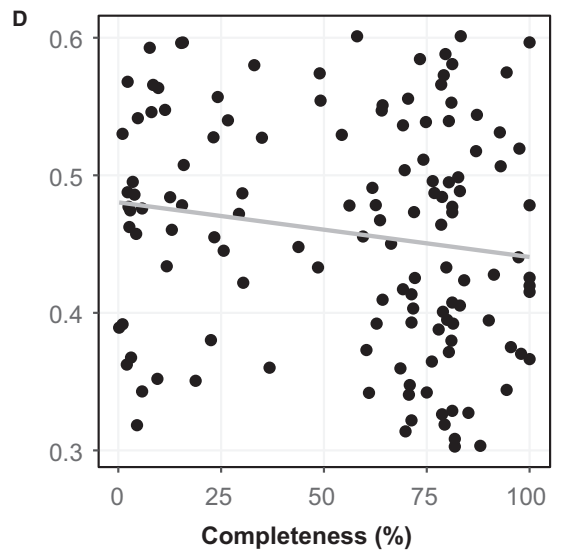
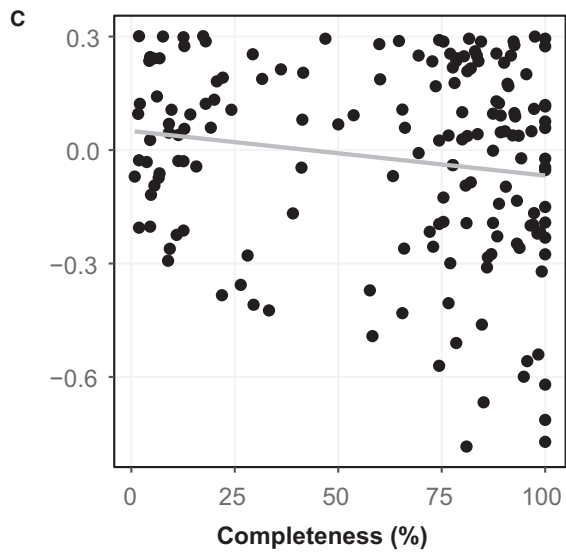
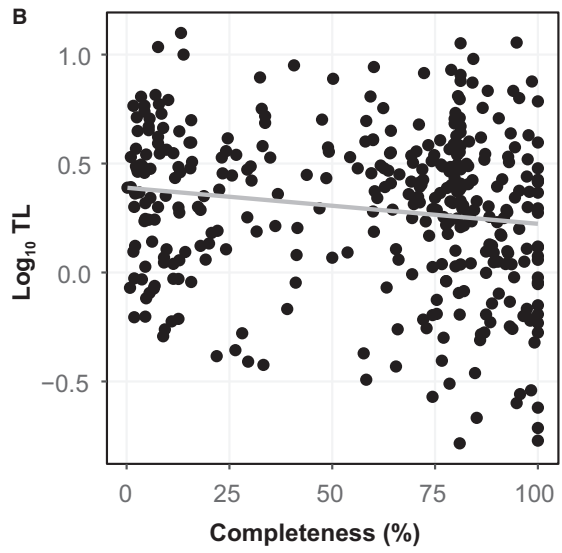
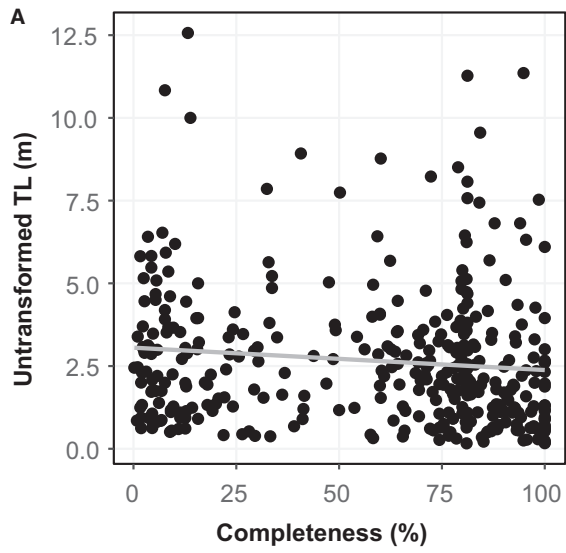
It is well established that the fossil record of nearly all organisms is dominated by occurrences from North America and western Europe (Jackson & Johnson 2001), for a suite of reasons that include: (1) the longer history of collecting fossils on these continents than elsewhere; (2) the relatively shorter distances between conurbations and fossil sites compared to other continents; and (3) the long-term prosperity of most fossil-bearing countries in these two continents. However, the northward drift of Pangaea during the Palaeozoic and early Mesozoic resulted in these

