Body Size Evolution in Crocodylians and Their Extinct Relatives

Pedro L Godoy, *Stony Brook University, Stony Brook, New York, USA*
Alan H Turner, *Stony Brook University, Stony Brook, New York, USA*

Advanced article

Article Contents

Crocodylians are currently facing evolutionary decline. This is evinced by the rich fossil record of their extinct relatives, crocodylomorphs, which show not only significantly higher levels of biodiversity in the past but also remarkable morphological disparity and higher ecological diversity. In terms of body size, crocodylians are mostly large animals (>2 m), especially when compared to other extant reptiles. In contrast, extinct crocodylomorphs exhibited a 10-fold range in body sizes, with early terrestrial forms often quite small. Recent research has shed new light on the tempo and mode of crocodylomorph body size evolution, demonstrating a close relationship with ecology, in which physiological constraints contribute to the larger sizes of marine species. Abiotic environmental factors can also play an important role within individual subgroups. Crocodylians, for instance, have been experiencing an average size increase during Cenozoic, which seems to be related to a long-term process of global cooling.

Introduction

For decades, numerous studies on animal macroevolution have turned their attention to patterns of body size. Two main reasons can explain this long-lasting interest. First, the intimate relationship of body size with ecology, physiology and biomechanics makes it a fundamental biological feature, with profound influence on an animal's life (Schmidt-Nielsen, 1984). Thus, by studying body size, researchers can explore many aspects of biology, ontogeny, diversity and evolutionary history. Second, body size is a trait accessible for most taxa, extant or extinct (McKinney, 1990), and can be obtained by directly measuring it or from estimations using a proxy (i.e. a part of the animal that can be consistently scaled to represent total body mass or length). **See also**: Ecological Consequences of Body Size; Macroevolution: Overview; Evolutionary Trends

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Consequently, evolutionary biologists and palaeontologists have been investigating the tempo and mode of body size evolution for a wide range of animal groups. Many studies have focused on groups with a large number of extant representatives, such as mammals, birds or insects (e.g. Gaston, 2000; Clauset and Erwin, 2008). This is expected as the extant biota provides important information on the evolutionary expansion that resulted in these species-rich groups. However, there are evolutionary questions that can only be fully addressed with evidence from extinct organisms (Hunt and Slater, 2016). For example, studies of extinction and decline rely mostly on data from fossil specimens, and extant timetrees (i.e. a phylogenetic tree scaled to time using only data from living organisms) cannot reliably reveal diversification histories (Louca and Pennell, 2020). Given that body size can play an important role in extinction selectivity (e.g. smaller-sized mammals were favoured during the K-Pg extinction event; Lyson *et al*., 2019), recognising body size patterns within groups of reduced extant diversity but a rich fossil record can prove useful in understanding complex macroevolutionary patterns. **See also**: Palaeoecology; Extinction; Extinction: K–Pg Mass Extinction

One such group is Crocodylomorpha (**Figures 1**, **2**), a group of archosaur reptiles that includes extant crocodylians and their extinct relatives. With more than 200 million years of evolution and about 500 species described to date, Crocodylomorpha is the largest group within the 'crocodylian-line' of archosaurs (Benton and Clark, 1988). But the vast majority of these taxa are already extinct, and only about 30 species of crocodylians exist today (Brochu and Sumrall, 2020). In particular, these numbers contrast enormously with those of birds, which are the extant representatives of the other major archosaur lineage, the 'bird-line' of archosaurs. There are more than 10,000 living species of birds (Jetz *et al*., 2012), represented by all sorts of sizes, shapes and

