Relative skull size evolution in Mesozoic archosauromorphs: potential drivers and morphological uniqueness of erythrosuchid archosauriforms

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Abstract: Little is known about the large-scale evolutionary patterns of skull size relative to body size, and the possible drivers behind these patterns, in Archosauromorpha. For example, the large skulls of erythrosuchids, a group of non-archosaurian archosauromorphs from the Early and Middle Triassic, and of theropod dinosaurs are regarded as convergent adaptations for hypercarnivory. However, few investigations have explicitly tested whether erythrosuchid and theropod skulls are indeed disproportionately large for their body size, and whether this trend is driven by hypercarnivory. Here, we investigate archosauromorph relative skull size evolution, examining the scaling relationships between skull and body size of Palaeozoic and Mesozoic archosauromorphs using a robust phylogenetic framework and characterizing the influence of potential drivers, such as taxonomy, diet, locomotory mode and inhabited biotope. Our results show that archosauromorph relative skull sizes are largely determined by phylogeny and that the other drivers have much weaker levels of influence. We find negative allometric scaling of skull size with respect to body size when all studied archosauromorphs are analysed. Within specific groups, skull size scales with positive allometry in non-archosaurian archosauromorphs and, interestingly, scales isometrically in theropods. Ancestral reconstructions of skull–femur size ratio reveal a disproportionately large skull at the base of Erythrosuchidae and proportionately sized skulls at the bases of Theropoda, Carnosauria and Tyrannosauridae. Relative skull sizes of erythrosuchids and theropods are therefore distinct from each other, indicating that disproportionately large skulls are not a prerequisite for hypercarnivory in archosauromorphs, and that erythrosuchids exhibit a bauplan unique among terrestrial Mesozoic carnivores.

Key words: relative skull size, Archosauromorpha, hypercarnivory, biotope, phylogeny, allometry.

The vertebrate head is a remarkable anatomical structure with a diverse array of functions. These include but are not limited to: feeding, housing and protecting the brain; sensing and interpreting external cues; display; and intra- and inter-specific aggression (Stephens et al. 2007; Openshaw & Keogh 2014; VanBuren et al. 2015; da Silva et al. 2018; Arbour et al. 2019). Head phenotypes are therefore the outcome of numerous selective pressures (Bright et al. 2016). Currently, our understanding of whether selective pressures have additive, interactive or constraining effects on head phenotypes is still incomplete (Watanabe et al. 2019; Felice et al. 2021). For example, skull size relative to the rest of the body is often hypothesized to be influenced by diet; disproportionately larger skulls showing positive allometric scaling are suggested as an adaptation for hypercarnivory in many lineages (Figueirido et al. 2010; Butler et al. 2019; Galatius et al. 2020). However, such hypotheses often fail to account for other drivers that may concurrently influence skull size. Characterizing phenotypic changes such as relative skull size over evolutionary time within a rigorous phylogenetic context, as well as understanding the role of potential drivers (e.g. diet, inhabited biotope and mode of locomotion) are crucial for understanding the origins and radiations of past
and present biodiversity (VanBuren et al. 2015; Benson et al. 2018).

Archosauromorpha represents an excellent group for studying large-scale evolutionary patterns and possible drivers of relative skull size. This highly successful clade includes archosaurs (dinosaurs, birds, pterosaurs and crocodylians) and their close relatives, and is represented today by over 10 000 bird and around 27 crocodylian species (Brusatte et al. 2010a; Nesbitt 2011; Grigg & Kirshner 2015; Ezcurra & Butler 2018; Ezcurra et al. 2020a). Archosaurs evolved in the middle–late Permian and rapidly diversified in the wake of the Permo-Triassic mass extinction to dominate terrestrial ecosystems for almost the entirety of the Mesozoic (Benton 2004; Langer et al. 2010; Nesbitt 2011; Foth et al. 2016a, 2021; Ezcurra & Butler 2018). Lineages from this clade have also repeatedly radiated into other biotopes, with pterosaurs and birds (and possibly a few non-avian theropod maniraptoran dinosaurs) independently evolving active flight (Rayner 1988; Pei et al. 2020) and members of groups such as Crocodylomorpha, Phytosauria, Tanystropheidae and Proterosuchidae evolving semi or fully aquatic lifestyles (Stocker et al. 2017; Wilberg et al. 2019; Ezcurra et al. 2020b). In addition, today most major archosauromorph clades have well-resolved phylogenies that enable macroevolutionary investigations within robust phylogenetic frameworks (e.g. Ezcurra 2016; Benson et al. 2018; Godoy et al. 2019; O’Brien et al. 2019; Pradelli et al. 2021).

One pattern of particular interest concerns the repeated occupation of terrestrial hypercarnivorous niches (a diet comprising more than 70% meat; Holliday & Steppan 2004), by distantly related archosauromorphs throughout the Mesozoic. This niche is thought to have been occupied in the Early and Middle Triassic by erythrosuchids, a non-archosaurian archosauromorph clade of quadrupeds characterized by large skulls with a subrectangular profile (e.g. Butler et al. 2019; Ezcurra et al. 2020a, 2021; Maidment et al. 2020). Middle and Late Triassic hypercarnivorous niches are thought to have been filled by non-crocodylomorph loricatan (pseudosuchian archosaurs traditionally referred to as ‘rauisuchians’ sensu Nesbitt & Desojo 2017) which probably assumed both quadrupedal and bipedal postures (e.g. Prestosuchus chiniquensis and Postosuchus kirkpatricki respectively; Chatterjee 1985; Weinbaum 2011, 2013; Mastrantonio et al. 2019; Desojo et al. 2020a). Multiple groups of theropod dinosaurs are regarded as the apex predators of Jurassic and Cretaceous food webs, such as megalosauroids in the former period and abelisaurids and tyrannosaurids in the latter (Therrien & Henderson 2007; Brusatte et al. 2012; Novas et al. 2013; Hendrickx & Mateus 2014). The large skulls exhibited by these archosauromorph groups are therefore deemed to be convergent adaptations for hypercarnivory (Chatterjee 1985; Nesbitt et al. 2013; Butler et al. 2019; Ezcurra et al. 2021). However, the hypothesis that their skulls are indeed disproportionately large with respect to body size, and are also convergent with each other, has currently received little explicit testing (Therrien & Henderson 2007; Butler et al. 2019).

In this study, we investigate relative skull sizes of Palaeozoic and Mesozoic archosauromorphs to: (1) understand the influence of potential drivers (taxonomy, diet, locomotion and biotope) on relative skull size; (2) understand scaling relationships between skull and body size according to these potential drivers; and (3) reconstruct relative skull size evolution across Archosauromorpha. We achieve these aims using a robust phylogenetic framework that includes the construction of a novel informal supertree that is independently time-scaled using two distinct methods. This also enables better identification of whether relative skull size evolution, at both higher-level and more exclusive clades, is constant and directional, or indicates evolutionary radiations (i.e. increase in morphological diversity at the base of major clades) followed by stasis. Our study represents the first comprehensive investigation of large-scale patterns of skull size evolution across the Palaeozoic and Mesozoic in archosauromorphs.

