Subaqueous foraging among carnivorous dinosaurs

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Abstract

Secondary aquatic adaptations independently evolved more than thirty times from terrestrial vertebrate ancestors[1,2]. For decades, non-avian dinosaurs were believed to be an exception to this pattern. Only a few species have been hypothesized as partly or predominantly aquatic[3,4,5,6,7,8,9,10,11]. However, these hypotheses remain controversial[12,13] largely due to the difficulty of identifying unambiguous anatomical adaptations for aquatic habits in extinct animals. In this study, we demonstrate that the relationship between bone density and aquatic ecologies across extant amniotes provides a reliable inference of aquatic habits in extinct species. We use this approach to evaluate the distribution of aquatic adaptations among non-avian dinosaurs. We find strong support for aquatic habits in spinosaurids, associated with a remarkable increase in bone density, which precedes the evolution of more conspicuous anatomical modifications, a pattern also observed in other aquatic reptiles and mammals[14,15,16]. Spinosaurids are revealed to be aquatic specialists with surprising ecological disparity, including subaqueous foraging behavior in *Spinosaurus* and *Baryonyx,* and non-diving habits in *Suchomimus*. Adaptation to aquatic environments appeared in spinosaurids during the Early

Cretaceous, following their divergence from other tetanuran theropods during the Early Jurassic[17].

Main text

Secondary adaptations to aquatic lifestyles, such as wading behavior (shoreline specialist and/or only partially submerged habit), subaqueous foraging (fully submerged behavior), and deep diving, evolved multiple times in every major amniote group[1,2]. Aquatic habits are widespread among extant birds, ranging from subaqueous foragers to waders. Moreover, water-related ecologies have deep evolutionary roots on the avian stem lineage, occurring in some of the earliest (i.e., Early Cretaceous) ornithuromorphs[18,19]. Therefore, the scarcity of evidence for aquatic adaptation in non-avian dinosaurs, which comprise the deep evolutionary stem lineage of birds, is striking.

Non-avian dinosaurs are generally hypothesized to have been restricted to terrestrial environments, with only a few proposed exceptions. Suggestions as to why dinosaurs did not evolve aquatic adaptations as frequently as other amniotes include constraints imposed by the musculoskeletal anatomy of the pelvis, hind limb, and tail[20]. However, the discovery of a new skeleton of the predatory dinosaur *Spinosaurus aegyptiacus* has challenged this long-held narrative[9,11]: the conical dentition, retracted nostrils, shortened hindlimbs, paddle-like feet, and fin-like tail, together with more ambiguous evidence from isotopic analyses[21,22] are consistent with an aquatic lifestyle. This has sparked a heated debate regarding the degree of ecological specialization in *Spinosaurus*, which has been described as actively pursuing prey in waters[11], with alternative proposals suggesting a more terrestrial or “wader-heron” model based on anatomical observations and 3D digital models[e.g.12,13,23]. Aquatic habits have also been suggested for a handful of other dinosaurs based on gut contents (other spinosaurids[24], and ornithomimosaurs[6,8]) or anatomical proxies (halszkaraptorine dromaeosaurids[10], compsognathids[5], and various ornithischians[3,4,7]), but remain ambiguous and controversial. This illustrates the inherent challenges of reconstructing ecomorphological relationships in vertebrates[25] and the resulting difficulties in inferring ecological traits in extinct species.

Adaptation to aquatic habits, such as subaqueous foraging or deep diving, constitutes a major evolutionary transition, often culminating into fundamental transformation of the body plan[25]. Nevertheless, even in groups that exhibit a high degree of aquatic specialization, such as cetaceans and many marine reptiles, this transformation occurred gradually over millions or tens of millions of years. Some extant species, and the early fossil members of even the most specialized aquatic groups, can show relatively subtle skeletal changes[14,15,16,26,27]. As such, many aquatic taxa possess few anatomical indicators of water-related ecology, and instead share numerous traits with land animals (e.g., *Hippopotamus*, and the earliest cetaceans[14,15,26,27]). It is therefore plausible that dinosaurs currently considered to have been terrestrial based on anatomical proxies and phylogenetic bracketing might instead represent the early stages of an evolutionary transition towards more specialized aquatic ecologies (e.g. early cetaceans), or amphibious animals (e.g., *Hippopotamus* and *Tapirus*) that evolved relatively limited anatomical transformations despite spending much of their lives in water.

