Palaeontology
The Palaeontological Association
Registered Charity No. 11683330

Spatiotemporal sampling patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact on diversity

Journal:	*Palaeontology*
Manuscript ID	PALA-07-18-4277-OA.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Mannion, Philip; Imperial College, Department of Earth Science and Engineering Chiarenza, Alfio; Imperial College, Department of Earth Science and Engineering Godoy, Pedro; University of Birmingham, School of Geography, Earth and Environmental Sciences Cheah, Yung Nam; Imperial College, Department of Earth Science and Engineering
Key words:	crocodiles, Crocodylomorpha, fossil record bias, Pull of the Recent, divergence times, diversity, spatiotemporal sampling
Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.	
Supplementary Information.xls	

SCHOLARONE™
Manuscripts

Spatiotemporal sampling patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact on diversity

Philip D. Mannion[1], Alfio Alessandro Chiarenza[1], Pedro L. Godoy[2] and Yung Nam Cheah[1]

[1]Department of Earth Science and Engineering, Imperial College London, South Kensington Campus, London, SW7 2AZ, UK; philipdmannion@gmail.com, a.chiarenza15@imperial.ac.uk, cheah.nam@gmail.com

[2]School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, B15 2TT, UK; pedrolorenagodoy@gmail.com

RRH: CROCODYLOMORPH FOSSIL RECORD
LRH: MANNION ET AL.

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.

Keywords: crocodiles; Crocodylomorpha; divergence times; diversity; fossil record bias; Pull of the Recent; spatiotemporal sampling

INTRODUCTION

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 and

McGowan 2007; Alroy 2010), spatial bias is also an important factor, but has received relatively little attention (though see Allison and Briggs 1993; Noto 2011; Vilhena and 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 and Briggs 1993; Vilhena and 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 geographic spread of the fossil record (Bush et al. 2004; Barnosky et al. 2005; Vilhena and 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 million year (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 and 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 in order to reconstruct temporal patterns in crocodylomorph palaeobiodiversity (Markwick 1998; Mannion et al. 2015; Pol and 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, e.g. 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. 2012a, b). A growing body of work has attempted to quantitatively estimate fossil specimen completeness, applying this to an array of Paleozoic to early Cenozoic tetrapods (Mannion and Upchurch 2010; Brocklehurst et al. 2012; Walther and Fröbisch 2013; Brocklehurst and Fröbisch 2014; Cleary et al. 2015; Verrière et al. 2016; Davies et al. 2017; Tutin and 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.

MATERIALS AND METHODS

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 4th July 2017 (Mannion et al. 2018a).

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 utilised 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 metres; (B) taxa between 2 and 4 metres; (C) taxa between 4 and 6 metres; and (D) taxa larger than 6 metres.

Mannion and 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 utilized 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 and 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, e.g. if one humerus was completely preserved, then all humeral characters were considered as '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 utilized 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 million years) 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, i.e. 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 thus they are not grouped together as Indo-Madagascar, nor are they incorporated with Africa, with rifting having separated these areas by the latest Cretaceous (Ali and Aitchison 2008). India is incorporated within Asia from the Eocene onwards, following their collision (Ali and 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 29th May 2018 (Mannion et al., 2018b).

All previous equivalent studies of fossil specimen completeness have been restricted to Paleozoic to early Cenozoic (Palaeogene) taxa (e.g. Brocklehurst et al. 2012; Brocklehurst and 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 et al. 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 crocodylomorph-bearing collections [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 Graeme Lloyd (http://www.graemetlloyd.com/methgd.html). 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.

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 and Lloyd 2015). The complete dataset is available in Mannion et al. (2018a).

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 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 an 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 crocodylomorph-bearing collections (CBCs) in all of our analyses (Spearman's rho (rs) = 0.72–0.86), completeness and numbers of CBCs are only significantly correlated when using 9 myr bin-level analyses, after applying generalized differencing (rs = 047; 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 (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–early Maastrichtian 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 with average completeness of 61%), Asia (68 species: 56%), Australasia (25 species: 35%), Europe (70 species: 69%), India (one species: 15%), Madagascar (six 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 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 and Hutchison 1980) and 79° S (late Eocene of Antarctica; Willis and 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 subpolar 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–Quaternary, 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–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). 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–Jurassic, and usually comprises two or 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 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 meters) are the least complete.

The average completeness of several well-recognised crocodylomorph subclades does not strongly deviate from the overall pattern (Fig. 11), with Notosuchia (72 species with 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 (rs = 0.51) and, especially, pterosaurs (rs = 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 utilise the character completeness metric (Mannion and 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 and Butler 2017); (3) pterosaurs = 59% (Dean et al. 2016); (4) pelycosaurs = 70% (Brocklehurst and Fröbisch 2014); (5) Cretaceous–Palaeogene eutherian mammals = 73% (Davies et al. 2017); (6) crocodylomorphs = 81% (this study); and (7) anomodonts = 82% (Walther and 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 and 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 and Fröbisch 2014; Verrière et al. 2016; Tutin and Butler 2017).

This greater weighting of the skull is largely consistent across crocodylomorph phylogenetic data sets (e.g. Brochu and 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, and 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 and Behrensmeyer 1984; Brand et al. 2003). Lagerstätten likely 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. ≥80%) skeletons. There might also be an upper limit of body size for good fossil preservation (Cleary et al. 2015); for example, Mannion and 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 standardisation 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 record comprises a high number of species from several palaeocontinents, eight 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 geographic 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 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 and 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 and Valdes 2006; Zachos et al. 2008). Also, if 'taphonomic control taxa' (i.e. taxa with an approximately similar preservation potential as crocodylomorphs; *sensu* Bottjer and Jablonski 1988) are present, then we might infer that the absence of crocodylomorphs in this area is genuine (Markwick 1994; Matsumoto and 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 and 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 Paleozoic and early Mesozoic resulted in these palaeocontinental regions (as well as much of Asia) lying primarily outside of the tropics from the Jurassic onwards (Allison and 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 and 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 and 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 likely 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 and Briggs 1993; Jackson and Johnson 2001; Kidwell and Holland 2002; Bush and Bambach 2004; Vilhena and Smith 2011; Kemp and 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 million year 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 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 and Cau 2011; Rabi and Sebők 2015), notosuchian remains are only known from Gondwana during the Mesozoic. Until recently, no definitive representatives of Notosuchia have been identified from deposits older than the Aptian (Pol and 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 and Larsson 2009; O'Connor et al. 2010), Asia (Wu et al. 1995), South America (Pol and 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 and 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* as 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 and Storrs 2012; Delfino and 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 *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. 'thoracosaurs') 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; Goldman et al. 2014; Lee and 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 complete sampling of extant taxa extends the stratigraphic 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 and 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 of these have a putative fossil record, and most of them (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 seven of these 15 species are known from fairly complete fossil skeletons (>70%), the remaining eight 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.

ACKNOWLEDGEMENTS

We are grateful for the efforts of all those who have generated crocodylomorph fossil data, as well as those who have entered this data into the Paleobiology Database (especially John Alroy, Matthew Carrano, Anna Behrensmeyer, and Mark Uhen). We also thank all those who facilitated collections access for the compilation of crocodylomorph body size data. Jonathan Tennant also provided us with information on the preserved skeletons of several fossil crocodylomorphs. Silhouettes of representative crocodylomorphs in figures are modified from illustrations by Evan Boucher, Scott Hartman, and Nobumichi Tamura, hosted at Phylopic (http://phylopic.org), where all license information is available. Comments from Mario Bronzati, Sally Thomas, and an anonymous reviewer improved an earlier version of this work. PDM was supported by a Leverhulme Trust Early Career Fellowship (ECF-2014-662) and a Royal Society University Research Fellowship (UF160216). AAC was supported by an Imperial College London Janet Watson Departmental PhD Scholarship. PLG was supported by a University of Birmingham-CAPES Joint PhD Scholarship (3581-14-4). This is Paleobiology Database official publication number XXX.

DATA ARCHIVING STATEMENT

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

REFERENCES

AGNOLIN, F. L., EZCURRA, M. D., PAIS, D. F. and SALISBURY, S. W. 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology*, **8**, 257–300.

ALI, J. R. and AITCHISON, J. C. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth Science Reviews*, **88**, 145–166.

ALLISON, P. A. and BRIGGS, D. E. G. 1993. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology*, **21**, 65–68.

ALROY, J. 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, **53**, 1211–1235.

ALROY, J. 2013. Online paleogeographic map generator. http://paleodb.org/?a=mapForm.

BARNOSKY, A. D., CARRASCO, M. A. and DAVIS, E. B. 2005. The impact of the species-area relationship on estimates of paleodiversity. *PLoS Biology*, **3**, e266.

BATEZELLI, A. 2017. Continental systems tracts of the Brazilian Cretaceous Bauru Basin and their relationship with the tectonic and climatic evolution of South America. *Basin Research*, **29**, 1–25.

BEARDMORE, S. R. 2017. The effect of body size on skeletal articulation and completeness in Jurassic Ichthyopterygia (Reptilia). *Paläontologische Zeitschrift*, **91**, 577–587.

BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T. and FURRER, H. 2012a. Float or sink: modelling the taphonomic pathway of marine crocodiles (Mesoeucrocodylia, Thalattosuchia) during the death–burial interval. *Palaeobiodiversity and Palaeoenvironments*, **92**, 83–98.

BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T., FURRER, H. and JOHNSON, C. 2012b. Death, decay and disarticulation: Modelling the skeletal taphonomy of marine reptiles demonstrated using *Serpianosaurus* (Reptilia; Sauropterygia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **337–338**, 1–13.