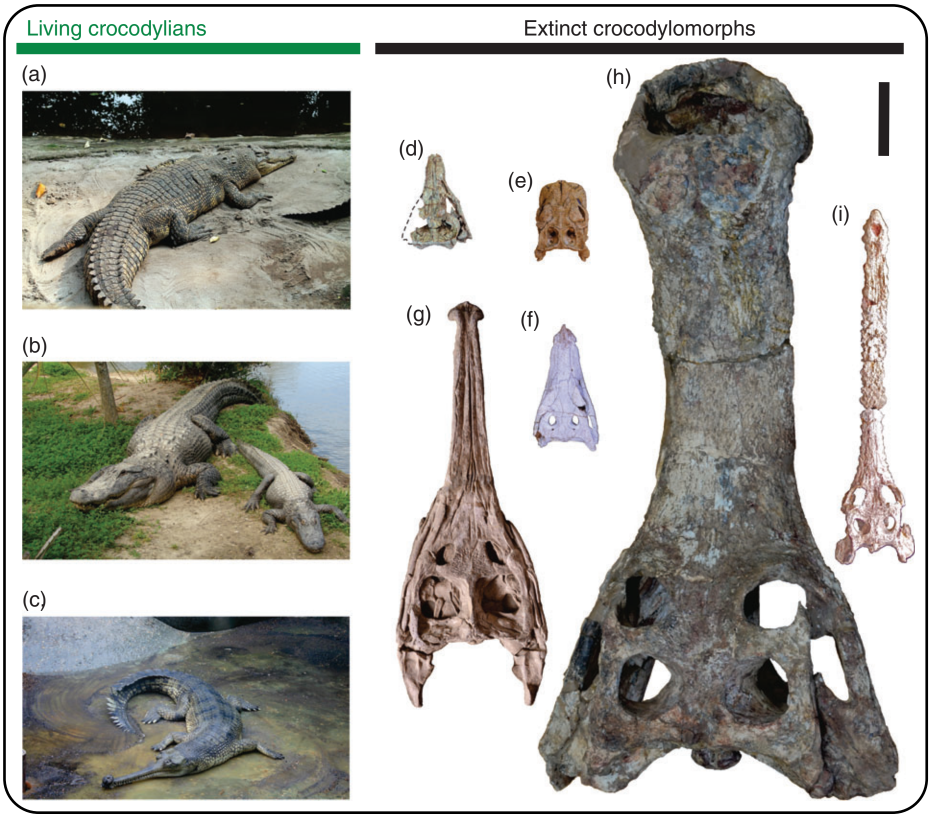

Figure 1 On the left, examples of extant crocodylians, which show similar overall body plan and ecology: (a) *Crocodylus porosus*. (b) *Alligator mississippiensis*. (c) *Gavialis gangeticus*. On the right, skulls of some extinct crocodylomorph in dorsal view, illustrating the morphological and size variation exhibited by the group: (d) *Dibothrosuchus elpahros*. (e) *Simosuchus clarki*. (f) *Montealtosuchus arrudacamposi*. (g) *Steneosaurus bollensis*. (h) *Sarcosuchus imperator*. (i) *Ikanogavialis gameroi*. All skulls of extinct crocodylomorphs are to the same scale (scale bar = 15 cm). Source: Photographs of living crocodylians taken by Ilham Nurwansah, J. Philipp Krone, and Ryan Somma

colours (Pigot *et al*., 2020). Thus, when compared to their feathered cousins, it can seem fair that crocodylians have received the label of ‘living fossils’ by the general public. However, upon closer inspection, the rich evolutionary history of Crocodylomorpha provides abundant evidence of a remarkable morphological variation, dismissing their reputation as a group that remained unchanged for millions of years. **See also**: **Reptilia (Reptiles)**

Species from the different subgroups of Crocodylomorpha can be used to illustrate the often unappreciated morphological and ecological diversities of the group (**Figures 1**, **2**). Crocodylia is perhaps the most familiar subgroup, given that it includes the extant species. Here, it is worth mentioning that, throughout this article, the term ‘crocodylian’ refers solely to members of the crown-group Crocodylia, whereas ‘crocodylomorphs’ has a much broader meaning. Most crocodylians share an overall similar body plan and ecology, but some exceptions are known from fossils. Gavialoids such as *Piscogavialis* and *Ikanogavialis* were extremely long-snouted (and possibly salt-water tolerant; Salas-Gismondi *et al*., 2016). *Mourasuchus* had a strange-looking flat and broad rostrum, which until today puzzles palaeontologist about its function (Cidade *et al*., 2019). The giant South American caiman *Purussaurus* had a massive narial opening – big enough to put one’s head into it (Aureliano *et al*., 2015)

But perhaps the best examples of more extreme ecologies and body shapes come from subgroups that are completely extinct. Thalattosuchia is a crocodylomorph subgroup that thrived during the Jurassic period – 201.3 to 145 million years ago (Ma) (**Figure 2**). Most of its members lived in the seas, which is something already different from modern crocodylians (Bronzati *et al*., 2015). But some thalattosuchians were so well adapted to the life in the marine realm that they evolved paddle-like flippers and tail fins, similar to what is seen in cetaceans today. Furthermore, there is evidence suggesting that some species had salt glands and were viviparous (and, therefore, did not have to leave the water for laying eggs; Fernández and Gasparini, 2008; Herrera *et al*., 2017).

Notosuchia is another important subgroup (**Figure 2**), most members of which lived during the Cretaceous period (145–66 Ma), on continents of the Southern hemisphere (Bronzati *et al*., 2015). Contrary to crocodylians and thalattosuchians (but similar to the earliest evolving crocodylomorphs), the majority of notosuchians were terrestrial animals (Wilberg *et al*., 2019). In terms of morphological diversity (also known as morphological disparity), notosuchians represent the subgroup with the highest cranial shape disparity among all crocodylomorphs (Godoy, 2020). This high variability of skull shapes might be related to an extraordinary range of feeding strategies