MATERIAL AND METHOD

Skull and body size data collection

We collected data on basal skull length (anterior tip of the premaxilla to the posterior tip of the quadrate) and femur length across Palaeozoic and Mesozoic archosauromorphs. Skull length was our chosen proxy for skull size due to the ease of data collection on account of not relying on homologous landmarks between distantly related taxa, and due to its previous use in investigating cranial morphological disparity in extant archosaurs (Erickson et al. 2012; Foth et al. 2015; Shatkovska & Ghazali 2021). Femoral length was our chosen proxy for overall body size because while femur circumference scales more closely with body mass (Campione & Evans 2012; Campione et al. 2014; Maidment et al. 2020), femur length is also a reliable proxy for body mass that has been used extensively, is much easier to measure, and is much more widely reported than femur circumference in the literature (Carrano 2006; Sookias et al. 2012; Turner & Nesbitt 2013; VanBuren et al. 2015; Butler et al. 2019). Data were collected for a total of 223 species of archosauromorphs, 81 of which were drawn from Butler et al. (2019; and references therein). We added data from personal observations and the literature for a further 142 species, including non-archosaurian archosauromorphs, pseudosuchians, dinosaurs and pterosaurs. The characteristic parietosquamosal frills of ceratopsian dinosaurs
Building the archosauromorph supertree

To explore our data in a robust phylogenetic framework, we created an informal supertree for all sampled archosauromorphs. The supertree comprises 1307 species-level taxa and was built using the topology used by Butler et al. (2019; and references therein) with input from: a modified version of Ezcurra (2016) for non-archosaurian archosauromorphs and non-crocodylomorph pseudosuchians; Ezcurra et al. (2020a) for non-pterosaur pterosauromorphs; Godoy et al. (2019) for crocodylomorphs; Andres et al. (2014) and Longrich et al. (2018) for Pterosauria; Raven & Maidment (2017) for Stegosauria; Rivera-Sylva et al. (2018) for Ankylosauria; Williamson & Brusatte (2016) for Pachycephalosauria; VanBuren et al. (2015) for Ceratopsia; Xing & Xing (2014) and McDonald et al. (2017) for Ornithopoda; Cashmore et al. (2020; and references therein) for Saurisochthyla; Pol & Rauhut (2012) and Wang et al. (2017) for Ceratopsia; Rauhut & Pol (2019) for Carnosauria; Delcourt & Grillo (2018) for Tyrannosauroidea; Lee et al. (2014a) for Ornithomimosauria; Hartman et al. (2019) for Therizinosauria; Xu et al. (2010) for Alvarezsauroidea; Lamanna et al. (2014) and Funston et al. (2018) for Oviraptorosauria and; Pei et al. (2020) for Paraves. The complete tree can be found in Appendix S1. Stratigraphic ages for species were taken either from the literature or from the Paleobiology Database (https://paleobiodb.org) and can be found in Table S2. The supertree was time-scaled using two different approaches to facilitate robust investigations into relative skull size evolution. We used the minimum branch length (mbl) method (Laurin 2004) with the minimum branch duration set at 1 myr (hereafter mbl.1) and the cal3 method (Bapst 2013). The two time-scaling approaches were applied using functions timePaleoPhy and cal3TimePaleoPhy from the package paleotree (Bapst 2012) in R version 4.1.0 (R Core Team 2018). For the cal3 method, the sampling rate was randomly drawn from a uniform distribution of previously estimated rates for tetrapods (Lloyd et al. 2016; Bapst & Hopkins 2017), whereas diversification and extinction rates (which we assume here to be the same) were obtained using the function Rate2sProb and dividing them by the interval length. Prior to time-scaling, we randomly resolved all polytomies in the supertree generating 20 different fully resolved trees, which, after time-scaling, resulted in 40 time-scaled trees (20 for each time-scaling approach). Analyses were performed using pruned versions of the mbl.1 and cal3 trees that included only archosauromorphs for which we had collected skull and body size data. Example code used to perform all analyses in R can be found in Appendix S2.

Phylogenetic signal and potential drivers of skull size evolution

We tested for the presence of a phylogenetic signal in the ratio of skull length to femur length using the phyloSignal function of the package phylosignal (Keck et al. 2016), setting 999 999 replicates for each tree. We used Pagel’s lambda (λ) as our index for testing phylogenetic signal as it is relatively robust when using trees with poorly resolved branch length information (Münkemüller et al. 2012; Molina-Venegas & Rodríguez 2017).

We applied regression models to examine the relationship between skull length and femur length in all archosauromorphs, and to investigate the effects of different drivers on this relationship. To take the phylogenetic relationships of taxa into account, we used phylogenetic generalized least squares (PGLS) regressions with the gls function from the package nlme (Pinheiro et al. 2018). We selected four predictors for our models: (1) taxonomy; (2) dietary group; (3) locomotory mode; and (4) inhabited biotope.

For taxonomy, archosauromorphs were assigned to one of the following clades or grades, some of which are modified from their formal phylogenetic definitions for easier between-group comparisons: (1) Avialae, the clade containing Passer domesticus and all coelurosaurian dinosaurs more closely related to it than to Dromaeosaurus albertensis and Troodon formosus (Turner et al. 2012); anchiornithines are included in this clade following Pei et al. (2020); (2) ‘basal
archosauromorphs’, a paraphyletic group that comprises all non-archosaurian archosauromorphs (including tangasauroids, rauisuchids, aetosaurs, erpetosuchids, and protorothyrids; Ezcurra et al. 2020b), all non-crocdylophalosaurian pseudosuchians (including phytosaurs, gracilisuchids, aetosaurs, ornithosuchids, erpetosuchids, poposaurusids and non-crocdylophalosaurian loricatans; Brusatte et al. 2010a; Nesbitt et al. 2013; Ezcurra 2016; Müller et al. 2020) and all non-dinosaurian and non-pterosaurian avemetatarsalians (e.g. Scleromochlus tayloiri); (3) Ceratopsia, the clade comprising all marginocephalian dinosaurs that are more closely related to Triceratops horridus than to Pachycephalosaurus wyomingensis (You & Dodson 2004); (4) Crocodylophalosauria, the most inclusive clade containing Crocodylus niloticus but not Rauisuchus tiradentis, Gracilisuchus stipanicicorum, Prestosuchus chiniquensis or Aetosaurus ferratus (Nesbitt 2011; Irmis et al. 2013); (5) Dinosauria, the clade comprising the most recent common ancestor of Triceratops horridus and Passer domesticus and all its descendants (Brusatte et al. 2010b); Mesozoic avialans, however, are excluded from this category since their bauplans are adapted for flight; (6) basal Ornithischia, a paraphyletic group including all ornithischians that are not included within Ceratopsia, Ornithopoda or Thyreophora (e.g. Heterodontosaurus tucki); (7) Ornithopoda, the clade comprising all dinosaurs that are more closely related to Edmontosaurus regalis than to Triceratops horridus (Norman et al. 2004a); (8) Pterosauria, the clade comprising the most recent common ancestor of Preondactylus buffarini and Quetzalcoatlus northropi and all its descendants (Nesbitt 2011); (9) Sauripoda, the clade comprising all dinosaurs that are more closely related to Saltasaurus loricatus than to Passer domesticus (Galton & Upchurch 2004); (10) Theropoda, the largest clade containing Allosaurus fragilis but neither Plateosaurus engelhardti nor Heterodontosaurus tucki (Naish et al. 2020); members of Herrerasauria, all dinosaurs that share a more recent common ancestor with Herrerasaurus ischigualastensis than with Liliosternum liliosterni or Plateosaurus engelhardti (Langer 2004), are here included within Theropoda for simplicity despite growing evidence that this clade may represent non-theropod saurischians (Novas et al. 2021; and references therein); as with our Dinosauria clade, avialans are excluded from Theropoda here to rule out confounding effects from their highly derived bauplans; and (11) Thyreophora, the clade comprising all dinosaurs that are more closely related to Ankylosaurus magniventris than to Triceratops horridus (Norman et al. 2004b). Regression models were also performed on Archosauromorpha and Dinosauria with sauropodomorphs excluded to explore whether these dinosaurs had disproportionate effects on regression slopes due to their characteristically small skulls (Sander et al. 2010; Rauhut et al. 2011).

For diet, archosauromorphs were categorized as either carnivores or herbivores. This dichotomy is a simplification of the range of likely ecologies exhibited by extinct taxa but is necessary because of the difficulty in reliably assigning specific ecologies based on dietary proxies (see Bestwick et al. (2018) and Miller & Pittman (2021) for recent reviews) and allows straightforward analyses. For biotope, archosauromorphs were categorized as either terrestrial, aquatic (including semi-aquatic lifestyles) or aerial. For locomotion, archosauromorphs were categorized as either obligate bipeds, obligate quadrupeds, facultative bipedal quadrupeds or bipedal-flying. All assignments for diet, locomotion and biotope were based on the common consensus of the literature and of the authors. We note that our aerial biotope and bipedal-flying categories have the same assigned taxa: avialans and pterosaurs and a few theropods (complete category assignments for all archosauromorphs can be found in Table S1).