BEHRENSMEYER, A. K., KIDWELL, S. M. and GASTALDO, R. A. 2000. Taphonomy and paleobiology. *Paleobiology*, **26**, 103–147.

BELL, M. A. and LLOYD, G. T. 2015. strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology*, **58**, 379–389.

BENSON, R. B. J., MANNION, P. D., BUTLER, R. J., UPCHURCH, P., GOSWANI, A. and EVANS, S. E. 2013. Cretaceous tetrapod fossil record sampling and faunal turnover: implications for biogeography and the rise of modern clades. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 88–107.

BENSON, R. B. J., BUTLER, R. J., ALROY, J., MANNION, P. D., CARRANO, M. T. and LLOYD, G. T. 2016. Near-stasis in the long-term diversification of Mesozoic tetrapods. *PLoS Biology*, 14, e1002359.

BENTON, M. J. 2008. How to find a dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology*, **34**, 516–533.

BOTTJER, D. J. and JABLONSKI, D. 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios*, **3**, 540–560.

BRAND, L. R., HUSSEY, M. and TAYLOR, J. 2003. Decay and disarticulation of small vertebrates in controlled experiments. *Journal of Taphonomy*, **1**, 69–95.

BROCHU, C. A. 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Systematic Biology*, **46**, 479–522.

BROCHU, C. A. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. *Copeia*, **2000**, 657–673.

BROCHU, C. A. 2003. Phylogenetic approaches towards crocodylian history. *Annual Review of Earth and Planetary Sciences*, **31**, 357–397.

BROCHU, C. A. 2004. A new Late Cretaceous gavialoid crocodylian from eastern North America and the phylogenetic relationships of thoracosaurs. *Journal of Vertebrate Paleontology*, **24**, 610–633.

BROCHU, C. A. 2011. Phylogenetic relationships of *Necrosuchus ionensis* Simpson, 1937 and the early history of caimanines. *Zoological Journal of the Linnean Society*, **163**, S228–S256.

BROCHU, C. A. and STORRS, G. W. 2012. A giant crocodile from the Plio-Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of *Crocodylus* in Africa. *Journal of Vertebrate Paleontology*, **32**, 587–602.

BROCKLEHURST, N. and FRÖBISCH, J. 2014. Current and historical perspectives on the completeness of the fossil record of pelycosaurian-grade synapsids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **399**, 114–126.

BROCKLEHURST, N., UPCHURCH, P., MANNION, P. D. and O'CONNOR, J. 2012. The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. *PLoS ONE*, **7**, e39056.

BRONZATI, M., MONTEFELTRO, F. C. and LANGER, M. C. 2015. Diversification events and the effects of mass extinctions on Crocodyliformes evolutionary history. *Royal Society Open Science*, **2**, 140385.

BROWN, C. M., EVANS, D. C., CAMPIONE, N. E., O'BRIEN, L. J. and EBERTH, D. A. 2013. Evidence for Taphonomic Size Bias in a Model Mesozoic Terrestrial Alluvial-Paralic System. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 108–122.

BUSH, A. M. and BAMBACH, R. K. 2004. Did Alpha Diversity Increase during the Phanerozoic? Lifting the Veils of Taphonomic, Latitudinal, and Environmental Biases. *Journal of Geology*, **112**, 625–642.

BUSH, A. M., MARKEY, M. J. and MARSHALL, C. R. 2004. Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling-standardization. *Paleobiology*, **30**, 666–686.

CARVALHO, I. S., GASPARINI, Z. B., SALGADO, L., DE VASCONCELLOS, F. M. and MARINHO, T. S. 2010. Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **297**, 252–262.

CLEARY, T. J., MOON, B. C., DUNHILL, A. M. and BENTON, M. J. 2015. The fossil record of ichthyosaurs, completeness metrics and sampling biases. *Palaeontology*, **58**, 521–536.

CLOSE, R. A., BENSON, R. B. J., UPCHURCH, P. and BUTLER, R. J. 2017. Controlling for the species-area effect supports constrained long-term Mesozoic terrestrial vertebrate diversification. *Nature Communications*, **8**, 15381.

COHEN, K. M., FINNEY, S. C., GIBBARD, P. L. and FAN, J.-X. 2013. The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204 [updated here: http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.pdf].

COMPANY, J., PEREDA SUBERBIOLA, X., RUIZ-OMEÑACA, J. I. and BUSCALIONI A. D. 2005. A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *Journal of Vertebrate Paleontology*, **25**, 343–353.

DALLA VECCHIA, F. M. and CAU, A. 2011. The first record of a notosuchian crocodyliform from Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, **117**, 309–321.

DAL SASSO, C., PASINI, G., FLEURY, G. and MAGANUCO S. 2017. *Razanandrongobe sakalavae*, a gigantic mesoeucrocodylian from the Middle Jurassic of Madagascar, is the oldest known notosuchian. *PeerJ*, **5**, e3481

DAVIES, T., BELL, M., GOSWAMI, A. and HALLIDAY, T. J. D. 2017. Completeness of the eutherian mammal fossil record and implications for reconstructing mammal evolution through the Cretaceous-Palaeogene mass extinction. *Paleobiology*, **43**, 521–536.

DEAN, C. D., MANNION, P. D. and BUTLER, R. J. 2016. Preservational bias controls the fossil record of pterosaurs. *Palaeontology*, **59**, 225–247.

DELFINO, M. and ROSSI, M. A. 2013. Fossil crocodylid remains from Scontrone (Tortonian, Southern Italy) and the late Neogene Mediterranean biogeography of crocodylians. *Geobios*, **46**, 25–31.

DRISCOLL, D. A., DUNHILL, A. M., STUBBS, T. L. and BENTON, M. J. 2018. The mosasaur fossil record through the lens of fossil completeness. *Palaeontology* (doi: 10.1111/pala.12381).

DYKE, G. J., McGOWAN, A., NUDDS, R. and SMITH, D. 2009. The shape of pterosaur evolution: evidence from the fossil record. *Journal of Evolutionary Biology*, **22**, 890–898.

ESTES, R. and HUTCHISON, J. H. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **30**, 325–347.

FARLOW, J. O., HURLBURT, G. R., ELSEY, R. M., BRITTON, A. R. and LANGSTON JR, W. 2005. Femoral dimensions and body size of *Alligator mississippiensis*: estimating the size of extinct mesoeucrocodylians. *Journal of Vertebrate Paleontology*, **25**, 354–369.

FOOTE, M. 2001. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. *Paleobiology*, **27**, 602–630.

FOUNTAINE, T. M. R., BENTON, M. J., NUDDS, R. L. and DYKE, G. J. 2005. The quality of the fossil record of Mesozoic birds. *Proceedings of the Royal Society of London B*, **272**, 289–294.

FU, Q.-M., MING, S.-Y. and PENG, G.-Z. 2005. A new species of *Sunosuchus* from Zigong, Sichuan, China. *Vertebrata PalAsiatica*, **43**, 76–83.

GODOY, P. L., BRONZATI, M., ELTINK, E., MARSOLA, J. C. A., CIDADE, G. M., LANGER, M. C. and MONTEFELTRO, F. C. 2016. Postcranial anatomy of *Pissarrachampsa sera* (Crocodyliformes, Baurusuchidae) from the Late Cretaceous of Brazil: insights on lifestyle and phylogenetic significance. *PeerJ*, **4**, e2075.

GOLD, M. E. L., BROCHU, C. A. and NORELL, M. A. 2014. An Expanded Combined Evidence Approach to the *Gavialis* Problem Using Geometric Morphometric Data from Crocodylian Braincases and Eustachian Systems. *PLoS ONE*, **9**, e105793.

GREEN, R. E., BRAUN, E. L., ARMSTRONG, J., EARL, D., NGUYEN, N., HICKEY, G., et al. 2014. Three crocodilian genomes reveal ancestral patterns of evolution among archosaurs. *Science*, **346**, 1254449.

HARSHMAN, J., HUDDLESTON, C. J., BOLLBACK, J. P., PARSONS, T. J. and BRAUN, M. J. 2003. True and false gharials: a nuclear gene phylogeny of Crocodylia. *Systematic Biology*, **52**, 386–402.

HILL, A. and BEHRENSMEYER, A. K. 1984, Disarticulation patterns of some modern East African mammals. *Paleobiology*, **10**, 366–376.

HURLBURT, G. R., HECKERT, A. B. and FARLOW, J. O. 2003. Body mass estimates of phytosaurs (Archosauria: Parasuchidae) from the Petrified Forest Formation (Chinle Group: Revueltian) based on skull and limb bone measurements. *New Mexico Museum of Natural History and Science Bulletin*, **24**, 105–113.

IRMIS, R. B., NESBITT, S. J. and SUES, H-D. 2013. Early Crocodylomorpha. *Geological Society, London, Special Publications*, **379**, 275–302.

JABLONSKI, D., ROY, K., VALENTINE, J. W., PRICE, R. M. and ANDERSON, P. S. 2003. The Impact of the Pull of the Recent on the History of Marine Diversity. *Science*, **300**, 1133–1135.

JACKSON, J. B. C. and JOHNSON, K. G. 2001. Measuring Past Biodiversity. *Science*, **293**, 2401–2404.

JANKE, A., GULLBERG, A., HUGHES, S., AGGARWAL, R. K. and ARNASON, U. 2005. Mitogenomic analyses place the gharial (*Gavialis gangeticus*) on the crocodile tree and provide pre-K/T divergence times for most crocodilians. *Journal of Molecular Evolution*, **61**, 620–626.

JOUVE, S., BARDET, N., JALIL, N.-E., PEREDA SUBERBIOLA, X., BOUYA, B. and AMAGHZAZ, M. 2008. The oldest African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous–Tertiary Boundary. *Journal of Vertebrate Paleontology*, **28**, 409–421.