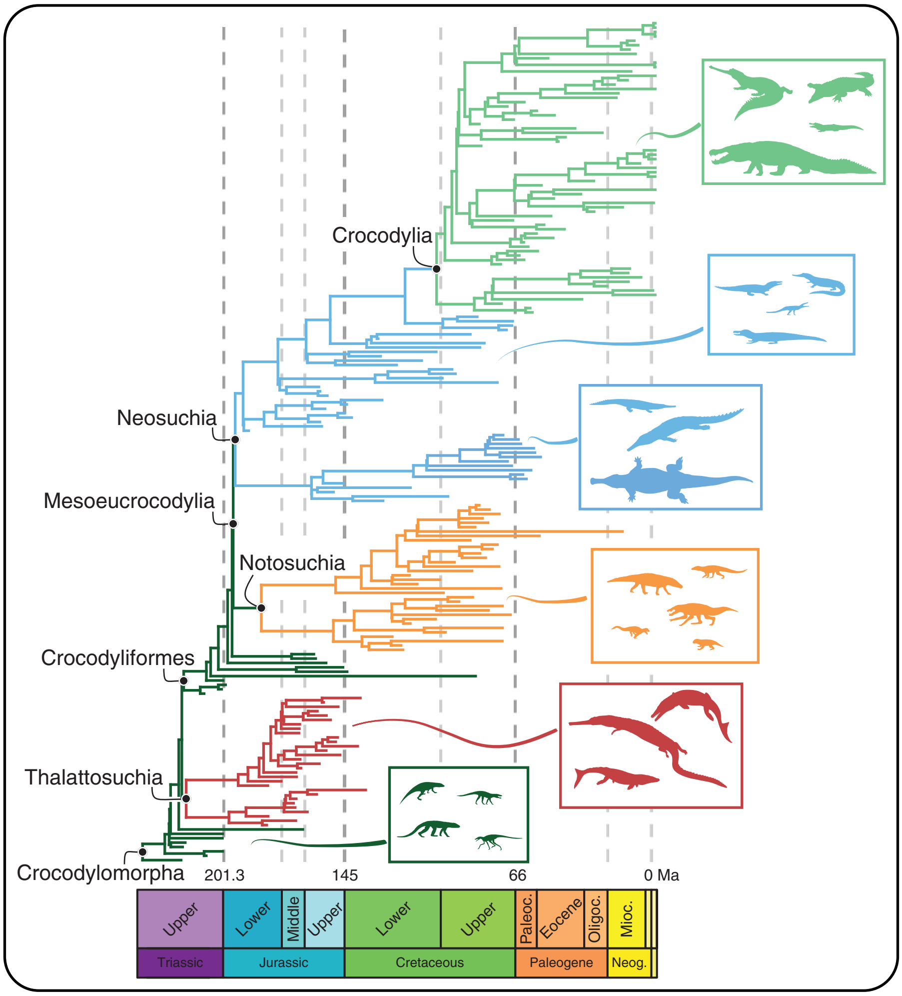

Figure 2 Phylogenetic relationships among most important crocodylomorph subgroups (shown in different colours). Silhouettes of some representatives of these groups are included in coloured boxes and are size-scaled to illustrate the diversity of body sizes in the group. Sources: Bronzati M, Montefeltro FC and Langer MC (2015) Diversification events and the effects of mass extinctions on Crocodyliformes evolutionary history. Royal Society Open Science 2: 140385; Godoy PL, Benson RB, Bronzati M and Butler RJ (2019) The multi-peak adaptive landscape of crocodylomorph body size evolution. BMC Evolutionary Biology 19: 167; Wilberg EW, Turner AH and Brochu CA (2019) Evolutionary structure and timing of majorhabitat shifts in Crocodylomorpha. Scientific Reports 9: 514.

experienced by notosuchians. While some were hypercarnivores, top-predators of their environments (Godoy *et al*., 2018), others were omnivores and even herbivores, with dentition so complex that resembled that of mammals (Melstrom and Irmis, 2019). **See also**: **Morphological Diversity: Evolution**

When the outstanding diversity of extinct crocodylomorphs is compared to the current status of such few remaining species, one can conclude that Crocodylomorpha is a group in evolutionary decline. The rich fossil record of Crocodylomorpha can help us document the patterns of this decline and better comprehend the processes behind it. As discussed above, body size is a feature that can summarise a myriad of other traits. Therefore, the study of crocodylomorph body size evolution offers us an excellent opportunity to understand long-term dynamics involved in the evolutionary history of such a unique group of animals.

Body Size Proxies

In order to estimate and understand patterns of body size evolution in deep geological time, palaeontologists and evolutionary biologists need data from extinct species. However, many fossil specimens do not preserve a complete skeleton, so total body size is often unobservable. To overcome this issue, a specific part of the skeleton is normally used to represent total body length or mass of the specimen, this is known as a body-size proxy. Using data from regression analyses, palaeontologists can estimate body size or mass from the selected proxy, and thus have body size information for as many species as possible. This is particularly important in the case of crocodylomorphs, given that the vast majority of the group's diversity is now extinct, which hampers direct observation of total body size. Consequently, most macroevolutionary studies that investigate long-term patterns of crocodylomorph body size rely on body size proxies (e.g. Turner and Nesbitt, 2013; Godoy *et al*., 2019; Solórzano *et al*., 2019; Gearty and Payne, 2020).

Different parts of the skeleton can be used as proxies of crocodylomorph total body length or mass (Farlow *et al*., 2005; Godoy *et al*., 2019; O'Brien *et al*., 2019), even though caution is recommended when performing estimations of extinct species, given the dissimilar body proportions between subgroups (Young *et al*., 2016). Postcranial elements have the disadvantage of being more susceptible than skulls to deformation during the fossilisation process (O'Brien *et al*., 2019). Furthermore, crocodylomorph postcrania have historically received less attention by palaeontologists, which makes information from cranial bones more frequently available (Mannion *et al*., 2019). As a consequence, cranial measurements are more commonly used as body size proxies for crocodylomorphs. For example, the figures within this article were constructed with data from Godoy *et al*. (2019), which uses a cranial measurement (dorsal orbito-cranial length) as a proxy for total body length. In addition, it is worth mentioning that, throughout this article, body size information about extinct crocodylomorph species are mostly estimated rather than direct observations.

Through-time Patterns of Crocodylomorph Body Size

Most of the oldest crocodylomorphs, such as *Litargosuchus* and *Hesperosuchus* (Irmis *et al*., 2013), were relatively small animals, especially when compared to other crocodylomorphs in subsequent time periods. But this is also true for comparisons made with other archosaurs of the Late Triassic (237–201.3 Ma), indicating that crocodylomorphs occupied niches of relatively smaller sizes in those terrestrial ecosystems (Turner and Nesbitt, 2013). Indeed, considering the entire evolutionary history of Crocodylomorpha, the Late Triassic witnessed the lowest mean value of body sizes (**Figure 3a**). Subsequently, the end-Triassic extinction event had a significant impact on terrestrial tetrapods. Crocodylomorpha was one of the few archosaur clades that survived this extinction (Mannion *et al*., 2015), but there is currently no evidence suggesting that their smaller body sizes had a decisive influence on this survivorship (Allen *et al*., 2019; Godoy *et al*., 2019). **See also**: **Extinction: End-Triassic Mass Extinction**

During the Jurassic period, some of the most significant crocodylomorph subgroups originated and diversified, including Thalattosuchia, Neosuchia and possibly Notosuchia (although there is no fossil record of notosuchians for the period, most studies estimate a Jurassic origin for the group; Bronzati *et al*., 2015; Turner *et al*., 2017). Thalattosuchians (e.g. *Steneosaurus*, *Metriorhynchus*, and others) first appear in the fossil record in the Early Jurassic (Toarcian) and had their diversity apex in the Middle and Late Jurassic. These predominantly marine crocodylomorphs were large-bodied animals (**Figure 3c, d**), with an average size of about 5 m, while some species reached nearly 8 m (Young *et al*., 2016). Considering that thalattosuchians are the most abundant crocodylomorphs in the Middle Jurassic, this resulted in an increase in average and maximum size (**Figure 3a**).