A total of 15 models were used in our approach, including a no predictor model, single predictor models, and a model for a two, three and four-way combination of predictors. Each of the 15 models was fitted to all 40 trees. We initially performed a stepwise removal model to remove all non-significant interaction terms from our multi-predictor models. This resulted in all interaction terms being removed (i.e. all predictors were analysed as additive fixed factors). We compared the mean average and median AIC scores from each model to assess how well they explained our data.

Subsequent PGLS regressions were performed on each subset of the archosauromorph dataset according to taxonomy, diet, locomotory mode and biotope. To test the additional hypothesis that hypercarnivory is a driver behind large relative skull sizes, PGLS was also performed on terrestrial basal archosauromorph carnivores and terrestrial dinosaur carnivores. The non-crocdylophalosaurian loricatans Prestosuchus chiniquensis and Postosuchus kirkpatricki were included as part of the former carnivore subset due to the lack of sampled taxa from this group of Middle–Late Triassic predatory archosauromorphs. This, however, still enables comparisons between Triassic carnivores and Jurassic and Cretaceous carnivores. To reduce computational demands, all ‘subset PGLS regressions’ were performed using just one randomly chosen tree from each timescaling approach (i.e. one mbl.1 tree and one cal3 tree).

Relative skull size evolution

To investigate relative skull size evolution in Archosauromorpha, one randomly chosen tree from each timescaling approach was pruned in R to include only archosauromorphs with sampled skull length and femur length data. Pruning has no effect on the topological relationships of remaining archosauromorphs. Ancestral reconstructions of log skull-length/log femur-length ratio
(henceforth: skull–femur ratio) were subsequently mapped onto each of the pruned supertrees. Maximum likelihood estimations were achieved using the contMap function in phytools (Revell 2012). In addition, to help determine whether ratio changes through evolutionary time are continuous or are better explained by evolutionary radiations (i.e. most significant shifts associated with the origin of major clades), we calculated ancestral skull–femur ratios along with variance and upper and lower 95% confidence intervals for 16 specific nodes (the same for each tree), using the anc.ML function in phytools. These nodes represent ratio estimates for the most recent common ancestor of a particular clade. For consistency with our PGLS and scaling analyses, nodes were selected to represent the following clades: Avialae, Ceratopsia, Crocodylomorpha, Dinosauria, basal Ornithischia, Ornithopoda, Pterosauria, Sauropodomorpha, Theropoda and Thyreophora. The taxonomic contents of these groups were not modified for this analysis. To further aid in identifying evolutionary changes we selected additional nodes that represented the following clades: Archosauromorpha (all saurians more closely to Proterosaurus than to Lepidosauria; Dilkes 1998), Archosauromorpha, the least inclusive clade containing Crocodylus niloticus and Passer domesticus; Sereno 2005), Avemetatarsalia (the most inclusive clade containing Passer domesticus but not Crocodylus niloticus; Benton 1999), and Pseudosuchia (the most inclusive clade containing Crocodylus niloticus but not Passer domesticus; Sereno 2005). We also selected nodes that represented Erythrosuchidae (all taxa more closely related to Erythrosuchus africanus than to Proterosaurus fergusi or Passer domesticus; Ezcurra et al. 2010), Loricata (the most inclusive clade containing Crocodylus niloticus but not Poposaurus gracilis, Ornithosuchus longidens or Aetosaurus ferratus; Nesbitt 2011), Abelisauridae (theropod dinosaurs more closely related to Carnotaurus sastrei than to Ceratosaurus nasicornis; Tykoski & Rowe 2004), Carnosauria (theropod dinosaurs more closely related to Allosaurus fragilis and to Megalosaurus bucklandii than to Passer domesticus; Raubut & Pol 2019) and Tyranosauroida (all theropod dinosaurs more closely related to Tyrannosaurus rex than to Ornithomimus velox, Deinonychus antirrhopus or Allosaurus fragilis; Holtz 2004) to understand skull size evolution in unrelated apex predators from across the Mesozoic, and how they compare with each other.

RESULTS

Phylogenetic signal and performance of predictor models

Across the full dataset of 223 archosauromorphs, there is a strongly significant phylogenetic signal in the skull–femur ratio for all time-calibrated trees (all \( \lambda > 0.84; p < 0.0001 \)). Phylogenetic signal results for all 40 time-calibrated trees can be found in Table S3.

Comparisons between the AIC scores for all 15 predictor models fitted to archosauromorph skull–femur lengths generally show similar levels of support (Fig. 1; AIC scores for all 40 trees from all predictor models can be found in Table S4). All models except one exhibit mean average AIC scores between 1.2 and −40.98 and median scores between −24.18 and −69.96 (Fig. 1; Table S4). The exception is the biotope model which shows the weakest level of support (i.e. higher AIC values; mean 77.7, median 53.1; Fig. 1). The ‘taxonomy + diet + locomotory mode’ model shows marginally the strongest level of support (mean −40.98, median −69.67; Fig. 1; Table S4). Method of time-calibration appears to have little effect on AIC scores for each model. Hereafter, only results from one randomly chosen tree from each time-scaling approach from the no predictor model are presented.

PGLS scaling relationships

For all studied archosauromorphs, skull length statistically significantly correlates with femur length for both time-scaled trees (\( p < 0.0001 \); Fig. 2). When slopes are considered, skull length scales with negative allometry with respect to femur length (\( a = 0.81 \pm 0.077 \) and \( 0.809 \pm 0.088 \) for the mbl1 and cal3 trees, respectively; Fig. 2; Table 1). Archosauromorph skulls therefore become disproportionately smaller with increasing body size (see Table S5 for full PGLS results). When archosauromorphs are categorized into subsets according to taxonomic group, we find that skull length is strongly correlated with femur lengths in all groups except in basal Ornithischia (\( p = 0.461 \) and 0.421 for the mbl1 and cal3 ornithischian trees, respectively; Table 1), probably due to its small sample size (\( n = 6 \)). When slopes are considered, skull length scales with positive allometry in basal archosauromorphs for both time-scaling methods (Table 1). Skull length scales with negative allometry for both time-scaling methods in ceratopsians, dinosaurs and sauropodomorphs (Table 1). Avialan skull length scales with negative allometry in the cal3 tree, but scales with isometry in the mbl1 tree (Table 1). Skull length scales isometrically with femur length in both time-calibrated trees in crocodylomorphs, ornithopods, pterosaurs, theropods and thyreophorans (Table 1; see Fig. S1 for regression lines and 95% confidence intervals for each taxonomic group; also see Fig. S2 for regression lines and 95% confidence intervals for all predictor subsets that show different scaling relationships between the mbl1 and cal3 trees). In the Archosauromorpha and Dinosauria with excluded sauro-

DINOSAURS, bases on the origin of major clades, we calculated ancestral skull–femur ratios along with variance and upper and lower 95% confidence intervals for 16 specific nodes (the same for each tree), using the anc.ML function in phytools. These nodes represent ratio estimates for the most recent common ancestor of a particular clade. For consistency with our PGLS and scaling analyses, nodes were selected to represent the following clades: Avialae, Ceratopsia, Crocodylomorpha, Dinosauria, basal Ornithischia, Ornithopoda, Pterosauria, Sauropodomorpha, Theropoda and Thyreophora. The taxonomic contents of these groups were not modified for this analysis. To further aid in identifying evolutionary changes we selected additional nodes that represented the following clades: Archosauromorpha (all saurians more closely to Proterosaurus than to Lepidosauria; Dilkes 1998), Archosauromorpha, the least inclusive clade containing Crocodylus niloticus and Passer domesticus; Sereno 2005), Avemetatarsalia (the most inclusive clade containing Passer domesticus but not Crocodylus niloticus; Benton 1999), and Pseudosuchia (the most inclusive clade containing Crocodylus niloticus but not Passer domesticus; Sereno 2005). We also selected nodes that represented Erythrosuchidae (all taxa more closely related to Erythrosuchus africanus than to Proterosaurus fergusi or Passer domesticus; Ezcurra et al. 2010), Loricata (the most inclusive clade containing Crocodylus niloticus but not Poposaurus gracilis, Ornithosuchus longidens or Aetosaurus ferratus; Nesbitt 2011), Abelisauridae (theropod dinosaurs more closely related to Carnotaurus sastrei than to Ceratosaurus nasicornis; Tykoski & Rowe 2004), Carnosauria (theropod dinosaurs more closely related to Allosaurus fragilis and to Megalosaurus bucklandii than to Passer domesticus; Raubut & Pol 2019) and Tyranosauroida (all theropod dinosaurs more closely related to Tyrannosaurus rex than to Ornithomimus velox, Deinonychus antirrhopus or Allosaurus fragilis; Holtz 2004) to understand skull size evolution in unrelated apex predators from across the Mesozoic, and how they compare with each other.