KEMP, M. E. and HADLY, E. A. 2016. Rocking Earth's biodiversity cradle: challenges, advances, and prospects for conservation paleontology in the tropics. *Journal of Vertebrate Paleontology*, **36**, e1179640.

KIDWELL, S. M. and HOLLAND, S. M. 2002. The Quality of the Fossil Record: Implications for Evolutionary Analyses. *Annual Review of Ecology and Systematics*, **33**, 561–588.

LEE, M. S. Y. and YATES, A. M. 2018. Tip-dating and homoplasy: reconciling the shallow molecular divergences of modern gharials with their long fossil record. *Proceedings of the Royal Society of London, Series B*, **285**, 20181071.

MANNION, P. D. and UPCHURCH, P. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology*, **36**, 283–302.

MANNION, P. D., BENSON, R. B. J., UPCHURCH, P., BUTLER, R. J., CARRANO, M. T. and BARRETT, P. M. 2012. A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Global Ecology and Biogeography*, **21**, 898–908.

MANNION, P. D., BENSON, R. B. J., CARRANO, M. T., TENNANT, J. P., JUDD, J. and BUTLER, R. J. 2015. Climate constrains the history and biodiversity of crocodylians. *Nature Communications*, **6**, 8438.

MANNION, P. D., CHIARENZA, A. A., GODOY, P. L. and CHEAH, Y. N. 2018a. Data from: Spatiotemporal sampling patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact on diversity. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.668950m.

MANNION, P. D., CARRANO, M. T., ALROY, J. and BEHRENSMEYER, A. K. 2018b. Taxonomic occurrences of Crocodylomorpha recorded in the Paleobiology Database. Fossilworks. http://fossilworks.org.

MARCOT, J. D., FOX, D. L. and NIEBUHR, S. R. 2016. Late Cenozoic onset of the latitudinal diversity gradient of North American mammals. *Proceedings of the National Academy of Sciences, USA*, **113**, 7189–7194.

MARKWICK, P. J. 1994. "Equability", continentality, and Tertiary "climate": The crocodilian perspective. *Geology*, **22**, 613–616.

MARKWICK, P. J. 1998. Crocodilian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology*, **24**, 470–497.

MARTIN, J. E. and DELFINO, M. 2010. Recent advances in the comprehension of the biogeography of Cretaceous European eusuchians. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **293**, 406–418.

MARTIN, J. E., AMIOT, R., LÉCUYER, C. and BENTON, M. J. 2014. Sea surface temperature contributes to marine crocodylomorph evolution. *Nature Communications*, **5**, 4658.

MARTIN, J. E., DELFINO, M. and SMITH, T. 2016. Osteology and affinities of Dollo's goniopholidid (Mesoeucrocodylia) from the Early Cretaceous of Bernissart, Belgium. *Journal of Vertebrate Paleontology*, **36**, e1222534.

MATSUMOTO, R. and EVANS, S. E. 2010. Choristoderes and the freshwater assemblages of Laurasia. *Journal of Iberian Geology*, **36**, 253–274.

MONTEFELTRO, F. C., LARSSON, H. C. E., DE FRANCA, M. A. G. and LANGER, M. C. 2013. A new neosuchian with Asian affinities from the Jurassic of northeastern Brazil. *Naturwissenschaften*, **100**, 835–841.

NOTO, C. 2011. Hierarchical Control of Terrestrial Vertebrate Taphonomy Over Space and Time: Discussion of Mechanisms and Implications for Vertebrate Paleobiology. *In* ALLISON, P. A. and BOTTJER, D. J. (eds). *Taphonomy: Process and Bias Through Time (2nd edition)*. Springer Netherlands, 287–336.

OAKS, J. R. 2011. A time-calibrated species tree of Crocodylia reveals a recent radiation of true crocodiles. *Evolution*, **65**, 3285–3297.

O'CONNOR, P. M., SERTICH, J. J. W., STEVENS, N. J., ROBERTS. E. M., GOTTFRIED, M. D., HIERONYMUS, T. L., JINNAH, Z. A., RIDGELY, R., NGASALA, S. E. and TEMBA, J. 2010. The evolution of mammal-like crocodyliforms in the Cretaceous Period of Gondwana. *Nature*, **466**, 748–751.

PIRAS, P., DELFINO, M., DEL FAVERO, L. and KOTSAKIS, T. 2007. Phylogenetic position of the crocodylian *Megadontosuchus arduini* and tomistomine palaeobiogeography. *Acta Palaeontologica Polonica*, **52**, 315–328.

POL, D. and LEARDI, J. M. 2015. Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. *Publicación Electrónica de la Asociación Paleontológica Argentina*, **15**, 172–186.

POL, D., LEARDI, J. M., LECUONA, A. and KRAUSE, M. 2012. Postcranial anatomy of *Sebecus icaeorhinus* (Crocodyliformes, Sebecidae) from the Eocene of Patagonia. *Journal of Vertebrate Paleontology*, **32**, 328–354.

POL, D., NASCIMENTO, P., CARVALHO, M., RICCOMINI, A. B., PIRES-DOMINGUES, R. A. and ZAHER, H. 2014. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS ONE*, **9**, e93105.

RABI, M. and SEBŐK, N. 2015. A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. *Gondwana Research*, **28**, 1197–1211.

RAUP, D. M. 1972. Taxonomic diversity during the Phanerozoic. *Science*, **177**, 1065–1071.

RAUP, D. M. 1979. Biases in the fossil record of species and genera. *Bulletin of Carnegie Museum of Natural History*, **13**, 85–91.

R CORE TEAM. 2017. *R: A language and environment for statistical computing, v. 3.4.3*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

REES, P. M., NOTO, C. R., PARRISH, J. M. and PARRISH, J. T. 2004. Late Jurassic climates, vegetation, and dinosaur distributions. *Journal of Geology*, **112**, 643–653.

ROOS, J., AGGARWAL, R. K. and JANKE, A. 2007. Extended mitogenomic phylogenetic analyses yield new insight into crocodylian evolution and their survival of the Cretaceous-Tertiary boundary. *Molecular Phylogenetics and Evolution*, **45**, 663–673.

SAHNEY, S. and BENTON, M. J. 2017. The impact of the Pull of the Recent on the fossil record of tetrapods. *Evolutionary Ecology Research*, **18**, 7–23.

SALAS-GISMONDI, R., FLYNN, J. J., BABY, P., TEJADA-LARA, J. V., WESSELINGH, F. P. and ANTOINE, P.-O. 2015. A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceedings of the Royal Society of London, Series B*, **282**, 20142490.

SALISBURY, S. W., MOLNAR, R. E., FREY, E. and WILLIS, P. M. A. 2006. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. *Proceedings of the Royal Society of London, Series B*, **273**, 2439–2448.

SCHEYER, T. M., AGUILERA, O. A., DELFINO, M., FORTIER, D. C., CARLINI, A. A., SÁNCHEZ, R., CARRILLO-BRICEÑO, J. D., QUIROZ, L. and SÁNCHEZ-VILLAGRA, M. R. 2013 Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications*, **4**, 1907.

SELLWOOD, B. W. and VALDES, P. J. 2006. Mesozoic climates: general circulation models and the rock Record. *Sedimentary Geology*, **190**, 269–287.

SERENO, P. C. and LARSSON, H. C. 2009. Cretaceous Crocodyliforms from the Sahara. *Zookeys*, **28**, 1–143.

SMITH, A. B. and MCGOWAN, A. J. 2007. The shape of the Phanerozoic marine palaeodiversity curve: how much can be predicted from the sedimentary rock record of western Europe? *Palaeontology*, **50**, 765–774.

TENNANT, J. P., MANNION, P. D. and UPCHURCH, P. 2016. Environmental drivers of crocodyliform extinction across the Jurassic/Cretaceous interval. *Proceedings of the Royal Society of London, Series B*, **283**, 20152840.

TUTIN, S. L. and BUTLER, R. J. 2017. The completeness of the fossil record of plesiosaurs, marine reptiles from the Mesozoic. *Acta Palaeontologica Polonica*, **62**, 563–573.

TYKOSKY, R. S., ROWE, T. B., KETCHAM, R. A. and COLBERT, M. W. 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, **22**, 593–611.

VERRIÈRE, A., BROCKLEHURST, N. and FRÖBISCH, J. 2016. Assessing the completeness of the fossil record: comparison of different methods applied to parareptilian tetrapods (Vertebrata: Sauropsida). *Paleobiology*, **42**, 680–695.

VILHENA, D. A. and SMITH, A. B. 2013. Spatial Bias in the Marine Fossil Record. *PLoS ONE*, **8**, e74470.

WALTHER, M. and FRÖBISCH, J. 2013. The quality of the fossil record of anomodonts (Synapsida, Therapsida). *Comptes Rendus Paleovol*, **12**, 495–504.

WILBERG, E. W. 2015. What's in an Outgroup? The Impact of Outgroup Choice on the Phylogenetic Position of Thalattosuchia (Crocodylomorpha) and the Origin of Crocodyliformes. *Systematic Biology*, **64**, 621–637.

WILBERG, E. W. 2017. Investigating patterns of crocodyliform cranial disparity through the Mesozoic and Cenozoic. *Zoological Journal of the Linnean Society*, **181**, 189–208.

WILLIS, P. M. A. and STILWELL, J. D. 2000. A probable piscivorous crocodile from Eocene deposits of McMurdo Sound, East Antarctica. *Antarctic Research Series*, **76**, 355–358.

WU, X.-C., SUES, H.-D. and SUN, A. 1995. A plant-eating crocodyliform reptile from the Cretaceous of China. *Nature*, **376**, 678–680.