Because of the difficulty of inferring aquatic habits from skeletal morphology alone, proxies that reveal ecological adaptations in extinct taxa are required. Osteohistological features such as variation in bone density provide one such possibility. Osteosclerosis occurs widely as an adaptation to aquatic life in extant amniotes[26,27,28,29], and has been used to infer aquatic ecologies in extinct tetrapods such as crocodyliforms, avialans, marine reptiles, and cetaceans [15,26,27].

Osteosclerosis involves additional deposition of bone mass per volumetric unit leading to the presence of a thick bone cortex with dense trabecular networks infilling the medullary cavity[2,26,27,28,29]. This results in increased body density, facilitating buoyancy control during subaqueous immersion related to either submerged aquatic foraging (e.g., in underwater pursuit divers), concealment, or refuge[14,15,16,26,27,28,29]. Although previously used for paleoecological inference, bone density has generally been used on single-clade-specific studies[e.g.30], and a phylogenetically broad test is required to validate the use of bone compactness as a proxy for aquatic adaptation in deep time, including in species outside of the extant crown clades such as non-avian dinosaurs.

We conduct phylogenetic comparative analyses of bone density data in a broad sample of amniotes, and use our findings to assess the extent of aquatic adaptations in non-avian dinosaurs. Our analyses provide evidence that one clade of dinosaurs, Spinosauridae, was ecologically adapted to life in water, representing the first known aquatic radiation among non-avian dinosaurs.

We quantify bone density in the femoral diaphysis and proximal region of dorsal ribs of 206 and 174 extant and extinct amniotes, respectively ($n_{\text{total observations}}$=380 with n=83 overlapping taxa between the two datasets; see Supplementary Dataset and Supplementary Table 1). Our dataset includes novel osteohistological data for non-avian dinosaurs (n_{femur}=36 and n_{rib}=12) and Mesozoic stem-avialans (n_{femur} =7) (see materials and methods, the Supplementary Dataset for the list of taxa and bone density values used in this study, Supplementary Table 2 for a list of spinosaurids and their investigated skeletal elements, and Extended Data Figures 1-7 for visualization of novel data used in this study).

We compared alternative explanations of variation in bone density using corrected Akaike information criterion (AICc)-based model comparison of phylogenetic multiple regressions[31], and also evaluated the influence of allometry using the maximum diameter of the femoral diaphysis and proximal region of the dorsal ribs as a size proxy. As ecological adaptations are often reflective of the most demanding biomechanical behavior (Liem's paradox[32]: while specialized animals are capable of less functionally demanding behaviors, less specialized taxa often cannot satisfy the requirements linked to functionally challenging habits, such as sustained flight or subaqueous foraging), taxa were scored using two categorical explanatory variables that encode the presence of (a) subaqueous foraging (0, unable; 1, able but infrequent; 2, frequent), and (b) flying (0, unable; 1, non-sustained flight; 2, sustained-flight) in a comprehensive evolutionary framework. We used two independently varying variables because flight and subaqueous foraging evolved at least partly independently of one another as indicated by the occurrence of both flying and flightless diving birds. Our datasets include extant and extinct taxa with undisputed aquatic adaptations, specifically marine mammals (cetaceans and pinnipeds) and non-archosaurian marine reptiles (ichthyosaurs, sauropterygians, including plesiosaurs, and mosasaurs), and aquatic archosaurs such as metriorhynchids, living crocodilians, and various clades of subaqueous foraging birds (penguins, auks, loons, grebes, and cormorants), in addition to extant and extinct terrestrial and flying archosaurs, lepidosaurs, and mammals (see Supplementary Dataset).

The best linear model is 'bone compactness ~ subaqueous foraging' (state 2: frequent subaqueous foraging) in both datasets (AICc_weight = 0.673 (femur) and 0.638 (rib); Table 1, Supplementary Tables 3-4). This indicates that frequent subaqueous foraging is associated with increased femoral and rib density across amniotes ($p<0.001$), a relationship that exhibits a strong phylogenetic signal (median $\lambda = 0.97$ (femur) and 0.969 (rib)). Infrequent subaqueous foraging and wading behavior are not significantly associated with variation in bone density (Table 1, Supplementary Tables 3-4), consistent with the observation that wading birds that feed in water but rarely submerge (e.g. herons, pelicans, gulls, flamingoes, some ducks) have similar compactness to non-aquatic taxa.