palaeocontinental regions (as well as much of Asia) lying primarily outside the tropics from the Jurassic onwards (Allison & Briggs 1993; Ziegler *et al.* 2003). As such, our potential sampling of palaeotropical non-marine fossil sites is dominated by Central America and Gondwana for most of crocodylomorph evolutionary history, and yet our sampling of these regions is extremely patchy (e.g. Benson *et al.* 2013; Kemp & Hadly 2016). Furthermore, rates of chemical weathering are generally higher in the tropics than at other latitudes, as a consequence of the higher temperatures and precipitation levels that characterize much of the tropics (Rees *et al.* 2004). This results in decreased fossil preservation (Behrensmeyer *et al.* 2000), as well as an increase in sedimentary rock breakdown (Kemp & Hadly 2016), and therefore acts as an additional filter to sampling palaeotropical biodiversity. In the rare instances that we do sample high palaeotropical crocodylomorph diversity prior to the Neogene (see Mannion *et al.* 2015) these localities usually represent semi-arid environments, inhabited by the ecologically unusual (i.e. predominantly terrestrial) notosuchians (Carvalho *et al.* 2010). Consequently, these geological, anthropogenic and taphonomic palaeotropical biases probably have a significant effect on our understanding of the evolutionary history of crocodylomorphs, as is also the case for most taxonomic groups (e.g. Allison & Briggs 1993; Jackson & Johnson 2001; Kidwell & Holland 2002; Bush & Bambach 2004; Vilhena & Smith 2013; Kemp & Hadly 2016).

#### *Does poor sampling obfuscate timings of crocodylomorph divergences and diversification?*

Clearly, the absence/paucity of sampling from certain time intervals, palaeocontinents and palaeolatitudes limits our understanding of patterns in biodiversity, both within time bins (e.g. preventing reconstructions of latitudinal biodiversity gradients) and between successive intervals (e.g. precluding assessments of temporal fluctuations in biodiversity). In particular, the scarcity of southern hemisphere and palaeotropical crocodylomorph occurrences for much of the group's 230 myr record significantly impacts upon our attempts to elucidate its evolutionary history. Below, we discuss how sampling affects our identification of the timing of several radiations and divergences within Crocodylomorpha.

The dearth of sampling of terrestrial crocodylomorphs during the Pliensbachian–Aalenian (190.8–170.3 Ma) impedes our understanding of the early evolution of the group, especially the origin of Neosuchia, with an approximately 20 myr gap between the oldest (*Calsoyasuchus* from the earliest Jurassic; Tykoski *et al.* 2002) and second oldest known neosuchian species (*Sunosuchus* from the Middle Jurassic; Fu *et al.* 2005) (note that this excludes





**TABLE 3.** Regression results for completeness and total length of species.

| Dataset                            | N   | Intercept | Slope   | <i>p</i> -value | Adjusted <i>R</i> <sup>2</sup> |
|------------------------------------|-----|-----------|---------|-----------------|--------------------------------|
| All species (TL untransformed)     | 363 | 3.055     | -0.006  | 0.034*          | 0.009                          |
| All species (log <sub>10</sub> TL) | 363 | 0.388     | -0.001  | 0.003*          | 0.021                          |
| Category A (log <sub>10</sub> TL)  | 167 | 0.05      | -0.001  | 0.038*          | 0.019                          |
| Category B (log <sub>10</sub> TL)  | 131 | 0.48      | -0.0003 | 0.075           | 0.016                          |
| Category C (log <sub>10</sub> TL)  | 39  | 0.701     | -0.0003 | 0.097           | 0.047                          |
| Category D (log <sub>10</sub> TL)  | 26  | 0.927     | -0.0004 | 0.406           | -0.011                         |

Results of ordinary least squares regressions of average crocodylomorph completeness on total length (TL) of species, using different datasets: including all species and untransformed TL values; all species and log-transformed TL values; species within size category A (smaller than 2 m) and log<sub>10</sub> TL; species within size category B (2–4 m) and log<sub>10</sub> TL; species within size category C (4–6 m) and log<sub>10</sub> TL; species within size category D (larger than 6 m) and log<sub>10</sub> TL.