ZACHOS, J. C., DICKENS, G. R. and ZEEBE, R. E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, **451**, 279–283.

ZIEGLER, A. M., ESHEL, G., REES, P. M., ROTHFUS, T. A., ROWLEY, D. B. and SUNDERLIN, D. 2003. Tracing the tropics across land and sea: Permian to present. *Lethaia*, **36**, 227–254.

FIGURES

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

FIGURE 2. Box-and-whisker plots showing the distribution of crocodylomorph completeness for different time intervals.

FIGURE 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 license information is available.

FIGURE 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, hosted at Phylopic (http://phylopic.org), where all license information is available.

FIGURE 5. Box-and-whisker plots showing the distribution of crocodylomorph completeness for each palaeocontinent.

FIGURE 6. Global palaeogeographic 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 palaeogeographic reconstructions from Fossilworks (http://fossilworks.org/ [Alroy 2013]) based on data in the Paleobiology Database (https://paleobiodb.org/) (Mannion et al. 2018b). Ages in parentheses refer to the palaeogeographic reconstruction date.

FIGURE 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: (A) Africa; (B) Asia; (C) Australasia; (D) Europe; (E) North America; (F) South America. Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman, and Nobumichi Tamura, hosted at Phylopic (http://phylopic.org), where all license information is available.

FIGURE 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, hosted at Phylopic (http://phylopic.org), where all license information is available.

FIGURE 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: (A) 50–60° N; (B) 40–50° N; (C) 30–40° N; (D) 20–30° N; (E) 10–20° N; (F) 0–10° N; (G) 0–10° S; (H) 10–20° S; (I) 20–30° S; (J) 30–40° S; (K) 40–50° S. Silhouettes of representative crocodylomorphs from selected palaeolatitudinal regions are modified from illustrations by Evan Boucher, Scott Hartman, and Nobumichi Tamura, hosted at Phylopic (http://phylopic.org), where all license information is available.

FIGURE 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.

FIGURE 11. Box-and-whisker plots showing the distribution of completeness for selected crocodylomorph subclades. Silhouettes of representative crocodylomorphs are modified from illustrations by Evan Boucher, Scott Hartman, and Nobumichi Tamura, hosted at Phylopic (http://phylopic.org), where all license information is available.

TABLES

TABLE 1. Correlation test results for time series comparisons.

Comparison	Raw data		Generalised differencing	
CCM vs TDE (stage; global)	rs = -0.30	*p* = 0.06	rs = 0.04	*p* = 0.82
CCM vs TDE (9 myr; global)	rs = -0.14	*p* = 0.53	rs = 0.34	*p* = 0.11
CCM vs CBCs (stage; global)	rs = -0.24	*p* = 0.13	rs = 0.04	*p* = 0.81
CCM vs CBCs (9 myr; global)	rs = -0.04	*p* = 0.84	rs = 0.47	*p* = 0.03*
TDE vs CBCs (stage; global)	rs = 0.86	*p* = 9.06^{e-13}*	rs = 0.78	*p* = 7.73^{e-8}*
TDE vs CBCs (9 myr; global)	rs = 0.84	*p* = 3.26^{e-7}*	rs = 0.72	*p* = 0.0002*
CCM vs TDE (9 myr; SAm)	rs = 0.55	*p* = 0.01*	rs = 0.69	*p* = 0.002*
CCM vs CBCs (9 myr; SAm)	rs = 0.21	*p* = 0.37	rs = 0.50	*p* = 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.

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

Comparison	Raw data		Generalised differencing	
Completeness vs TDE	rs = 0.04	*p* = 0.90	rs = 0.19	*p* = 0.61
Completeness vs CBCs	rs = 0.88	*p* = 0.0004*	rs = 0.77	*p* = 0.01*
TDE vs CBCs	rs = 0.25	*p* = 0.45	rs = 0.56	*p* = 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.

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

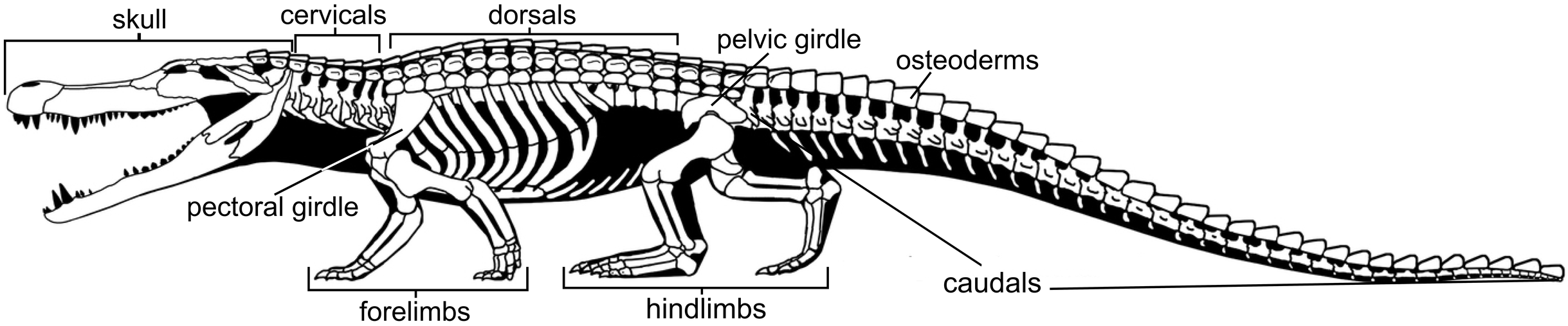
Dataset	N	Intercept	Slope	p-value	Adjusted R^2
All species (TL untransformed)	363	3.055	-0.006	0.034*	0.009
All species (log_{10} TL)	363	0.388	-0.001	0.003*	0.021
Category A (log_{10} TL)	167	0.05	-0.001	0.038*	0.019
Category B (log_{10} TL)	131	0.48	-0.0003	0.075	0.016
Category C (log_{10} TL)	39	0.701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

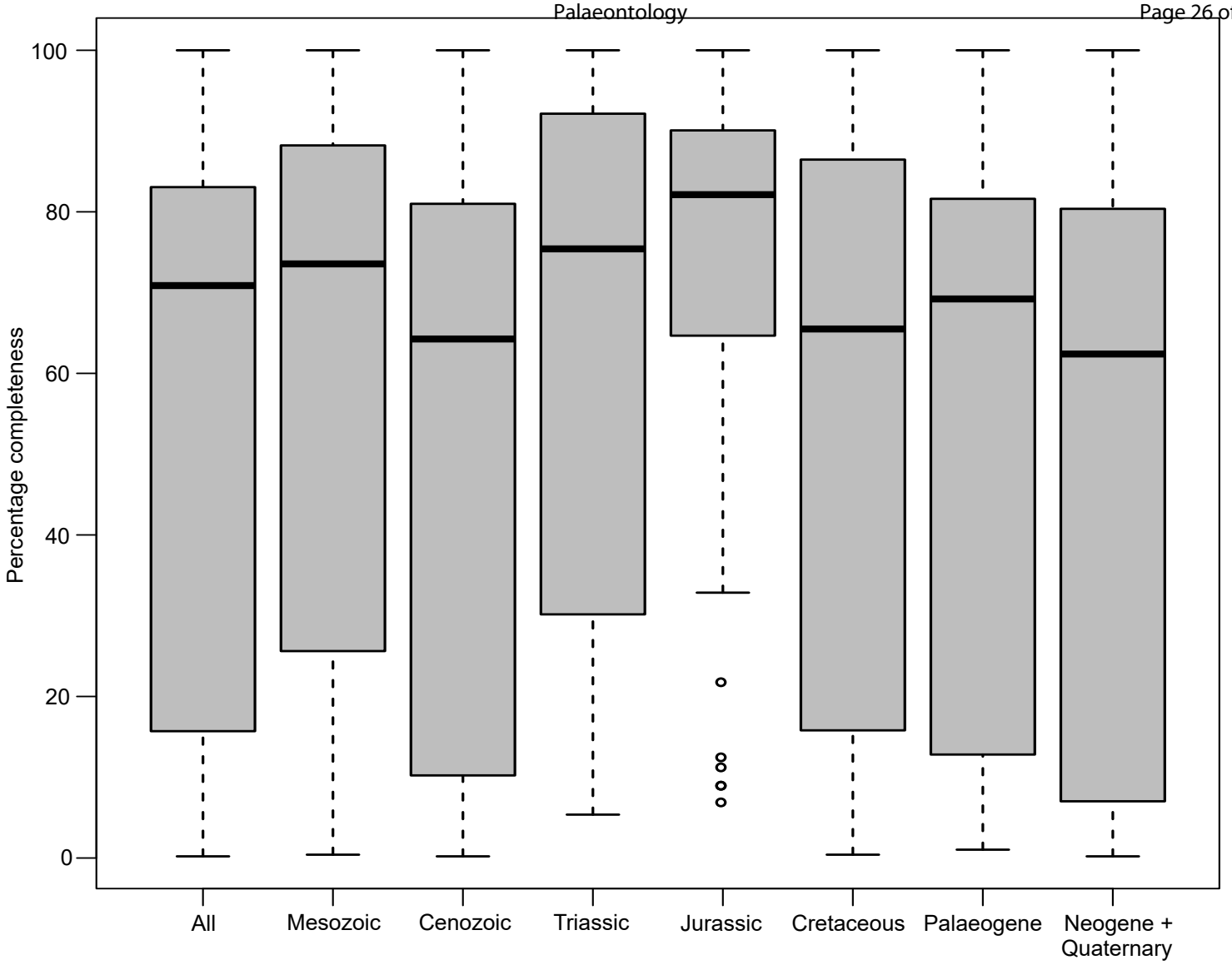
Results of OLS regressions of average crocodylomorph completeness on total length (TL) of species, using different datasets: including all species and untransformed TL values; all species and log-transformed TL values; species within size category A (smaller than 2 metres) and log_{10} TL; species within size category B (2 to 4 metres) and log_{10} TL; species within size category C (4 to 6 metres) and log_{10} TL; species within size category D (larger than 6metres) and log_{10} TL. *Significant at alpha (*p*-value) = 0.05.