On the opposite side of the body size spectrum are atoposaurid neosuchians (e.g. *Atoposaurus*, *Theriosuchus*, and others), which date back to the Middle Jurassic (Bajocian–Bathonian). They represent some of the smallest known crocodylomorphs, many of which have less than 1 m in total (Schwarz *et al*., 2017). Thus, as a consequence of the coexistence of large thalattosuchians and diminutive atoposaurids (as well as other small-bodied non-mesoeucrocodylian crocodyliforms, such as *Fruitachampsa*; Clark, 2011), the Late Jurassic witnessed the highest peak in body size variability (disparity) ever experienced by crocodylomorphs (**Figure 3b**).

While most thalattosuchians became extinct by the end of the Jurassic, the boundary with the Cretaceous is marked by a decrease in body size disparity (**Figures 2**, **3b**). Concomitantly, the diversification of notosuchians during the Early Cretaceous contributes to a drop in average size for crocodylomorphs (**Figures 2**, **3a**). Although Notosuchia exhibits extraordinary morphological variation (e.g. *Notosuchus*, *Araripesuchus*, *Baurusuchus* and others), which is reflected in the wide range of feeding strategies displayed by the group, most species were small- to medium-sized. Given the significant contribution of notosuchians to crocodylomorph biodiversity known for the Cretaceous (Mannion *et al*., 2015), it is not surprising that the mean body size of all crocodylomorphs during the period is similar to that of notosuchians (between 2 and 3 m; **Figure 3a, d**).

Important Cretaceous diversifications were not restricted to notosuchians. Two significant neosuchian lineages had their initial diversification events during the Late Cretaceous: Crocodylia and Dyrosauridae. In the case of crocodylians, the Late Cretaceous species, which represent the oldest records for the group, did not exhibit body sizes too disparate from those of notosuchians (**Figure 3c**). But dyrosaurids (e.g. *Dyrosaurus*, *Hyposaurus* and others) were predominantly large species, with mean size between 4 and 5 m (**Figure 3c**). Dyrosauridae probably represented the second crocodylomorph transition to the marine realm (Wilberg *et al*., 2019), although dyrosaurids did not evolve the highly specialised limb morphologies seen in some thalattosuchians. Consequently, when compared to the Early Cretaceous, the Late Cretaceous is characterised by a slight increase in crocodylomorph average size (**Figure 3a**).

As no clear disruption in body size patterns is seen through the Cretaceous-Paleogene (K-Pg) boundary (**Figure 3a, b**), the current data suggests no body size selectivity for crocodylomorphs during the K-Pg mass extinction event (Godoy *et al*., 2019). This is somehow consistent with previous examinations of the crocodylomorph fossil record, which proposed that they were not as affected by this extinction event as other tetrapod groups, more notably non-avian dinosaurs (Bronzati *et al*., 2015; Mannion *et al*., 2015). In addition, it contrasts with what has been reported for groups such as mammals and squamates, which seem to display a pattern of differential extinction of larger-bodied species through K-Pg (Longrich *et al*., 2012; Lyson *et al*., 2019).

The Cenozoic witnessed the rise of crocodylians, which established themselves as the dominant subgroup of crocodylomorphs. Other groups survived the K-Pg extinction event, such as dyrosaurids and notosuchians. But members of these groups