\*Significant at alpha (*p*-value) = 0.05.

the marine clade Thalattosuchia, whose position within Crocodylomorpha is uncertain; see Wilberg 2015).

Aside from *Chimaerasuchus*, from the Aptian–Albian of China (Wu *et al.* 1995), and fragmentary remains (primarily referred to *Doratodon*) from the Coniacian–Maastrichtian of Europe (Company *et al.* 2005; Dalla Vecchia & Cau 2011; Rabi & Sebök 2015), notosuchian remains are known only from Gondwana during the Mesozoic. Until recently, no definitive representatives of Notosuchia have been identified from deposits older than the Aptian (Pol & Leardi 2015). However, based on its sister taxon relationship with Neosuchia, which has its oldest known representative in the Early Jurassic (Tykoski *et al.* 2002), Notosuchia has an extremely long ghost lineage (~65 myr). If the group was primarily Gondwanan prior to the Aptian, then the limited opportunities to sample crocodylomorphs from the southern continents during this interval (Benson *et al.* 2013) might be the cause of this ghost lineage. The recent reinterpretation of fragmentary cranial remains (CCM = 7%) from the Bathonian (Middle Jurassic) of Madagascar as the earliest known notosuchian (Dal Sasso *et al.* 2017) is in keeping with this view. Furthermore, although their ‘sudden’ appearance in the Aptian of Africa (e.g. Sereno & Larsson 2009;

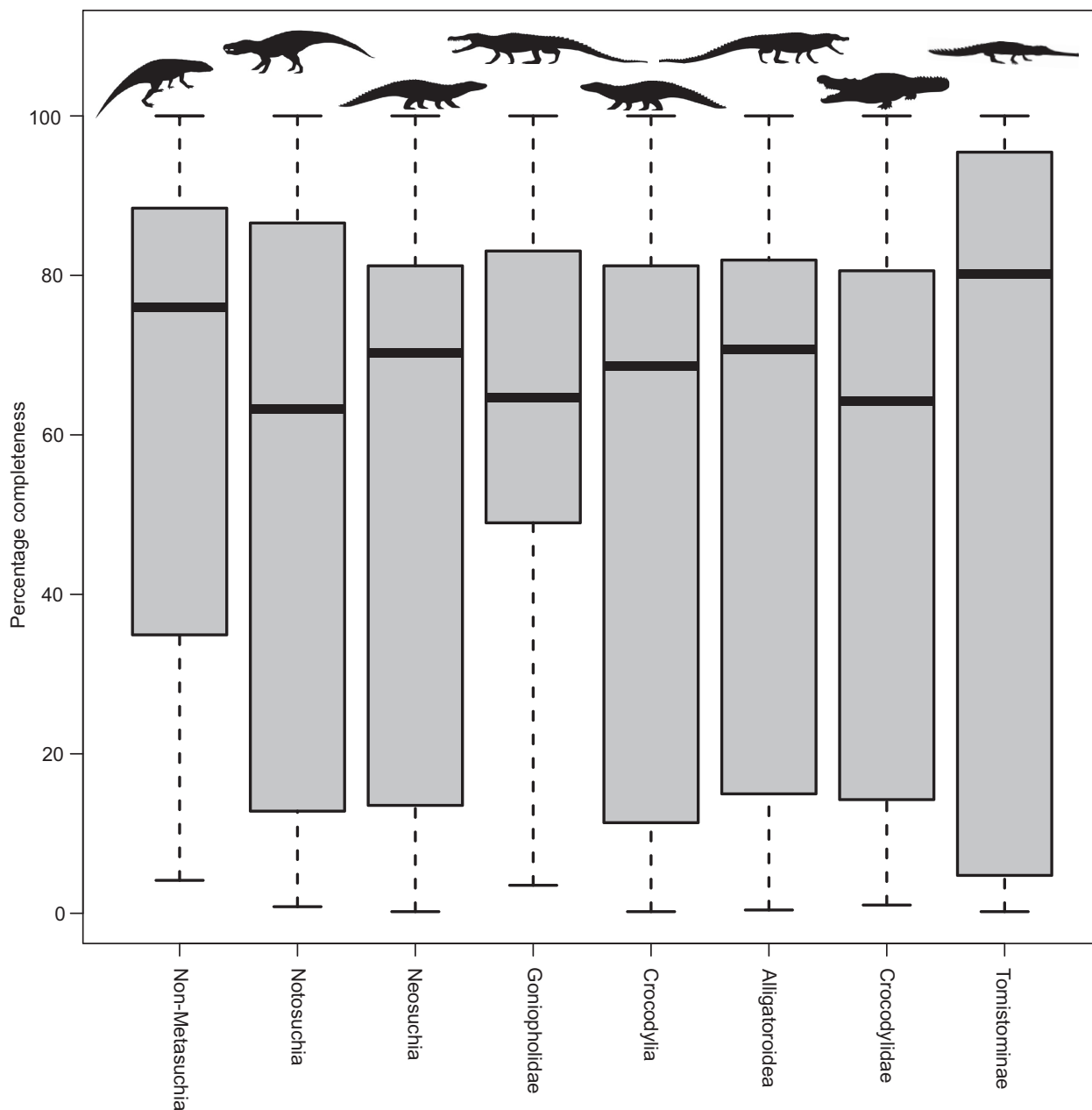
O’Connor *et al.* 2010), Asia (Wu *et al.* 1995), South America (Pol & Leardi 2015) and possibly Australia (Agnolin *et al.* 2010) might reflect a genuine notosuchian radiation (Pol *et al.* 2014; Bronzati *et al.* 2015), this seemingly instantaneous widespread distribution is perhaps indicative of an earlier, unsampled diversification.