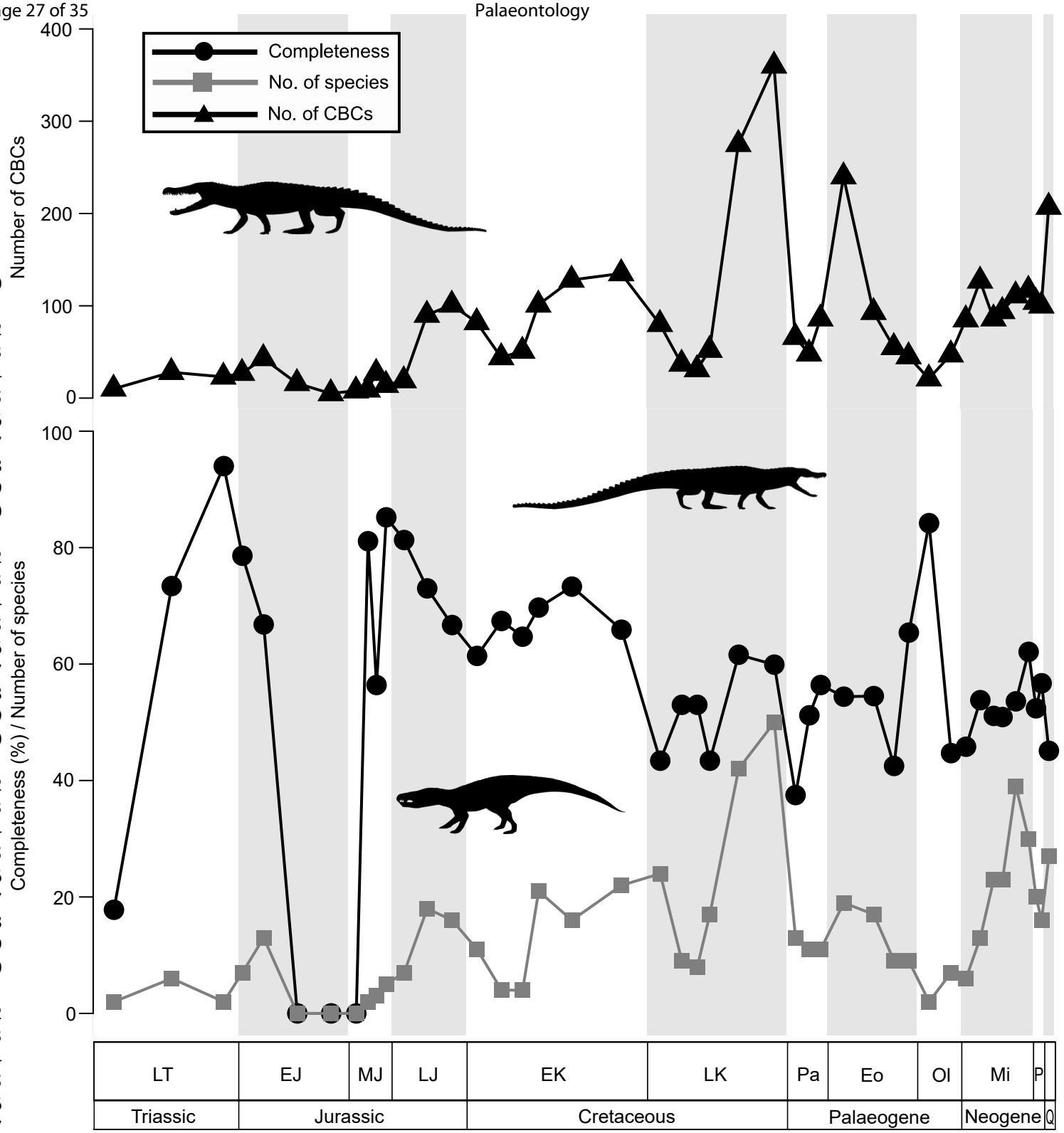
TABLE 4. Correlation test results for clade comparisons.

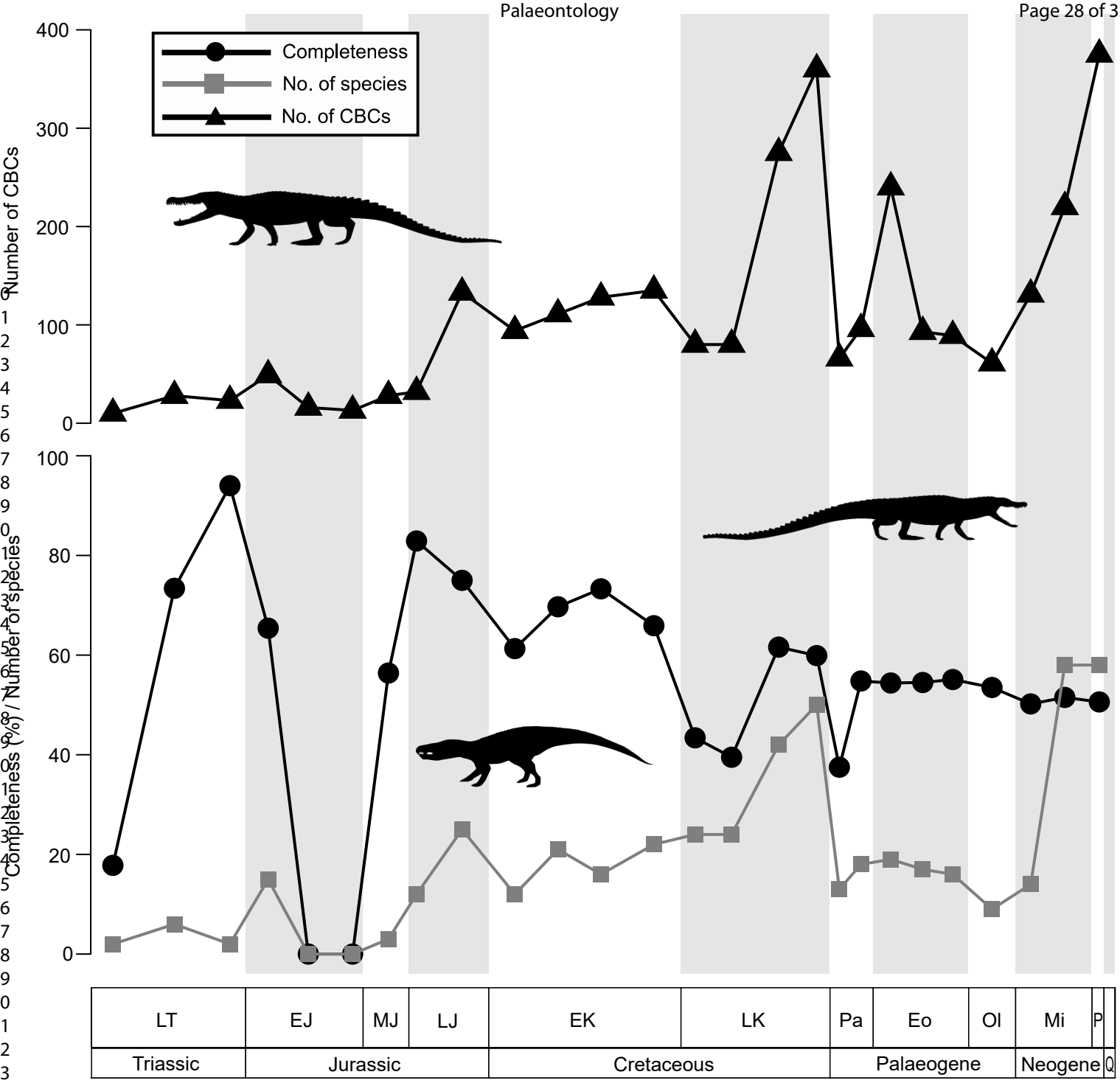
Comparison	Raw data		Generalised differencing	
Crocodylomorphs vs pterosaurs	rs = 0.75	$p = 5.23^{e-5}$*	rs = 0.26	$p = 0.25$
Crocodylomorphs vs sauropodomorphs	rs = 0.51	$p = 0.02$*	rs = -0.10	$p = 0.66$