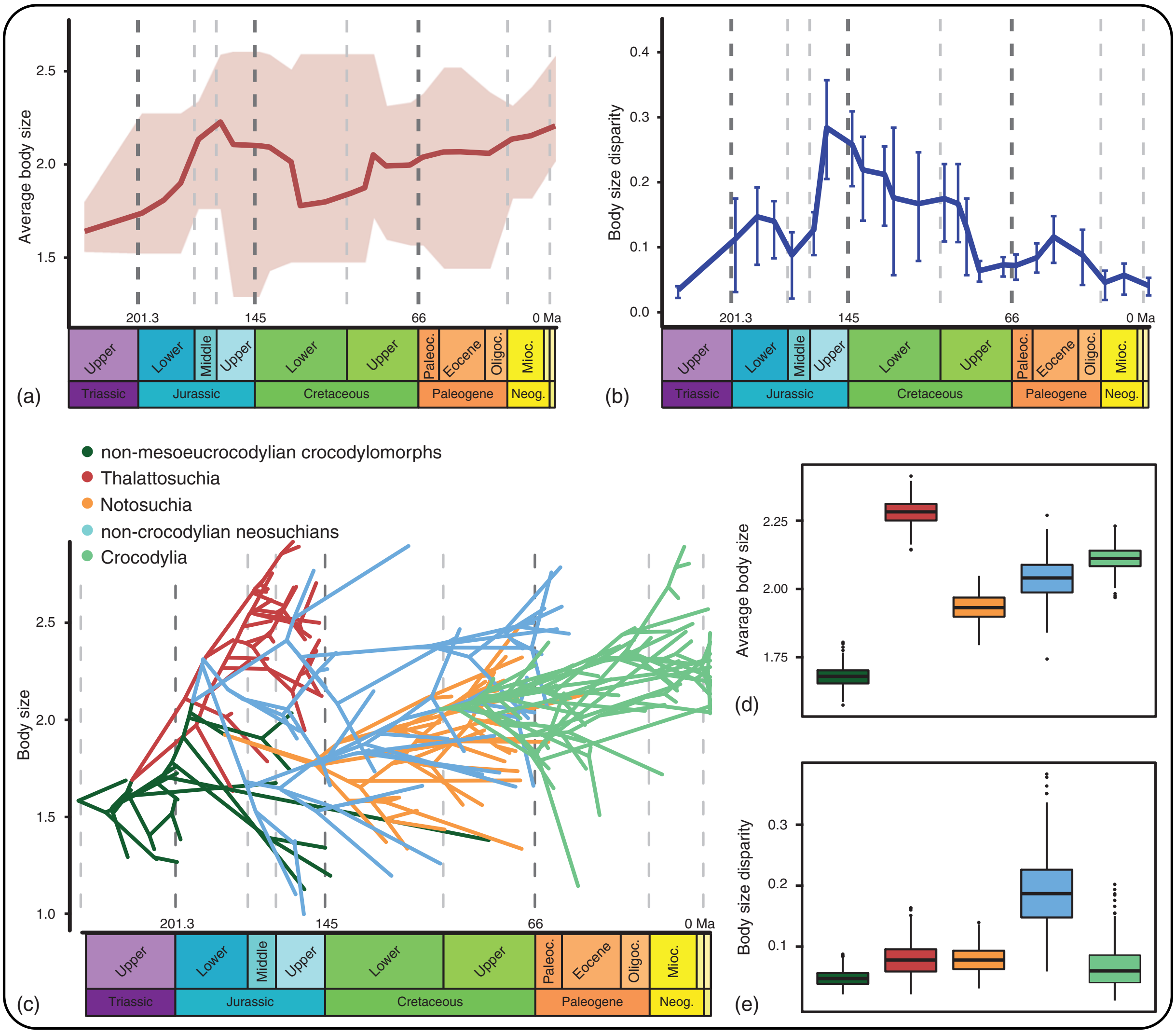

Figure 3 Patterns of crocodylomorph body size through time and between subgroups. Body size is represented by a cranial measurement (dorsal orbito-cranial length) after log-transformation. (a) Mean body size (red line) through time, with lower and upper limits (i.e. minimum and maximum size) of each time bin represented by light red shaded area. (b) Body size disparity (sum of variances) through time. Error bars represent bootstrapped values (500 replicates). (c) Phenogram with body size incorporated into crocodylomorph phylogeny, with most important crocodylomorph subgroups shown in different colours. (d) Mean body size of different subgroups (mean values were subjected to bootstraps and rarefaction; colour key same as panel c). (e) Body size disparity (sum of variances) of different subgroups (disparity values were subjected to bootstraps and rarefaction; colour key same as panel c). Data from Godoy PL, Benson RB, Bronzati M and Butler RJ (2019) The multi-peak adaptive landscape of crocodylomorph body size evolution. BMC Evolutionary Biology 19: 167.

were much rarer than crocodylians, and eventually became extinct – dyrosaurids in the Eocene (56–33.9 Ma) and notosuchians in the Miocene (23.03–5.33 Ma). Accordingly, patterns of crocodylomorph body size observed during the Cenozoic are most likely related to the evolutionary dynamics of crocodylians. For example, the very interesting pattern of increase in average size, coupled with a decrease in body size disparity, observed throughout almost the entire Cenozoic (**Figure 3a, b**) seems to governed by environmental factors, which are known to have significant influence on many aspects of crocodylian biology (such as physiology and biodiversity; Markwick, 1998a; Seymour *et al*., 2004; Mannion *et al*., 2015). This subject will be further explored in the last section of this article.

Body Size and Adaptive Landscapes

The relatively small size of the earliest crocodylomorphs, especially when compared to most extant crocodylians, might initially suggest that a generalised trend of size increase followed the end of the Triassic period, in a pattern known as ‘Cope’s rule’.

According to this rule, multiple lineages within a clade would exhibit a directional trend towards size increase through time (Stanley, 1973). However, as discussed above, crocodylomorph subgroups that diversified after the Late Triassic have experienced a much more complex body size evolution, with taxa exhibiting remarkable body size variation. This is best exemplified when the diminutive size of *Tsoabichi greenriverensis* (smaller than 1 m in total; Brochu, 2010) is compared to the massive body length of *Purussaurus brasiliensis* (that probably reached more than 10 m; Aureliano *et al*., 2015), both of which lived during the Cenozoic and are included in Caimaninae, a subclade within Crocodylia. This is consistent with previous work that found no support for a generalised, multilineage evolutionary trend towards larger or smaller sizes (Godoy *et al*., 2019).

Similarly, crocodylomorph body size evolution cannot be explained by unconstrained gradual evolution. Among the currently available statistical models of phenotypic evolution, Brownian motion (BM) is possibly the most widely employed and describes unconstrained evolution via random walks along independent phylogenetic lineages (Felsenstein, 1985). In the case of crocodylomorph body size evolution, model-fitting analyses found proportionally weak support for BM-based models received (Godoy *et al*., 2019), indicating that the body size variation in the group did not emerge from uniform, gradual evolution. **See also**: **Punctuated Equilibrium and Phyletic Gradualism**; **Evolutionary Trends**

The evolution of crocodylomorph body size is better understood within the paradigm of Simpsonian adaptive landscapes, in which trait variation emerges from the invasion of new adaptive zones (which are similar to ecological niches or zones of high fitness; Hansen, 1997). For modelling purposes, evolutionary biologists have borrowed from mathematics the formulation of Ornstein–Uhlenbeck (OU) processes, which allowed for the incorporation of constraints into evolutionary models, simulating the action of natural selection (Felsenstein, 1985). OU-based models can also account for multiple evolutionary regimes, which are analogous to adaptive zones, making them consistent with the concept of adaptive landscapes. In the case of Crocodylomorpha, multi-regime OU models received proportionally stronger support when fitted to body size data. This means that, along the group's evolutionary history, distinct selective pressures governed the evolution of body size, giving rise to the observed distribution of body sizes (Godoy *et al*., 2019). **See also**: **Evolution: Tempo and Mode**; **Simpson, George Gaylord**

Shifts between evolutionary regimes (or adaptive zone) can be associated with biotic or abiotic factors (Hansen, 1997). Examples of biotic factors could include the evolution of morphological features that allowed lineages to move into a new adaptive zone (these are often called 'key evolutionary innovations'). In the case of crocodylomorphs, there is evidence suggesting that intrinsic biological factors influenced the body size of specific subgroups. Shifts to new optimal body sizes zones are detected at the origin some subgroups (such as Thalattosuchia, Notosuchia, and Crocodylia; Godoy *et al*., 2019). Similarly, some of these same subgroups experienced diversification events close to or at their origin (Bronzati *et al*., 2015), indicating that lineage-specific adaptations are possibly linked to pulses of diversification and phenotypic variation. Particularly, in the case of Thalattosuchia, Notosuchia and Crocodylia, examples of such evolutionary innovations include, respectively, morphological modifications to the life in the marine realm (Fernández and Gasparini, 2008; Herrera *et al*., 2017), a highly modified feeding apparatus (Godoy *et al*., 2019; Melstrom and Irmis, 2019), and physiological adaptations for maximising submergence time, such as a pulmonary bypass shunt (Seymour *et al*., 2004).