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allometry in both time-calibrated trees (Table 1; Fig. S3; Table S5).

When categorized by diet, skull length is strongly correlated with femur length in both archosauromorph carnivores and herbivores for both time-calibrated trees (Fig. 3; Table 2). Carnivore skull lengths scale isometrically with respect to femur length for all time-scaled trees, while herbivore skull lengths scale with negative allometry (Fig. 3; Table 2). When categorized by locomotory mode, skull length is strongly correlated with femur length for all locomotory modes for both time-scaling methods (Table 3; see Fig. S4 for regression lines and 95% confidence intervals for each locomotory mode). Skull length scales with negative allometry for both time-calibrated trees in bipedal archosauromorphs, and with positive allometry in terrestrial archosauromorphs (Table 4; Fig. 4). Both terrestrial basal archosauromorph carnivores and terrestrial dinosaur carnivores exhibit statistically significant relationships between skull and femur lengths (Fig. 4; Table 5). Skull length scales isometrically with femur length from both time-calibrated trees in dinosaurs, while in basal archosauromorphs, skull length scales isometrically with femur length from the *mbl*1 tree, but scales with positive allometry from the *cal3* tree (Fig. 4; Table 5).

**Ancestral skull–femur ratio estimates**

The skull–femur ratio ancestral state estimates using the two time-calibrated trees show broadly similar estimated ratios across most archosauromorph lineages and for specific nodes of interest (Fig. 5; Table 6; see Table S6 for ancestral estimates, variance, and upper and lower 95% intervals for all nodes highlighted in Fig. 5, and for the complete ancestral estimate list of all 222 nodes from the two time-calibrated trees; see Fig. S6 for the locations of all 222 nodes within the two trees). The ancestral estimate of Archosauromorpha (node 1, Fig. 5) from the *mbl*1 tree indicates a skull equal in length to that of the femur...
FIG. 2. Phylogenetic generalized least squares (PGLS) regression of log skull-length and log femur-length for 223 extinct archosauromorph species (grey solid line). Taxonomic clades and grades that comprise the dataset are highlighted. Star symbols denote erythrosuchids. Dashed grey lines denote 95% confidence intervals (CIs). Regression line and CIs from the analysis that used the *mbl.1* time-scaled phylogeny. Taxa located above the regression line have disproportionately larger skulls and taxa located below the regression line have disproportionately smaller skulls. The theoretical isometric line ($a = 1$) is denoted by the dashed black line. PGLS results of all archosauromorphs from all 40 time-calibrated trees, as well as regression results of each taxonomic clade and grade from the *mbl.1* and *cal3* tree, can be found in Table S5.

**TABLE 1.** Phylogenetic generalized least squares (PGLS) regression results of log skull-length and log femur-length for all studied archosauromorphs and for assigned taxonomic groups within Archosauromorpha.

| Taxonomic group                     | df  | mbl.1 Slope | 95% CI | p     | cal3 Slope | 95% CI | p     |
|------------------------------------|-----|--------------|--------|-------|-------------|--------|-------|
| All archosauromorphs               | 222 | 0.81         | 0.077  | <0.0001 | 0.809       | 0.088  | <0.0001 |
| Avialae                            | 11  | 0.735        | 0.284  | 0.0002 | 0.622       | 0.267  | 0.0004 |
| Basal archosauromorphs             | 36  | 1.193        | 0.147  | <0.0001 | 1.209       | 0.145  | <0.0001 |
| Ceratopsia                         | 24  | 0.85         | 0.147  | <0.0001 | 0.801       | 0.107  | <0.0001 |
| Crocodylomorpha                    | 23  | 1.075        | 0.153  | <0.0001 | 1.112       | 0.16   | <0.0001 |
| Dinosauria                         | 116 | 0.761        | 0.114  | <0.0001 | 0.679       | 0.1    | <0.0001 |
| Basal Ornithischia                 | 5   | 0.424        | 1.445  | 0.461  | 0.401       | 1.245  | 0.421  |
| Ornithopoda                        | 16  | 0.894        | 0.242  | <0.0001 | 0.92        | 0.267  | <0.0001 |
| Pterosauria                        | 32  | 0.993        | 0.184  | <0.0001 | 0.926       | 0.273  | <0.0001 |
| Sauropodomorpha                    | 18  | 0.753        | 0.23   | <0.0001 | 0.774       | 0.191  | <0.0001 |
| Theropoda                          | 33  | 0.758        | 0.311  | <0.0001 | 0.81        | 0.294  | <0.0001 |
| Thyreophora                        | 15  | 1.242        | 0.414  | <0.0001 | 1.32        | 0.519  | <0.0001 |
| Archosauromorpha without Sauropodomorpha | 203 | 0.791        | 0.127  | <0.0001 | 0.771       | 0.087  | <0.0001 |
| Dinosauria without Sauropodomorpha | 97  | 0.817        | 0.129  | <0.0001 | 0.837       | 0.138  | <0.0001 |

Includes regression results using the *mbl.1* and *cal3* time-calibrated trees and 95% confidence interval (CI) range for each tree. See text for how each taxonomic group was defined in this study. Full results for each PGLS can be found in Table S5.
whereas the estimate from the *cal3* tree indicates a slightly longer skull (1.056 ± 0.05; Table 6). The ancestral *mbl*1 and *cal3* estimates for Erythrosuchidae (node 2) in contrast clearly show a disproportionately larger skull (Fig. 5; Table 6). The ancestral estimates for the most recent common ancestor of Archosauria (node 3) denotes a skull only very slightly longer than the femur, but while the same trend is observed in the most recent common ancestor of Pseudosuchia (node 17), the ancestral estimate for the most recent common ancestor of Avemetatarsalia (node 4) shows a skull and femur of equal length (Table 6). Ancestral estimates for the two major avemetatarsalian clades, Pterosauria and Dinosauria (nodes 5 and 6 respectively), show a strongly disproportionately large skull for the former and a skull and femur of equal length in the latter (Table 6). The ancestral estimate for Ornithischia (node 7, Fig. 5) from the *mbl*1 tree indicates a disproportionately short skull (albeit marginally), while the *cal3* tree indicates a skull equal in length to the femur.