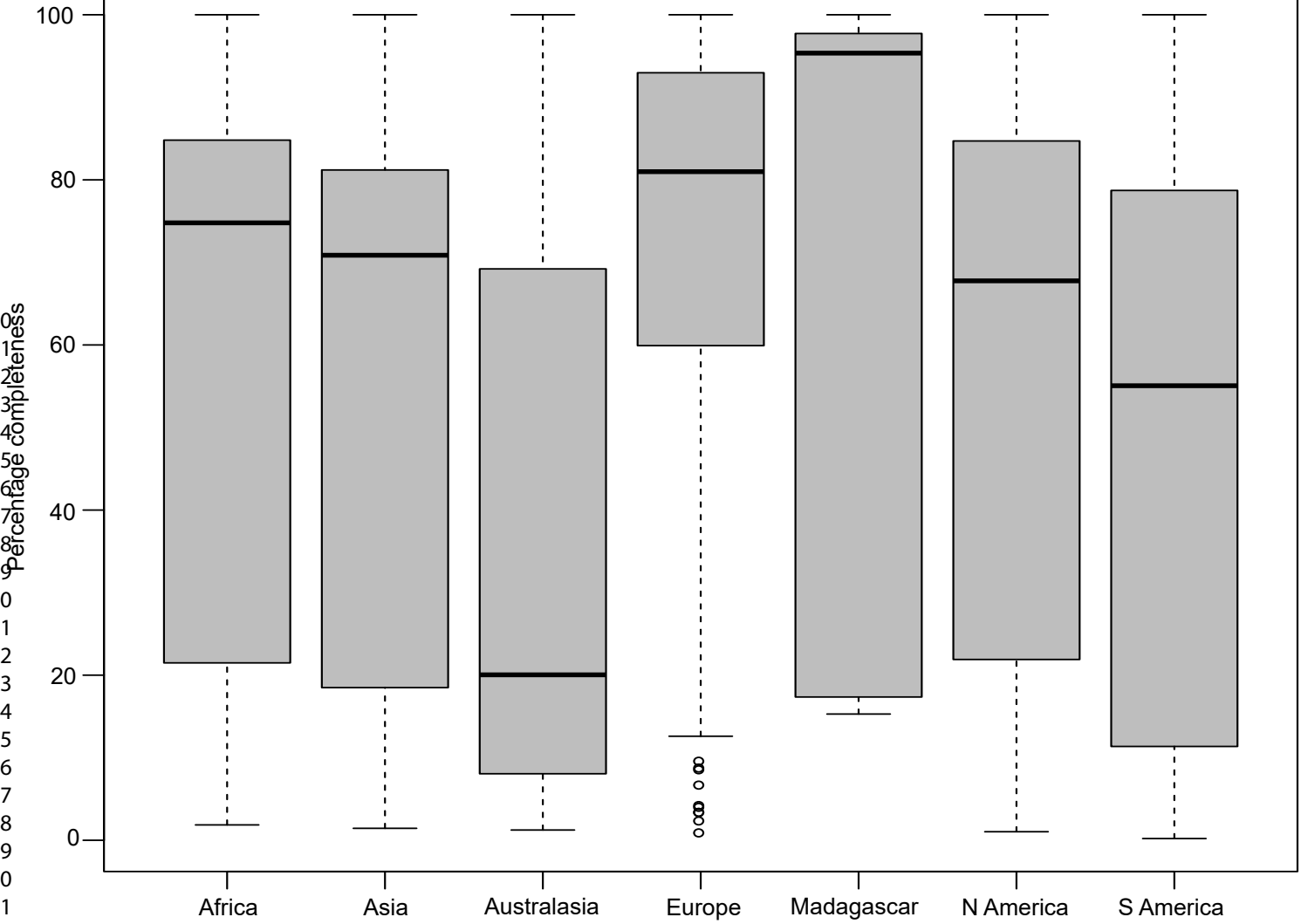
Statistical comparisons between global temporal fluctuations in Mesozoic crocodylomorph, pterosaur, and sauropodomorph dinosaur completeness. Spearman's rank correlation coefficients (rs) were calculated for each pairwise comparison based on the raw data and after generalized differencing. *Significant at alpha (*p*-value) = 0.05.

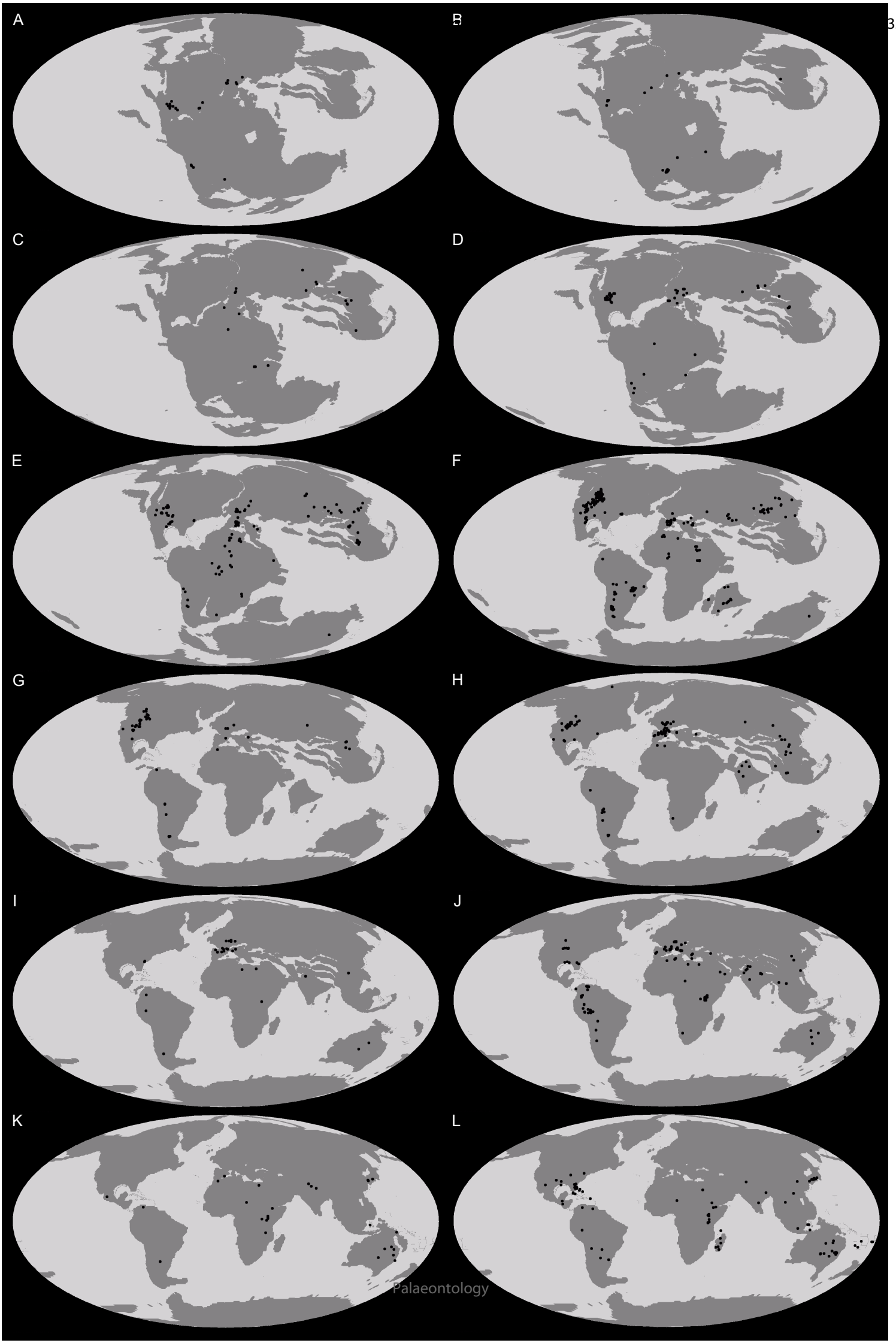

skull
cervicals
dorsals
pelvic girdle
osteoderms
pectoral girdle
caudals
forelimbs
hindlimbs