Abiotic factors, such as environmental or geologic changes, can also be associated with the diversification and the origin or expansion of morphological variation in many animal groups. In the case of crocodylomorphs, climatic and geologic variables, including temperature and sea-level changes, are thought to a have significant influence on through-time patterns of biodiversity (Markwick, 1998b; Mannion *et al*., 2015). However, it is unlikely that a single environmental factor drove crocodylomorph body size evolution, given that only non-significant or weak correlations were found between overall body size and temperature or latitudinal data (Godoy *et al*., 2019). This might reflect the fact that crocodylomorph subgroups inhabited many different ecosystems, living in highly contrasting climatic conditions (i.e. from oceans to semi-arid environments). It is thus expected that climate alone cannot explain the observed morphological variation of all crocodylomorphs. Nevertheless, within more constrained phylogenetic and/or temporal scales (such as within the same subgroup), different relationship between morphology and climate can arise. A good example is the strong correlation between body size and temperature exhibited by crocodylian species throughout the Cenozoic (see below).

Relationship between Crocodylomorph Body Size and Ecology

As discussed above, the distribution of body sizes within Crocodylomorpha can be at least partially explained by lineage-specific adaptations, which are associated with the emergence of important subgroups (e.g. Thalattosuchia, Notosuchia and Crocodylia). Ecology is another important biotic factor that helps us understand the adaptive landscape of body size evolution in the group. Crocodylomorphs experienced multiple ecological transitions throughout their evolutionary history. More specifically, shifts between terrestrial and more aquatic habitats, either in freshwater or marine ecosystems, happened repeatedly between and within subgroups (Wilberg *et al*., 2019). Even though we cannot directly observe the ecology of extinct species, it can be inferred based on their morphology and the sedimentary composition of the rocks in which fossils are found. **See also**: **Fossils and Fossilisation**; **Palaeoecology**

A clear distinction arises when the mean body size of crocodylomorphs is subdivided into three lifestyle categories (i.e. terrestrial, freshwater and marine; **Figure 4a**). Terrestrial crocodylomorphs are, on average, smaller than more aquatic ones, what is expected given the relatively small size of the earliest crocodylomorphs, as well as of most notosuchians (**Figure 3e**), which constitute the majority of terrestrial species. Freshwater forms occupy a niche of intermediate average body size but exhibit

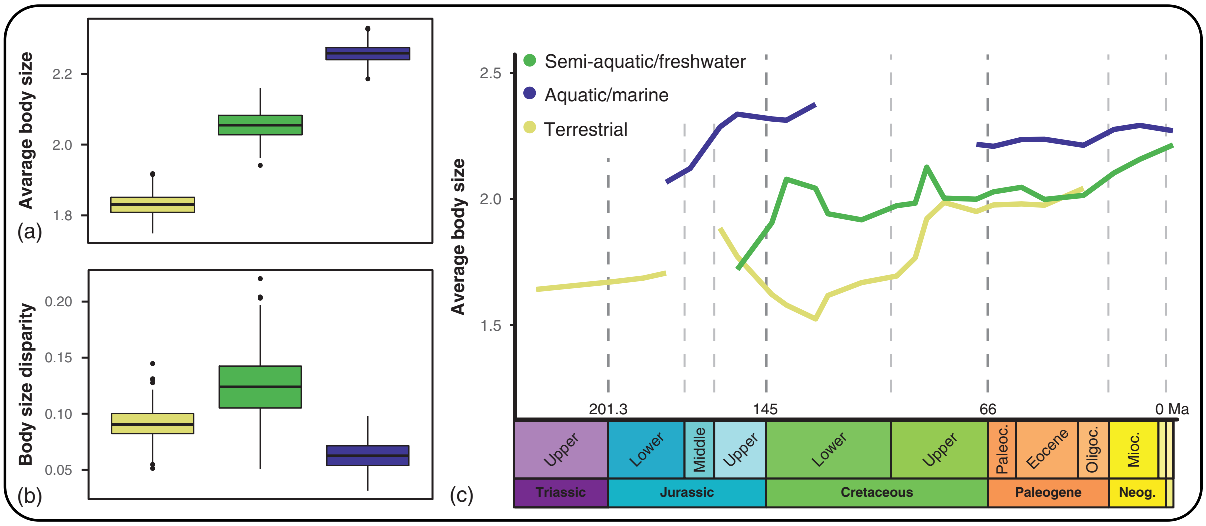

Figure 4 Body size patterns of different crocodylomorph lifestyles (terrestrial, semi-aquatic/freshwater and aquatic/marine). Body size is represented by a cranial measurement (dorsal orbito-cranial length) after log-transformation. (a) Mean body size of different lifestyles (mean values were subjected to bootstraps and rarefaction; colour key same as panel c). (b) Body size disparity (sum of variances) of different lifestyles (disparity values were subjected to bootstraps and rarefaction; colour key same as panel c). (c) Through-time variation of body size (mean values per time bin) for different lifestyles. Data for time bins with only one species are not displayed. Source: Data from Godoy PL, Benson RB, Bronzati M and Butler RJ (2019) The multi-peak adaptive landscape of crocodylomorph body size evolution. BMC Evolutionary Biology 19: 167.

higher variability (**Figure 4b**). This is consistent with the high disparity observed for neosuchians (**Figure 3e**), which are mostly semi-aquatic animals and include some species at the end of both sides of the body size spectrum (e.g. the diminutive atoposaurids, with less than 1 m, and the gigantic *Sarcosuchus imperator*; Godoy *et al*., 2019).