Divergence times within Crocodylia based on molecular data are generally in close agreement with the fossil record. Recent molecular analyses place the split between Alligatoroidea and Crocodyloidea + Gavialoidea at approximately 100–80 Ma (Roos *et al.* 2007; Oaks 2011; Green *et al.* 2014; though note that most morphological-only analyses place Gavialoidea outside of Crocodyloidea + Alligatoroidea). Cretaceous crocodylians have currently only been recovered from Laurasia and North Africa: alligatoroids are known from Campanian–Maastrichtian (83.6–66 Ma) deposits (and possibly from the Santonian (86.3–83.6 Ma) too), and crocodyloids and gavialoids both have a Maastrichtian record (e.g. Brochu 2003; Jouve *et al.* 2008; Martin & Delfino 2010). Given the generally poor early Late Cretaceous terrestrial fossil record (Benson *et al.* 2013), coupled with low numbers of crocodylomorph species and average completeness outside of South America during this interval, possible ghost lineages of <15 myr would not be too surprising.

Other splits within Crocodylia have even greater congruence. For example, the first fossil occurrences of alligatorines and caimanines are known from early Paleocene (66–61.6 Ma) deposits (Brochu 2011) and molecular divergence estimates place this alligatoroid split at or close to the K/Pg boundary (e.g. Roos *et al.* 2007). There are wide error margins for the timing of the Crocodylinae–Tomistominae split (63.7–39.8 Ma; Oaks 2011), but the earliest definitive fossils of both clades are from the Ypresian (56–47.8 Ma) (Brochu 2003; Piras *et al.* 2007). Oaks (2011) inferred the age of the most recent common ancestor of *Crocodylus* to be 13.6–8.3 Ma, and the oldest fossil remains attributable to the genus are from the Tortonian (11.6–7.2 Ma) (Brochu 2000; Brochu & Storrs 2012; Delfino & Rossi 2013). Similarly, a 9.8–6.7 Ma age was calculated for the most recent common ancestor of *Caiman* (Oaks 2011), and it first appears in the fossil record in the Tortonian (e.g. Salas-Gismondi *et al.* 2015). This overall congruence between morphological and molecular data might merely reflect the serendipity of the crocodylian fossil record (i.e. these divergences happened to occur during our short-lived opportunities to sample a particular place in time).

The only significant discrepancy between molecular and morphological data pertains to the timing of the

**FIG. 10.** Global patterns in total length (TL) of species plotted against completeness for: A, all species (TL untransformed); B, all species; C, species smaller than 2 m (size class A); D, species between 2–4 m (size class B); E, species between 4–6 m (size class C); F, species larger than 6 m (size class D). TL is logged in plots B–F.



**FIG. 11.** Box-and-whisker plots showing the distribution of completeness for selected crocodylomorph subclades. The median average completeness value is shown by the horizontal black bar in each plot. Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman and Nobumichi Tamura (<http://phylopic.org>).