![FIG. 3. Phylogenetic generalized least squares (PGLS) regression results of log skull-length and log femur-length for 233 extinct archosauromorph species assigned as either carnivores (violet solid line) or herbivores (turquoise solid line). Star symbols denote erythrosuchids. Dashed lines indicate 95% confidence intervals (CIs) for the corresponding diet. Regression lines and CIs from the analysis that used the *mbl*1 time-scaled phylogeny. Taxa located above the regression lines have disproportionately larger skulls and taxa located below the regression lines have disproportionately smaller skulls. The theoretical isometric line (a = 1) is denoted by the dashed black line.](image)

**TABLE 2.** Phylogenetic generalized least squares (PGLS) regression results of log skull-length and log femur-length for all studied archosauromorphs assigned to a dietary group.

| Diet       | *mbl*1 |          |          |          |          |          |          |          |          |          |          |
|------------|--------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
|            | df     | Slope    | 95% CI   | p        | Slope    | 95% CI   | p        |
| Carnivores | 123    | 1.05     | 0.094    | <0.0001  | 1.082    | 0.1      | <0.0001  |
| Herbivores | 98     | 0.777    | 0.083    | <0.0001  | 0.718    | 0.08     | <0.0001  |

Includes regression results using the *mbl*1 and *cal3* time-calibrated trees and 95% confidence interval (CI) range for each tree. See text for how each dietary group was defined in this study. Full results for each PGLS can be found in Table S5.
TABLE 3. Phylogenetic generalized least squares (PGLS) regression results of log skull-length and log femur-length for all studied archosauromorphs assigned to a locomotory mode.

| Locomotory mode         | df  | Slope   | 95% CI   | p       | Slope   | 95% CI   | p       |
|-------------------------|-----|---------|----------|---------|---------|----------|---------|
| Bipedal                 | 56  | 0.786   | 0.199    | <0.0001 | 0.781   | 0.176    | <0.0001 |
| Bipedal-quadrupedal     | 21  | 0.725   | 0.273    | <0.0001 | 0.862   | 0.182    | <0.0001 |
| Bipedal-flying          | 45  | 0.832   | 0.182    | <0.0001 | 0.832   | 0.294    | <0.0001 |
| Quadrupedal             | 97  | 1       | 0.096    | <0.0001 | 1.059   | 0.105    | <0.0001 |

Includes regression results using the mbl1 and cal3 time-calibrated trees and 95% confidence interval (CI) range for each tree. See text for how each locomotory mode was defined in this study. Full results for each PGLS can be found in Table S5.

TABLE 4. Phylogenetic generalized least squares (PGLS) regression results of log skull-length and log femur-length for all studied archosauromorphs assigned to an inhabited biotope.

| Biotope      | df  | Slope   | 95% CI   | p       | Slope   | 95% CI   | p       |
|--------------|-----|---------|----------|---------|---------|----------|---------|
| Aerial       | 45  | 0.832   | 0.182    | <0.0001 | 0.84    | 0.289    | <0.0001 |
| Aquatic      | 26  | 1.213   | 0.15     | <0.0001 | 1.222   | 0.129    | <0.0001 |
| Terrestrial  | 149 | 0.87    | 0.097    | <0.0001 | 0.853   | 0.094    | <0.0001 |

Includes regression results using the mbl1 and cal3 time-calibrated trees and 95% confidence interval (CI) range for each tree. See text for how each biotope was defined in this study. Full results for each PGLS can be found in Table S5.

FIG. 4. PGLS results of log skull-length and log femur-length for terrestrial basal archosauromorph carnivores (orange solid line) and terrestrial dinosaur carnivores (blue solid line). Star symbols denote erythrosuchids. Dashed lines indicate 95% confidence intervals (CIs) for the corresponding category. Regression lines and CIs from the analysis that used the mbl1 time-scaled phylogeny. Taxa located above the regression lines have disproportionately larger skulls and taxa located below the regression lines have disproportionately smaller skulls. Non-applicable archosauromorphs are greyed out for easier comparison. The theoretical isometric line (a = 1) is denoted by the dashed black line.
Ancestral estimates for several major dinosaurian clades, including the most recent common ancestors of Ceratopsia, Ornithopoda, Sauropodomorpha and Theropoda (nodes 9–12 respectively), indicate skulls and femora of equal length (Fig. 5; Table 6), which then exhibit steady directional changes in skull–femur ratio through evolutionary time. For example, the sauropodomorph ratio becomes smaller through time, while the ceratopsian ratio becomes slightly larger (Fig. 5). Multiple independent shifts towards disproportionately shorter or longer skulls are optimized in Theropoda and in Avialae (nodes 12 and 16 respectively; Fig. 5). For example, the ancestral estimates for Abelisauroida (node 13; Fig. 5; Table 6) indicate skulls and femora of equal length with multiple lineages independently evolving disproportionately smaller skulls. In contrast, ancestral estimates of Carnosauria and Tyrannosauroidea (nodes 14 and 15 respectively) indicate skulls and femora of equal length (Table 6) with little change exhibited by subsequent lineages and taxa (Fig. 5). The ancestral ratio estimate for Thyreophora (node 8) indicates a disproportionately short skull (Table 6), and the ratio in this clade exhibits little change through evolutionary time (Fig. 5). Interestingly, the ancestral estimates for Loricata and Crocodylomorpha (nodes 18 and 19 respectively) indicate skulls and femora of equal length (Table 6), with multiple lineages within the latter clade subsequently evolving disproportionately longer skulls (Fig. 5).

### DISCUSSION

#### Scaling relationships and drivers of relative skull size

Our results indicate that skull–femur ratios across Archosauromorpha are largely determined by phylogeny and indicate no clear support for any of our predictor models as an explanation behind the observed patterns. However, the biotope model provides a relatively poorer explanation for skull–femur ratios than other models. Multiple, unrelated selection pressures could explain the weak support for our predictor models, since multiple pressures acting on anatomical structures that perform multiple roles can result in morphologies that are not optimally adapted for a single role (Gould & Lewontin 1979; Fisher 1985; Ferry-Graham et al. 2002). Nevertheless, our results can still be discussed in ecological and evolutionary contexts.

Our scaling relationships are only slightly influenced by time-scaling method, thus our results from the two time-scaled trees can be discussed together. Relative skull size scaling with negative allometry for all studied archosauromorphs considered together contrasts with similar studies of extant mammalian clades. For example, skull sizes of multiple groups of marsupials (Macropodidae) and placentalts (Chiroptera, Primates, Rodentia, Ungulata) scale isometrically with respect to body size (Cardini & Polly 2013; Cardini et al. 2015; Cardini 2019), while skull sizes

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**TABLE 5.** Phylogenetic generalized least squares (PGLS) regression results of log skull-length and log femur-length for terrestrial basal archosauromorph carnivores and terrestrial dinosaur carnivores.

| Category             | mbl.1 df | mbl.1 Slope | mbl.1 95% CI  | mbl.1 p  | cal3 Slope | cal3 95% CI  | cal3 p  |
|----------------------|----------|-------------|---------------|----------|------------|---------------|----------|
| Basal archosauromorphs | 19       | 1.149       | 0.154         | <0.0001  | 1.244      | 0.178         | <0.0001  |
| Dinosaurs            | 32       | 0.784       | 0.341         | <0.0001  | 0.804      | 0.369         | <0.0001  |

Includes regression results using the mbl.1 and cal3 time-calibrated trees. Includes 95% confidence interval (CI) range. Full results for each PGLS can be found in Table S5.
of other placentals (Carnivora, Cetacea) scale with positive allometry (Slater & Van Valkenburgh 2009; Tarnaglini et al. 2017; Law et al. 2018). Skull sizes also scale with positive allometry in a few unrelated extant avian lineages, although these relationships are less clear (Bright et al. 2016; Linde-Medina 2016; Tokita et al. 2016). Our results therefore indicate that relative skull size relationships may not be universal between major groups of distantly related amniotes and that focusing on scaling relationships of data subsets may enable identification of more informative patterns.

With regard to taxonomic subsets, it is unsurprising that basal archosauromorph skulls scale with positive allometry, given that several distinct groups, including erythosuchids, proterochampsids, proterosuchids and phytosaurs are frequently cited as having disproportionately large skulls (e.g. Stocker & Butler 2013; Butler et al. 2019; Ezcurra et al. 2020b). There is also emerging evidence of disproportionately large skulls in basal aetosaurs (e.g. Revueltosaurus callenderi; Parker et al. 2021). However, this study provides some of the first quantitative evidence that the skulls of these lineages are indeed disproportionately larger for their size in comparison to other archosauromorphs (Butler et al. 2019). Since all our studied basal archosauromorphs are from the Triassic, this allometric relationship highlights the uniqueness of not only Triassic archosauromorphs but Triassic ecosystems in general.