Finally, fully aquatic species are usually large-bodied. Transitions to marine habitats are seen in thalattosuchians, dyrosaurids (within Neosuchia) and crocodylians (independently in gavialoids and tomistomines). These species are usually large-bodied animals (about 5 m on average), with some reaching almost 8 m (such as *Machimosaurus rex*; Young *et al*., 2016). Through-time patterns of body size (**Figure 4c**) show that marine crocodylomorphs originated at sizes larger than terrestrial and semi-aquatic ones, with average size values never at levels lower than the other two ecological categories (Gearty and Payne, 2020).

To explain these differences, it has been proposed that strong selective pressures imposed physiological constraints on the body size of marine crocodylomorphs (Gearty and Payne, 2020). Indeed, body size regime shifts towards larger sizes are often associated with more aquatic lifestyles (Godoy *et al*., 2019). Furthermore, marine crocodylomorphs exhibit lower disparity (**Figure 4d**), indicating that the size ranges of these species are evolutionary constrained. One of the reasons might be related to heat loss in aquatic environments. Experiments performed by Smith (1976) show larger individuals of *Alligator mississippiensis* cool down more slowly than smaller ones. Given the higher rates of heat transfer in water (when compared to the air), heat loss is expected to be a bigger issue for more aquatic species. Consistently, Gearty and Payne, (2020) found that heat loss imposes a lower size limit of 10 kg to marine crocodylomorphs. Furthermore, species between 10 and 100 kg have relatively low lung capacity, reducing their diving time (Seymour *et al*., 2004; Gearty and Payne, 2020). Thus, larger crocodylomorphs would also have physiological advantages over smaller ones.

Environmental Drivers of Crocodylian Body Size

Although abiotic factors alone cannot explain the distribution of body sizes of all crocodylomorphs, some environmental variables do appear to influence the trajectories of body size evolution within crocodylomorph subgroups (Godoy *et al*., 2019). This is the case for the crocodylomorph crown-group (Crocodylia), for which a strong correlation ($R^2 = 0.828$, $p < 0.0005$) between body size and temperature was found (**Figure 5a, b**). This is not particularly unexpected when considering the long-recognised influence of temperature on the physiology and biology of extant crocodylian (Allsteadt and Lang, 1995; Lakin *et al*., 2020). Similarly, temperature is thought to have played an important role in defining through-time biodiversity patterns of crocodylian biodiversity (Markwick, 1998b; Mannion *et al*., 2015; de Celis *et al*., 2019).

In this case, mean body size values of crocodylians increased as the globe cooled throughout the Cenozoic (we use oxygen isotope [δ^{18}O] as a proxy for palaeotemperature – higher δ^{18}O values indicate lower temperatures; **Figure 5a**; Zachos *et al*., 2008). Concomitantly, a decrease in body size disparity is observed during the same time period (**Figure 3b**). Both phenomena can be understood as a consequence of a sustained process of extinction