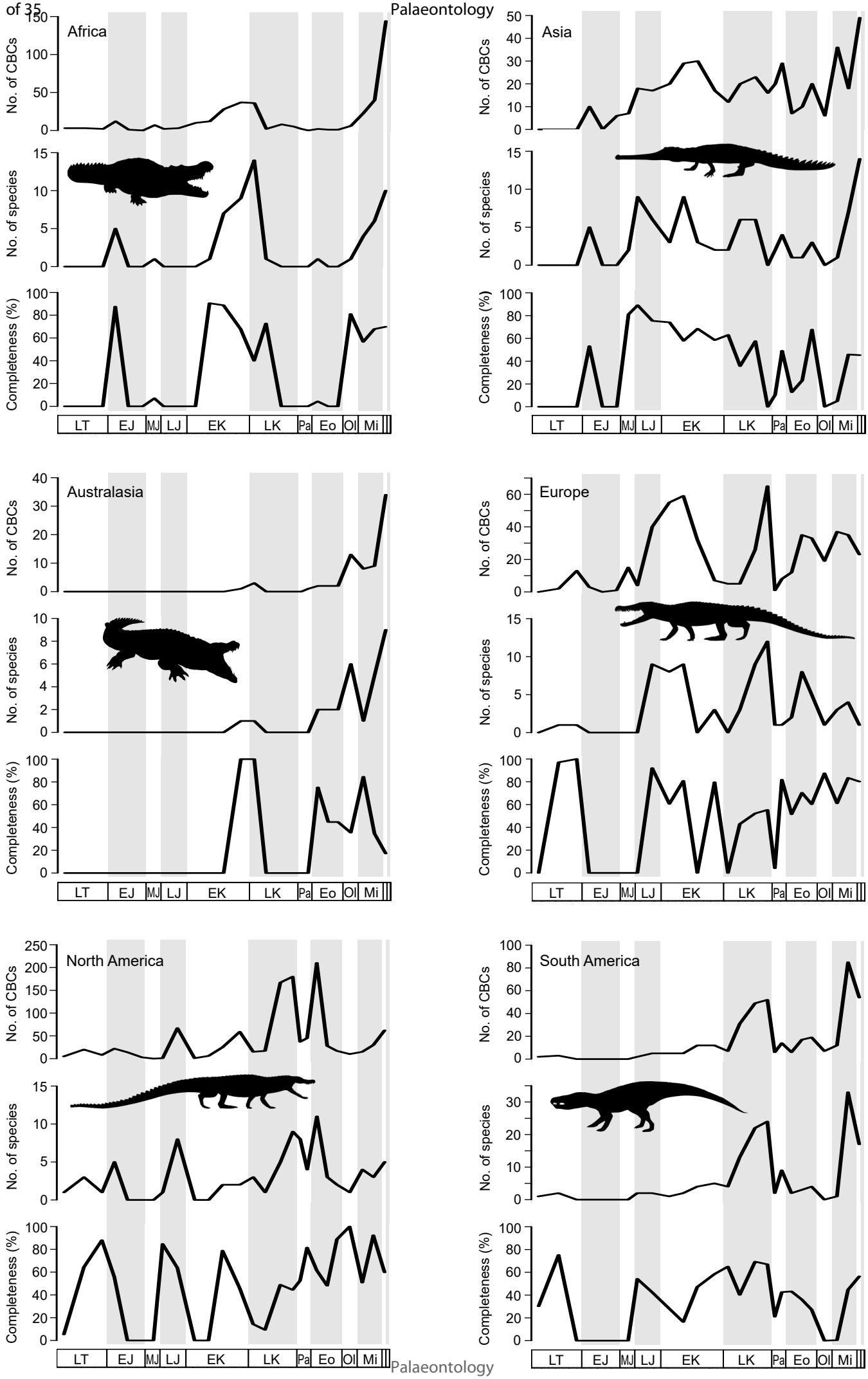

Percentage completeness
100
80
60
40
20
0
All
Mesozoic
Cenozoic
Triassic
Jurassic
Cretaceous
Palaeogene
Neogene + Quaternary

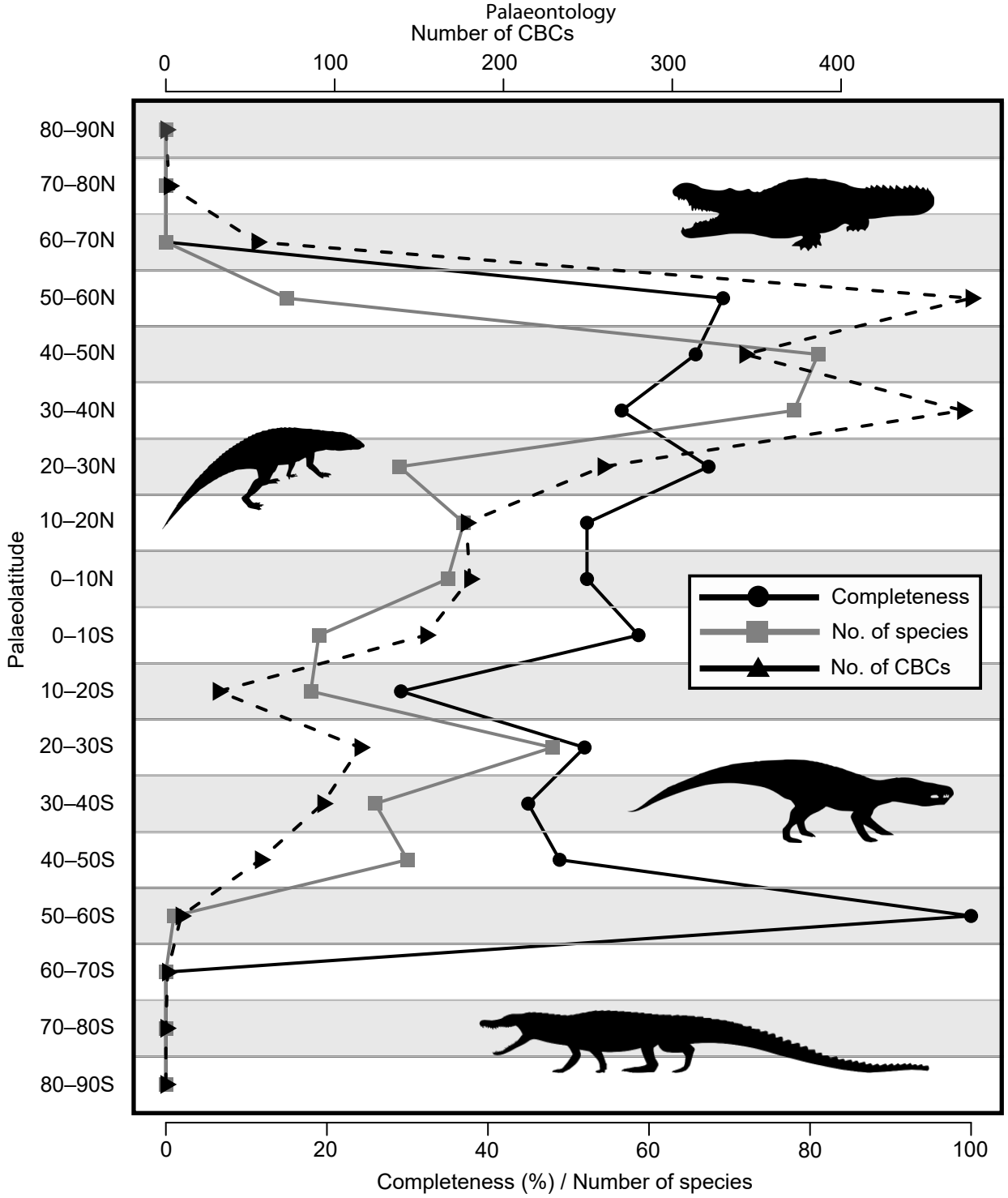

Completeness
No. of species
No. of CBCs
Number of CBCs
400
300
200
100
0
Completeness (%) / Number of species
100
80
60
40
20
0
LT
EJ
MJ
LJ
EK
LK
Pa
Eo
Ol
Mi
P
Triassic
Jurassic
Cretaceous
Palaeogene
Neogene
Q

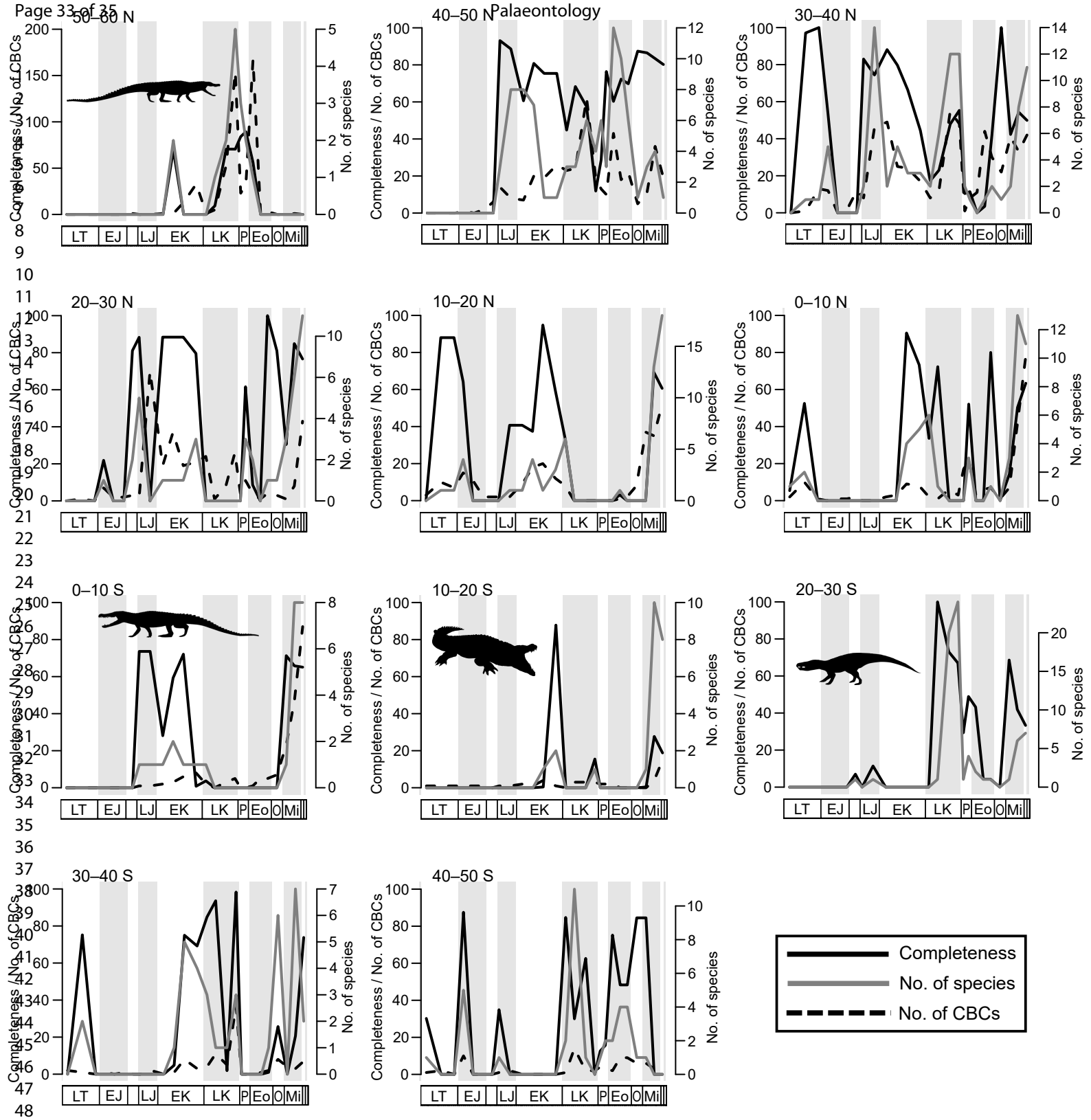

Completeness
No. of species
No. of CBCs
Number of CBCs
Completeness (%) / Number of species
400
300
200
100
0
100
80
60
40
20
0
LT
EJ
MJ
LJ
EK
LK
Pa
Eo
Ol
Mi
P
Triassic
Jurassic
Cretaceous
Palaeogene
Neogene
Q