A more surprising result perhaps, given the huge morphological disparity exhibited by the clade, is the number of archosaurian groups that exhibit isometric scaling of skull length with respect to femur length. For example, the relationship in non-avialan theropods contrasts with that found by Therrien & Henderson (2007), in which skull lengths scaled with positive allometry with respect to body length. However, that study used a considerably smaller sample size in terms of both number of species and number of represented theropod subclades. Due to the nature of the fossil record, over half of our theropod sample were coelurosaurs; those species more closely related to Passer domesticus than to Allosaurus fragilis (sensu Turner et al. 2012). Coelurosaurian theropods exhibit rapid and sustained morphological changes moving crownward towards Avialae, such as miniaturization (the main exceptions being tyrannosaurids and ornithomimosaurs), truncation of the snout and modifications of the limb bones, which are all likely to have influenced relative skull size (Bhullar et al. 2012; Benson & Choiniere 2013; Dececchi & Larsson 2013; Brusatte et al. 2014; Lee et al. 2014b, 2020; Puttick et al. 2014; Foth et al. 2016b; Nebreda et al. 2021). This larger coverage of taxa potentially explains the difference between our results and those of Therrien & Henderson (2007), and highlights the importance of thorough species sampling.

### Table 6

| Node no. | Node label              | mbl.1 ancestral ratio estimate | ±95% CI   | cal3 ancestral ratio estimate | ±95% CI   |
|---------|-------------------------|-------------------------------|-----------|-------------------------------|-----------|
| 1       | Archosauromorpha        | 1.033                         | 0.059     | 1.056                         | 0.050     |
| 2       | Erythrosuchidae         | 1.146                         | 0.027     | 1.163                         | 0.002     |
| 3       | Archosaurus             | 1.043                         | 0.040     | 1.064                         | 0.032     |
| 4       | Avemetatarsalia         | 1.036                         | 0.042     | 1.049                         | 0.049     |
| 5       | Pterosauria             | 1.174                         | 0.051     | 1.154                         | 0.083     |
| 6       | Dinosaurs               | 1.000                         | 0.046     | 0.994                         | 0.060     |
| 7       | Ornithischia            | 0.953                         | 0.043     | 0.961                         | 0.052     |
| 8       | Thyreophora             | 0.941                         | 0.038     | 0.943                         | 0.042     |
| 9       | Ceratopsia              | 0.994                         | 0.210     | 1.006                         | 0.012     |
| 10      | Ornithopoda             | 0.963                         | 0.043     | 0.992                         | 0.063     |
| 11      | Sauropodomorpha         | 0.984                         | 0.046     | 0.964                         | 0.410     |
| 12      | Theropoda               | 0.998                         | 0.052     | 0.970                         | 0.042     |
| 13      | Abelisauroida           | 0.960                         | 0.060     | 0.943                         | 0.122     |
| 14      | Carnosauria             | 0.969                         | 0.063     | 0.982                         | 0.115     |
| 15      | Tyrannosaurida          | 0.982                         | 0.053     | 0.991                         | 0.072     |
| 16      | Avialae                 | 0.974                         | 0.037     | 0.985                         | 0.046     |
| 17      | Pseudosuchia            | 1.046                         | 0.042     | 1.064                         | 0.032     |
| 18      | Loricata                | 1.038                         | 0.050     | 1.050                         | 0.050     |
| 19      | Crocodylomorpha         | 1.024                         | 0.049     | 1.031                         | 0.087     |

Node numbers correspond to those indicated in Figure 5. Full ancestral estimate reconstructions can be found in Table S6. All values to 3 d.p.
Another surprising result is the isometric scaling found for Crocodylomorpha. The Mesozoic witnessed the highest morphological and ecological diversity of crocodylomorphs, particularly in the Jurassic and Cretaceous, including: small cursorial forms; specialized herbivores; semi-aquatic and fully marine piscivores and carnivores; and terrestrial apex predators (Young et al. 2010; Stubbs et al. 2013; Ösi 2014; Melstrom & Irmis 2019; Wilberg et al. 2019; Montelferto et al. 2020). A range of skull morphologies is thereby exhibited by Mesozoic crocodylomorphs, from the short stubby rostra of notosuchians such as Simosuchus clarki to the gracile elongate rostra of thalattosuchians such as Cricosaurus suevicus (Felice et al. 2021; Stubbs et al. 2021). It is therefore possible that these morphological extremes effectively balance the overall trend and that greater focus on specific crocodylomorph lineages may reveal further interesting patterns.

Focusing on specific ornithischian lineages reveals interesting patterns, namely negative allometric scaling in ceratopsians, while ornithopods and thyreophorans scale isometrically. Our ceratopsian relationship contrasts with previous research that found ceratopsian skulls to scale isometrically (VanBuren et al. 2015). As both studies have very similar ceratopsian samples, these differences could be due to the choice of time-scaling methods. For example, both studies used the mbl method and our mbl.1 tree produced a slope with confidence intervals only just outside the theoretical slope of isometry. Our cal3 tree, a method not used by VanBuren et al. (2015), in contrast produced a slope with a much lower gradient. Nevertheless, these results are still worth mentioning within evolutionary and ecological contexts. It is likely that the negative scaling relationship is being driven by the appearance of disproportionately large skulls very early in ceratopsian evolutionary history, such as Psittacosaurus major and Psittacosaurus sinensis, although the exact reasons behind this are unclear (Ostrom 1966; Sereno et al. 2007; VanBuren et al. 2015).

With regard to the dietary subsets, carnivores exhibiting proportionally larger skulls than herbivores is unsurprising as larger skulls have more jaw muscle attachment sites for higher bite forces, are capable of wider gaps, and have greater resistance to biomechanical stress and strain, all of which aid in the capture and killing of prey (Slater & Van Valkenburgh 2009; Fabre et al. 2016; McCurry et al. 2017; Galatius et al. 2020). In contrast, consumption of fibrous and tough plant material often correlates with modified postcranial structures that enable effective digestion including, but not exclusive to, elongate intestinal tracts, gastric mills and increased trunk size (Barrett 2014; and references therein). However, the isometric scaling of carnivore skull size contrasts with several groups of mammalian carnivores that exhibit positive allometric scaling of skull size with respect to both body size and the size of preferred prey (e.g. carnivorans and cetaceans; Slater & Van Valkenburgh 2009; Tamagnini et al. 2017; Galatius et al. 2020; but see Law et al. 2018). Isometric scaling could be explained by the scaling relationships of our terrestrial carnivore subsets. The isometric dinosaur carnivore scaling relationship may have been influenced by the relative lack of spinosaurids and carcharodontosauroids (lineages that are regarded as hypercarnivorous and which show evidence of proportionately large skulls; Sereno et al. 1998; Sues et al. 2002; Novas et al. 2013) due to incomplete preservation. Carnivores that probably filled mesopredator niches (such as dromaeosaurids and troodontids; Wick et al. 2015) would have experienced lower selection pressure for larger skulls, occurred in greater numbers, and may therefore have lowered the slope gradient (Tamagnini et al. 2017; Galatius et al. 2020). Nevertheless, we include taxa from these hypothesized hypercarnivorous lineages where preservation allowed, as well as other lineages of large theropods such as tyrannosaurs and ceratosaurs (Benson et al. 2018). In addition, recent evidence that suggests a semi-aquatic lifestyle for some spinosaurids (Ibrahim et al. 2020), potentially excluding them from this terrestrial subset. We therefore regard our terrestrial dinosaur carnivore sampling range and the resulting slope to be representative despite the limitations of the fossil record.