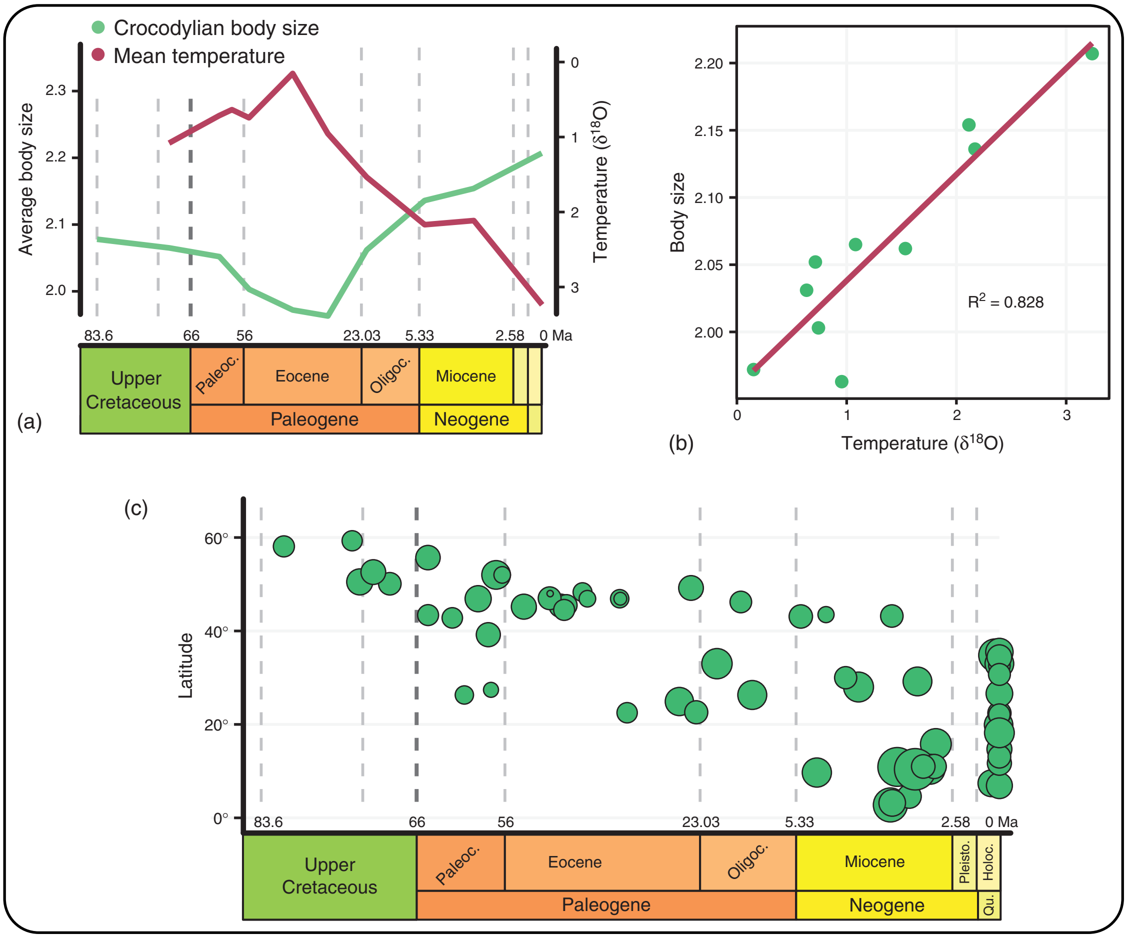

Figure 5 Body size patterns of crocodylians. Body size is represented by a cranial measurement (dorsal orbito-cranial length) after log-transformation. (a) Mean body size (green line) through time, plotted with environmental temperature data (red line). Temperature is represented by $\delta^{18}O$ data (lower values indicate higher temperatures). (b) Mean body size regressed against temperature, indicating a strong correlation (significant coefficient of determination (R^2) = 0.828). (c) Through-time variation of crocodylian latitudinal distribution. Body size is incorporated into the plot as different-sized circles. Latitude values are absolute (i.e. without distinction between north and south). For extant crocodylians, maximum latitudinal range was considered. Sources: Godoy PL, Benson RB, Bronzati M and Butler RJ (2019) The multi-peak adaptive landscape of crocodylomorph body size evolution. BMC Evolutionary Biology 19: 167; Zachos JC, Dickens GR and Zeebe RE (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451: 279–283.

of lineages and/or species of smaller sizes, especially from the end of the Eocene until today (**Figure 3a**). In other words, the extinction of small-bodied crocodylomorphs through the Cenozoic structured the observed pattern of average size increase coupled with a decrease in disparity.

But what can explain the extinction of smaller species? Although higher rates of extinction rates are expected for crocodylians at both sides of the body size spectrum (Solórzano *et al.*, 2019), smaller forms seem to be affected the most (Godoy *et al.*, 2019). A clue to the answer might be on the latitudinal distribution of crocodylians during the Cenozoic (**Figure 5c**). There is a clear pattern of geographic range contraction, with early Cenozoic crocodylians inhabiting subpolar regions (at more than 60°N), while extant species are restricted to a band of nearly 40° at either side of the Equator (Mannion *et al.*, 2015). Considering that temperature is one of the main factors influencing modern species' distribution (Markwick, 1998a), it is expected that the decreasing temperatures through the Cenozoic would reduce the latitudinal range of crocodylians.

Larger crocodylians have proportionally lower food requirements (per kilogram) than smaller ones (Seymour *et al.*, 2013). Larger species also have the advantage of being able to handle larger preys, and thus needing to seek for food much less frequently. Furthermore, smaller crocodylomorphs have lower potential dispersal capabilities, making them more susceptible to extinctions due to local unfavourable conditions (Nicolaï and Matzke, 2019). Therefore, in an increasingly competitive world, with fewer suitable habitats available due to global cooling, strong selective pressures against smaller crocodylians can be presumed. In the long-term (i.e. throughout the Cenozoic), this eventually resulted in the differential extinction of smaller-sized species (Godoy *et al.*, 2019).

Conclusions

Despite their reputation, extant crocodylians are not ‘living fossils’, as illustrated by the remarkable diversity exhibited by their crocodylomorph relatives. In terms of body size, crocodylomorphs displayed striking size variation over 200 million years of evolutionary history, spanning from species that were less than 1 m long, to giants stretching over 10 m. Macroevolutionary studies have demonstrated that body size evolution in the group does not exhibit a widespread pattern of size increase or decrease, and it cannot be explained by unconstrained gradual evolution (BM) either. Instead, the body size variation observed is more consistent with the concept of adaptive landscapes, with various optimal body sizes, which vary according to multiple factors. Among these factors, ecological lifestyle emerges as an important component, given that aquatic crocodylomorphs tend to be larger than terrestrial ones. This relationship between ecology and body size can be explained by physiological constraints associated with thermoregulation and lung capacity. Another important factor is environmental temperature, especially in the case of crocodylians (which include the living species). As the planet became cooler during the Cenozoic (i.e. during the last 66 million years), species became larger on average. Concomitantly, geographic ranges of crocodylians contracted over time, resulting in the differential extinction of smaller-sized species.

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Glossary

Adaptive landscape The conceptual framework upon which biologists study evolutionary changes in response to natural selection. As selective pressures in a changing environment act on evolving species, these would move to new ‘adaptive peaks’ (or adaptive zones), resulting in changes in the genotype (Wrightian Adaptive Landscape) or phenotypic traits (Simpsonian Adaptive Landscape).

Archosauria The clade consisted of extant crocodylians and birds, as well as all the extinct species that are more closely related to these two groups of animals, including dinosaurs, pterosaurs and extinct crocodylomorphs.

Crocodylia A crown-group, which means that it is the clade that includes all extant crocodylians (alligators, caimans, crocodiles and gharials), as well as all the descendants of their most recent common ancestor.

Crocodylomorpha The clade that includes all species (extant or extinct) that are more closely related to crocodylians than to other archosaurs, such as birds, dinosaurs and pterosaurs.

Evolutionary models Statistical models that attempt to characterise the process or processes of biological evolution, often with respect to organismal trait values or phylogenetic tree shape.

Macroevolution Originally, the evolution of taxa above the species level. Currently, refers to the deep-time evolutionary processes related to the origin and diversification of major clades.

Neosuchia The clade formed by the crocodylomorphs that are closer to extant crocodylians than to notosuchians. Besides the crown-group Crocodylia, Neosuchia also includes some extinct species, such as the marine *Dyrosaurus* and the gigantic *Sarcosuchus*.

Notosuchia A clade formed only by extinct crocodylomorphs, which were mostly terrestrial, small- to medium-sized species that lived mainly in the southern continents of the Cretaceous period. Some examples are the carnivore *Baurusuchus*, the omnivore *Araripesuchus*, and the herbivore *Simosuchus*.

Thalattosuchia A clade formed only by extinct crocodylomorphs, which were mostly aquatic, medium- to large-sized species, most of which lived in the seas of the Jurassic period. Some examples are *Cricosaurus*, which had flippers and a tail fin, and the gigantic *Machimosaurus*.

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