*Tomistoma–Gavialis* split, but in this regard the fossil record of gavialoids (extending back into the Campanian; Brochu 2004) substantially predates molecular estimates (29–16.1 Ma; Oaks 2011). Reconciling this discordance is partly dependent on resolving whether *Gavialis* is the sister taxon to all other extant crocodylians (morphological analyses) or to *Tomistoma* (molecular and combined analyses). However, it would also require the re-interpretation of ‘basal’ gavialoids (e.g. ‘thoracosaur’) from the latest Cretaceous–Palaeogene as ‘basal’ eusuchians, rather

than as close relatives of Gavialidae, for these divergence dates to be correct (e.g. see discussion in Brochu 1997; Harshman *et al.* 2003; Janke *et al.* 2005; Oaks 2011; Gold *et al.* 2014; Lee & Yates 2018).

#### *Extant taxa and the Pull of the Recent*

The ‘Pull of the Recent’ was originally coined by Raup (1979) to describe the phenomenon whereby the relatively

**TABLE 4.** Correlation test results for clade comparisons.

| Comparison                         | Raw data |                        | Generalized differencing |      |
|------------------------------------|----------|------------------------|--------------------------|------|
|                                    | rs       | p                      | rs                       | p    |
| Crocodylomorphs vs pterosaurs      | 0.75     | $5.23 \times 10^{-5*}$ | 0.26                     | 0.25 |
| Crocodylomorphs vs sauropodomorphs | 0.51     | 0.02*                  | -0.10                    | 0.66 |

Statistical comparisons between global temporal fluctuations in Mesozoic crocodylomorph, pterosaur, and sauropodomorph dinosaur completeness. Spearman's rank correlation coefficients (rs) were calculated for each pairwise comparison based on the raw data and after generalized differencing.

\*Significant at alpha ( $p$ -value) = 0.05.

complete sampling of extant taxa extends the stratigraphical ranges of geologically younger taxa to the present day across intervening time intervals in which fossils of those taxa are absent (Jablonski *et al.* 2003). Although these taxa must have been present during these time intervals, and thus would have contributed to diversity, no equivalent extension can be applied to extinct taxa; therefore, range-through data can lead to the artificial appearance of an exponential rise in diversity towards the present day (Foote 2001; Jablonski *et al.* 2003). Although this particular issue is not pertinent to our study, and most recent studies have suggested that the effect is limited (Jablonski *et al.* 2003; Sahney & Benton 2017), the Pull of the Recent has also been used as a more general term to describe factors that might lead to better sampling of the fossil record in younger relative to older rocks.

One aspect of this pertains to the identification of extant species in the fossil record. Of the 24 living species of Crocodylia, 15 have a putative fossil record, and most of these (13) are present in Quaternary deposits, meaning that there is little influence of the Pull of the Recent on crocodylian diversity in its original meaning. However, the average CCM of fossil remains of these 15 species is 41%, which is considerably lower than the average value for all crocodylomorphs (56%), Cenozoic species (51%), and also Neogene taxa (48%). Whereas 7 of these 15 species are known from fairly complete fossil skeletons (>70%), the remaining 8 species are all known from fossil skeletons that are less than 9% complete (average of <4%). Their low completeness might therefore suggest that these species can be more readily recognized in the fossil record because we have complete skeletons of living members, and thus we only need a small portion of the skull to make an identification. However, an alternative interpretation is that some of these fragmentary fossil remains are attributed to extant taxa primarily because their provenance closely matches the species' present-day distribution, rather than through shared autapomorphies.

## CONCLUSIONS

The fossil record of crocodylomorphs is heavily biased through both time and space, especially in the palaeotropics. In general, Mesozoic species are known from more complete fossil specimens than their Cenozoic counterparts, with an overall trend of decreasing average completeness through time. Our understanding of nearly all diversification and extinction 'events' in crocodylomorph evolutionary history is essentially driven by regional patterns, with no global sampling signal. These spatiotemporal biases might also explain several long phylogenetic ghost lineages, including the origin and radiation of Notosuchia. The close congruence between the fossil record and crocodylian divergence dates based on molecular data might merely be fortuitous, i.e. divergences happened to occur during our ephemeral spatiotemporal sampling windows.

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## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.668950m>

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