Locomotor mode may also help to explain scaling similarities and differences between archosauromorph carnivores and mammalian carnivores. For example, the vast majority of theropods are bipedal and therefore have a centre of mass located around the hips allowing the animal to maintain balance (Henderson 1999; Maidment et al. 2014). Theoretical modelling has shown that even small morphological changes to the skulls and/or forelimbs of bipedal dinosaurs can move the centre of mass anteriorly, resulting in a top-heavy animal (Maidment et al. 2014; Barrett & Maidment 2017). Bipedality therefore probably imposes stronger constraints on skull size than quadrupedality. This is further exemplified by the quadrapedal erythrosuchids (Erythrosuchus africanus, Garjainia prima and Shansisuchus shansisuchus), which not only have the most disproportionately large skulls among terrestrial archosauromorph carnivores, but also among all terrestrial taxa in this study. In contrast, the two non-crocdylomorph loricatans Postosuchus and Prestosuchus have relative skull sizes more similar to those of hypercarnivorous theropods than to erythrosuchids. In fact, hypothesized Triassic mesopredators such as ornithosuchids (von Baczko 2018) exhibit proportionately longer skulls than the aforementioned loricatans (although loricatan skulls are alternatively much deeper; Chatterjee 1985; Weinbaum 2011; Mastrantonio et al. 2019). These scaling relationships between basal archosauromorphs and dinosaurs, and their skull–femur length ratios, indicate
that disproportionately large skulls are not a prerequisite for hypercarnivory and further highlights the morphological uniqueness of erythrosuchids.

With regard to the biotope subsets, different scaling relationships between our subsets are broadly similar to morphological studies of extant and extinct squamate skulls that found that mode of life (terrestrial, fossorial, semi-aquatic etc.) was a strong driver of skull shape and size (Fabre et al. 2016; da Silva et al. 2018). It is likely that the negative allometry seen in the scaling of terrestrial archosauromorph skulls is driven by the disproportionately small skulls of sauropodomorphs and thyreophorans (Christiansen 1999). Isometric scaling of a similar pattern observed in extant bats (Chiroptera; Cardini & Polly 2013). Powered flight has independently evolved in archosauromorphs at least twice (at the base of Pterosauria and near the base of Aves), and possibly even three or more times (at least once within Deinonychosauria, such as in Microraptor zhaoianus; Pei et al. 2020), with each clade exhibiting marked modifications and reductions of skeletal elements for balance and flight efficiency (Bell et al. 2011; Benson et al. 2014, 2018; Lee et al. 2014b; Tokita 2015; Witton 2015). For example, the hind limbs of pterosaurs and bats are directly connected to the forelimbs via the brachypatagium and are thus part of the flight apparatus, while avialan hind limbs are not involved in flight and can move independently of the forelimbs (Tokita 2015). It is therefore interesting that morphological adaptations for flight do not change skull scaling relationships from the ancestral state, not just in archosauromorphs, but in all aerial amniotes.

Disproportionately large skulls and positive allometric scaling in unrelated aquatic archosauromorphs can be explained by ecomorphological convergence. Extant crocodilians are all semi-aquatic and also exhibit disproportionately large skulls (VanBuren et al. 2015; Butler et al. 2019). This seems to be the result of some degree of cranial elongation driven by heterochronous modifications in craniofacial ontogeny that facilitated seizing prey via unilateral biting motions (Erickson et al. 2012; Walmsley et al. 2013; McCurry et al. 2015; Morris et al. 2019; Lee et al. 2020), and by reduced limb sizes since elongated neural spines of the caudal vertebrae enable swimming via axial muscle-derived propulsion (Pol et al. 2012; Grigg & Kirshner 2015; Molnar et al. 2015; Henderson 2018). Shifts from terrestrial to semi or fully aquatic lifestyles in extinct archosauromorphs have occurred at least once in each of the following clades: Tanystropheidae, Proterosuchidae; Proterochampsia; Phytosauria; and Crocodylomorpha (Ezcurra 2016; Willberg et al. 2019; Brown et al. 2020; Ezcurra et al. 2020b). In most cases (not tanystropheids and at least some non-proterochampsid proterochampsians) these lineages exhibit some level of convergence with crocodilians and with each other, resulting in disproportionately large skulls (Stocker & Butler 2013; Trotteyn et al. 2013; Wynd et al. 2019; Brown et al. 2020; Ezcurra et al. 2020b; Felice et al. 2021; Stubbs et al. 2021). Selection for larger skull–femur ratios would also be greater in semi-aquatic taxa as they are more likely to spend time in water, in which smaller limbs and larger axial muscles, to reduce drag and combat locomotion-induced stresses, respectively, would be more advantageous (Biewener 2005; Montgomery et al. 2013; Molnar et al. 2015).

Relative skull size evolution

The isometric, or near-isometric, ancestral skull–femur ratio estimates for the majority of our higher-level clades (i.e. above family level) indicates that minimal changes in relative skull size occur prior to the origin of a clade and that greater changes occur soon after the clade has appeared. This indicates that deviations of the ancestral skull–femur ratio probably happened once phylogenetic diversifications occurred, during a phase of ecomorphological expansion. For example, the isometric estimate for the ancestral sauropodomorph is quickly followed by a conspicuous ratio decrease in the lineage that includes all sauropodomorphs except for its two earliest-diverging members, Buriolestes schultzi and Eoraptor lunensis. This is consistent with developmental timing shifts and bauplan changes that began to occur around this time such as: the shortening and anterior rotation of cranial bones associated with the braincase (e.g. jugal); increasing trunk size; elongation of the neck and development of columnar limbs (Christiansen 1999; Sander et al. 2010; Rauhut et al. 2011; Sookias et al. 2012; Turner & Nesbitt 2013; Barrett & Maidment 2017; Fabbri et al. 2021; Pradelli et al. 2021). These changes are likely to have co-evolved with dietary shifts to bulk herbivory as sauropodomorphs became among the dominant herbivores of the latest Triassic and Early Jurassic (Christiansen 1999; Sander et al. 2010; Rauhut et al. 2011; Fabbri et al. 2021).

However, this is perhaps not the case for clades where multiple taxa and lineages exhibit independent changes in relative skull size. In pterosaurs for example, the abrupt decrease and almost immediate subsequent increase in relative skull size around the centre of the pterosaur tree is probably influenced by anurognathids; a family from the Middle–Upper Jurassic characterized by very small wingspans (<1 m) and short, box-like skulls (Bennett 2007; Bestwick et al. 2018). This morphology is hypothesized as an adaptation for a unique lifestyle among pterosaurs, that is, catching insects on the wing with their mouths open (Bestwick et al. 2018; and references therein). However, the influence of topological
uncertainties cannot be ruled out as other phylogenies recover anurognathids as one of the earliest branching groups (e.g. Lü et al. 2010; Rodrigues et al. 2015), which is likely to minimize these abrupt increase and decrease events due to a longer anurognathid ghost lineage. The repeated evolution of disproportionately large skulls in pterosaurs, particularly in derived lineages, could be due to multiple non-mutually exclusive selection pressures including less reliance on terrestrial locomotion as flight becomes more efficient, thereby reducing the size of the hind limbs (Witton & Habib 2010; Venditti et al. 2020), and the occupation of new niches as early-diverging lineages were small and most likely insectivorous while more deeply nested lineages became carnivores and piscivores (Bestwick et al. 2020). These patterns reflect the huge disparity in pterosaur relative skull sizes and may indicate fewer phylogenetic constraints from these flying reptiles relative to other archosauromorphs.

The multiple, independent skull–femur ratio decreases in theropods (including avialans) similarly indicate unappreciated patterns in body plan evolution. It is tempting to suggest that these decreases denote dietary shifts towards facultative or obligate herbivory such as in ornithomimosaurs and oviraptorosaurs (Barrett 2014). However, this is unlikely to be the sole explanation for two main reasons: (1) there is limited evidence that herbivory is a major driver in altering theropod skull and body sizes (Zanno & Makovicky 2013; Button & Zanno 2020); and (2) there are large theropods in our dataset (total body length >6 m) that show quantitative evidence of carnivory and have disproportionately short, yet deep, skulls, such as the abelisaurids Carnotaurus sastrei and Skorpiovenator bustingorryi (Bonaparte et al. 1990; Canale et al. 2009; Mazetta et al. 2009). Furthermore, our results show limited evidence of relative skull size increases in supposed hypercarnivorous lineages such as tyrannosaurids. These patterns suggest that hypercarnivory and herbivory are not necessary prerequisites for disproportionately large and small skulls, respectively, in theropods. Incorporating other skull size proxies in future investigations, such as skull depth, may help corroborate this emerging view.