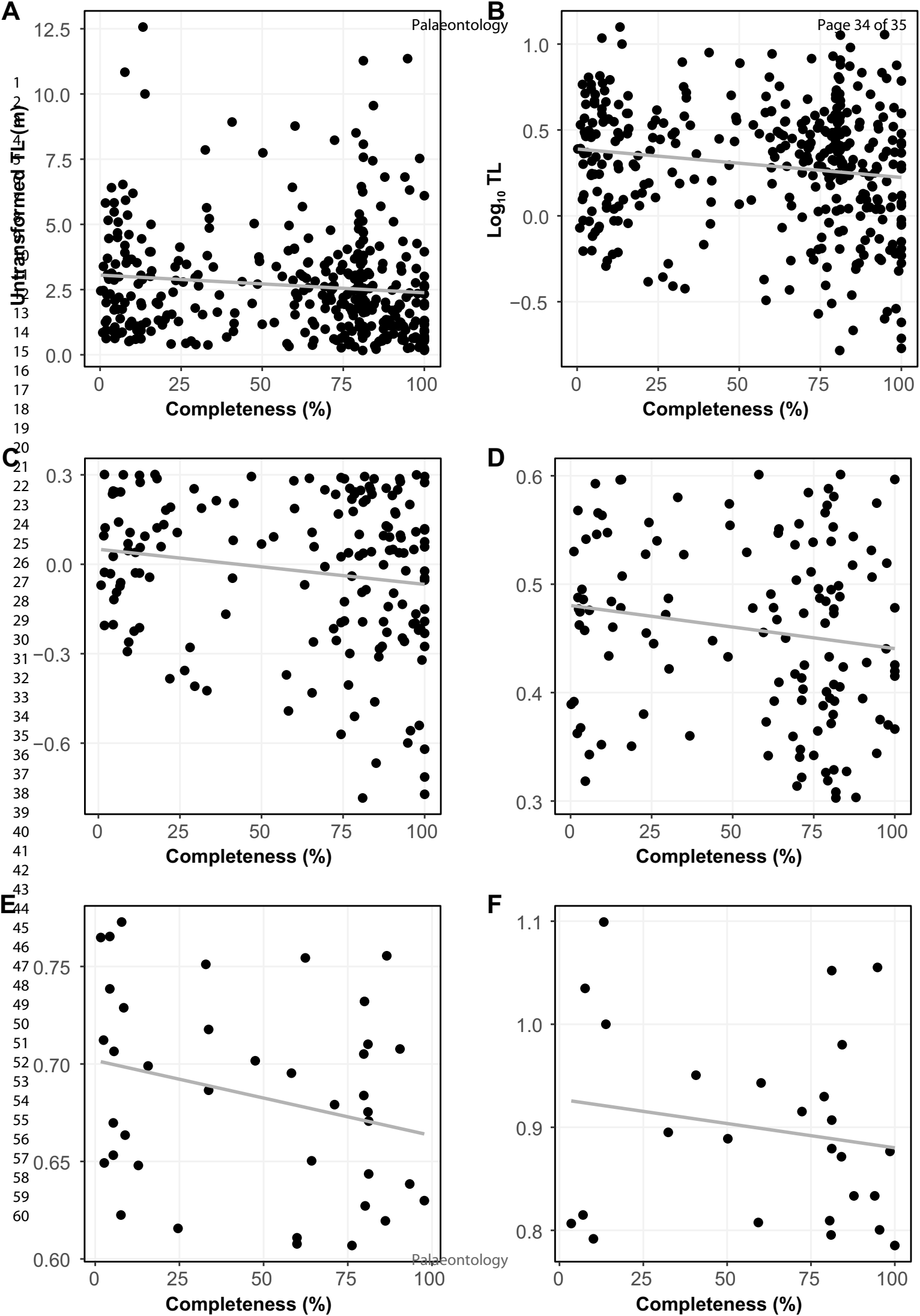

Percentage completeness
100
80
60
40
20
0
Africa
Asia
Australasia
Europe
Madagascar
N America
S America

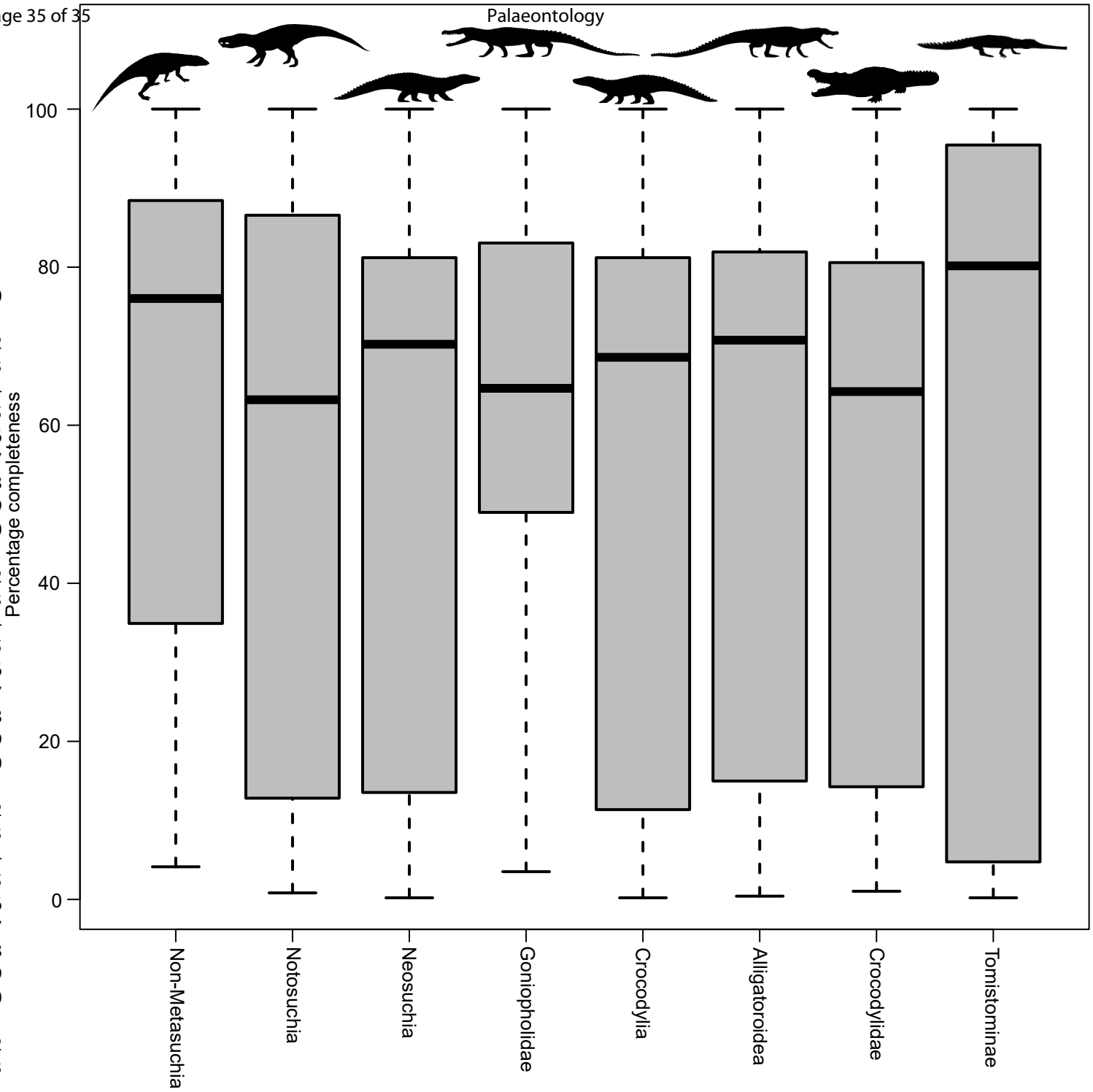

A
B
C
D
E
F
G
H
I
J
K
L


Africa
Asia
Australasia
Europe
North America
South America
No. of CBCs
No. of species
Completeness (%)
LT
EJ
MJ
LJ
EK
LK
Pa
Eo
Ol
Mi


Number of CBCs
0
100
200
300
400
80–90N
70–80N
60–70N
50–60N
40–50N
30–40N
20–30N
10–20N
0–10N
0–10S
10–20S
20–30S
30–40S
40–50S
50–60S
60–70S
70–80S
80–90S
Palaeolatitude
Completeness
No. of species
No. of CBCs
0
20
40
60
80
100
Completeness (%) / Number of species


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
Completeness / No. of CBCs
No. of species
LT
EJ
LJ
EK
LK
P
Eo
O
Mi
Completeness
No. of species
No. of CBCs


A
Untransformed TL (m)
12.5
10.0
7.5
5.0
2.5
0.0
0
25
50
75
100
Completeness (%)
B
Log10 TL
1.0
0.5
0.0
−0.5
0
25
50
75
100
Completeness (%)
C
0.3
0.0
−0.3
−0.6
0
25
50
75
100
Completeness (%)
D
0.6
0.5
0.4
0.3
0
25
50
75
100
Completeness (%)
E
0.75
0.70
0.65
0.60
0
25
50
75
100
Completeness (%)
F
1.1
1.0
0.9
0.8
0
25
50
75
100
Completeness (%)


Percentage completeness
100
80
60
40
20
0
Non-Metasuchia
Notosuchia
Neosuchia
Goniopholidae
Crocodylia
Alligatoroidea
Crocodylidae
Tomistominae