Similar patterns in other non-theropod carnivores also cast doubt on the necessity for disproportionately large skulls. For example, the decrease in skull–femur ratio estimates between the slightly disproportionately large skull of the ancestral pseudosuchian and the subequal skull and femur lengths of the ancestral loricatan and crocodylomorph (Table S6) is contrary to what would be expected from a lineage containing a paraphyletic assemblage of hypothesized apex predators such as Prestosuchus and Postosuchus (Chatterjee 1985; Nesbitt 2011; Nesbitt et al. 2013; Desojo et al. 2020a). In contrast, the ancestral Erythrosuchidae ratio estimate (Table S6) indicates that disproportionately large skulls are probably a synapomorphic trait for this clade (Ezcurra et al. 2013; Butler et al. 2019; Maidment et al. 2020). It can therefore be argued that the skull–femur ratios of carnivorous early loricatans are more like those of carnivorous theropods, such as tyrannosaurids, than those of erythrosuchids and that the erythrosuchid bauplan is morphologically unique among terrestrial archosauromorph carnivores with respect to their hugely disproportionately large skulls, short neck and quadrupedality. Further investigations into relative skull size convergence between distantly related archosauromorph carnivores, or even between archosauromorph and mammalian carnivores, could use non-uniform evolutionary models such as SURFACE as they do not require a priori assumptions on where regime shifts are located in the phylogeny (Ingram & Mahler 2013; Godoy et al. 2019).

It is worth noting that some of our skull–femur ratio estimates could be affected by limitations of the fossil record. For example, the high Pterosauria ancestral estimates are probably influenced by the absence of non-pterosaurian pterosauriforms in our dataset due to their extremely rare and poorly preserved nature, with the earliest-known pterosaurs from the late Norian already exhibiting a highly modified bauplan capable of active flight (Dalla Vecchia 2013; Dean et al. 2016; Britt et al. 2018; Ezcurra et al. 2020a). The absence of earlier pterosauriforms may thereby artificially affect the ancestral Pterosauria estimate. Similarly, the fossil record of early ornithischians from the Triassic and Early Jurassic is very poor or even null (Irms et al. 2007; Baron 2017; but see Desojo et al. 2020b), which in our dataset creates a ghost lineage of approximately 35–40 myr from the base of Dinosauria to the earliest included ornithischian. This long ghost lineage is likely to have caused the ratio estimate differences between our two time-scaled trees. There is some published evidence that silesaurids, traditionally viewed as the sister group to Dinosauria, may actually be a paraphyletic assemblage of Triassic ornithischians that would greatly reduce the length of this ghost lineage (Cabreira et al. 2016; Müller & García 2020). However, the lack of preservation of complete skulls also prevented their inclusion here. New, well-preserved fossil material and greater resolution of phylogenetic relationships will further improve the robustness of future studies.

CONCLUSION

Relative skull size in archosauromorphs is strongly phylogenetically structured, with diet, locomotory mode and biotope found as much weaker drivers of the observed scaling trends. Most significant changes in relative skull size occur soon after the origin of most terrestrial archosauromorph clades, which is indicative of an ecomorphological expansion (or evolutionary radiation) followed by relative
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**SUPPORTING INFORMATION**

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12599):

Fig. S1. PGLS results of log skull-length and log femur-length for each extinct archosauriform taxonomic group used in this study. A, Avialae; B, basal archosauriforms; C, Ceratopsia; D, Crocodylomorpha; E, Dinosauria; F, basal Ornthischia; G, Ornithopoda; H, Pterosauria; I, Sauropodomorpha; J, Theropoda; K, Thyreophora. Avialans are not included in the Dinosauria and Theropoda panels. Star symbols denote eurytherosuchids. Dashed lines denote 95% confidence intervals (CIs). Regression lines and CIs from the analysis that used the mbl.1 time-scaled phylogeny. The theoretical isometric line (a = 1) is denoted by the dashed black line in each panel. Non-applicable archosauriforms in each panel are greyed out. Taxonomic assignments for all archosauriforms can be found in Table S1.

Fig. S2. PGLS results of log skull-length and log femur-length for each assigned archosauriform category that produced different scaling relationships after using the mbl.1 and cal3 time-scaled phylogenies. A, avialans; B, bipedal-quadruped archosauriforms; C, terrestrial basal archosauriforms carnivores. In all panels the cal3 regression line is denoted by a green solid line and the mbl.1 regression lines in panels A–C are denoted by a blue, yellow and orange solid line respectively. Dashed lines denote 95% confidence intervals (CIs). The theoretical isometric line (a = 1) is denoted by the dashed black line in each panel. Non-applicable archosauriforms in each panel are greyed out. PGLS regression results can be found in Table S5.

Fig. S3. PGLS results of log skull-length and log femur-length for: A, Archosauromorpha; B, Dinosauria that include and exclude sauropodomorphs. In both panels the sauropodomorph-excluded regression line is denoted by a scarlet solid line and the sauropodomorph-included regression lines in panels A and B are denoted by a grey and blue solid line respectively. Dashed lines denote 95% confidence intervals (CIs). The theoretical isometric line (a = 1) is denoted by the dashed black line in each panel. Non-applicable archosauriforms in each panel are greyed out. PGLS regression results can be found in Table S5.

Fig. S4. PGLS results of log skull-length and log femur-length for each assigned locomotory mode of extinct archosauriforms. A, aerial; B, aquatic; C, terrestrial. Dashed lines denote 95% confidence intervals (CIs). Regression lines and CIs from the analysis that used the mbl.1 time-scaled phylogeny. The theoretical isometric line (a = 1) is shown as a dashed black line in each panel. Non-applicable archosauriforms in each panel are greyed out. Locomotory assignments for all archosauriforms can be found in Table S1.

Fig. S5. PGLS results of log skull-length and log femur-length for each assigned biotope of extinct archosauriforms. A, aerial; B, aquatic; C, terrestrial. Dashed lines denote 95% confidence intervals (CIs). Regression lines and CIs from the analysis that used the mbl.1 time-scaled phylogeny. The theoretical isometric line (a = 1) is denoted by the dashed black line in each panel. Non-applicable archosauriforms in each panel are greyed out. Biotope assignments for all archosauriforms can be found in Table S1.

Fig. S6. Ancestral character-state reconstructions of log skull-length/log femur-length ratio evolution for 223 archosauriforms from mapping ratios onto time-calibrated supertrees with label numbers of all 222 nodes. A, reconstruction using the mbl.1 dating method. B, reconstruction using the cal3 dating method. Ancestral node estimates, along with the variance and upper and lower 95% confidence intervals for both trees can be found in Table S6.

Table S1. Skull and femur length data of studied archosauriforms with taxonomy, diet, locomotion and biotope assignments.
Table S2. First and last appearance data (in millions of years) of archosauromorphs used to time-scale the supertree used in our analyses.

Table S3. Phylogenetic signal results, using Pagel’s lambda, of archosauromorph log skull-length/log femur-length ratio from the 40 randomly resolved, time-calibrated trees used for the model fitting analysis.

Table S4. Phylogenetic generalized least squares regression and predictor model fitting results of all 15 predictor models on archosauromorph log skull-length and log femur-length from 40 randomly resolved, time-calibrated trees.

Table S5. Phylogenetic generalized least squares regression results of archosauromorph log skull-length and log femur-length from subsets according to: taxonomic group; diet; locomotory mode; biotope; terrestrial basal archosauromorph carnivores and terrestrial dinosaur carnivores.

Table S6. Estimated ancestral archosauromorph log skull-length/log femur-length ratios for selected nodes from the mbl 1 and cal3 time-calibrated trees.

Appendix S1. Nexus file for undated archosauromorph tree.

Appendix S2. Example R code.

Appendix S3. cal3 trees (taxa dropped, 20 trees).

Appendix S4. mbl 1 trees (taxa dropped, 20 trees).

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