Models that include flight or shaft diameter as additional covariates receive less support from AICc (Table 1, Supplementary Tables 3-4). This indicates that evidence for an amniote-wide common allometry in bone density, or for association of flight with decreased skeletal density, is weak, and that those effects are secondary to that of aquatic adaptation (see Table 1, Supplementary Tables 3-4, Extended Data Figures 8-9). Nevertheless, negative allometry in bone compactness (reduction of bone density with size increase) is found in flying taxa when analyzed separately (volant extant birds, Cretaceous enantiornithines, pterosaurs; Table 1, Supplementary Tables 3-4). This shows the importance of skeletal weight reduction in association with or preceding the origin of active flight[33,34]: postcranial bones of predatory dinosaurs typically show an open medullary cavity, a trait inherited by birds (see Figure 1, Extended Data Figures 1-9)[14,34]. Large-bodied terrestrial amniotes have relatively high femoral compactness related to graviportality: trabeculae invade the medullary cavity to support increased weight in graviportal mammals[15,27,35,36] and sauropod dinosaurs (Figure 1, Extended Data Figures 1-7 and Supplementary Tables 5-6). Deep diving animals, such as ichthyosaurs, mosasaurs, living cetaceans and seals, are characterized by lower bone density when compared to shallow-water subaqueous foragers: the compact bone cortex of deep divers is replaced by cancellous bone characterized by extensive trabeculae and vascularization[2,27] (Figure 1, Extended Data Figure 1-7, and Supplementary Tables 5-6), hypothesized as counteracting compression in deep waters and increases in metabolism[1,2]. High bone density is therefore an excellent indicator for the initial stages of aquatic adaptation, but poorly distinguishes between wading, deep diving, and terrestrial habits. These limitations can be overcome using anatomical observations because deep diving show other transformations of the body plan, such as presence of fins and flippers. Graviportal animals can be distinguished from aquatic species by the presence of columnar limbs, an anatomical trait which is generally missing among subaqueous foragers. Furthermore, graviportality does not affect rib compactness (see Supplemental dataset, and Extended Data Figures 1-7). These analyses therefore demonstrate that bone density is a powerful proxy of shallow subaqueous foraging across amniotes.

We used this relationship to establish quantitative predictions of subaqueous foraging in a range of non-avian dinosaurs, including groups that were previously suggested to be linked to water[4,6,8,9,10,11], using phylogenetically flexible discriminant analyses with all amniotes in our sample (see materials and methods). We repeated analyses across 100 informal supertrees with varying branch lengths to account for stratigraphic uncertainty. The informal consensus trees include a novel phylogenetic analysis of Tetanurae modified from recently published datasets[17,37], including new observations of the *Spinosaurus* neotype (Figures 1, 2, 3, Supplementary Figure 1; see Supplementary Materials). Our analyses include novel osteohistological data for the spinosaurids *Baryonyx*[24], *Suchomimus*[9,38], and *Spinosaurus*[9,11], as well as other tetanuran theropods (see Supplementary Materials for ontogenetic assessments of these taxa and other carnosaurs analyzed in this study; Figure 1, Extended Figure 10, Supplementary Figures 2,3).

The correct classification rates of our phylogenetically flexible discriminant analyses ranges are 84-85% (femora) and 83-84% (ribs) (Figure 2,3; see Supplementary Materials, Supplementary Tables 7–10). This increases to 90% in both datasets when excluding graviportal and deep diving taxa (Figure 2,3; see Supplementary Tables 7–10). Contrary to previous hypotheses, our analyses indicate that Spinosauridae is the only clade of non-avian dinosaurs with unambiguous evidence of subaqueous foraging. Within Spinosauridae, disparate ecomorphologies were found. *Spinosaurus* (median probability for subaqueous foraging = 100% (femur) and 95% (rib)) and *Baryonyx* (= 98% (femur) and 96% (rib)) were predicted as subaqueous foragers. In contrast, *Suchomimus* was found as non-subaqueous-forager (= 31% (femur)), similar to other terrestrial non-avian dinosaurs (Figures 1–3, Extended Data Figure 10, Supplementary Tables 7–10). Considering the similar body size between the skeletally mature specimen of *Suchomimus* (G51) and the neotypic skeletally immature individual of *Spinosaurus*, and that our analytical approach accounts for size variation, these results can be confidently attributed to ecological adaptations, rather than the influence of allometry. This is also supported by the presence of open medullary cavities in postcranial elements of other large bodied, bipedal predatory dinosaurs such as femora of *Tyrannosaurus*, *Tyrannotitan*, *Torvosaurus*, and a large carcharodontosaurid rib, contrasting with the osteosclerotic bones of *Baryonyx* and *Spinosaurus* (Figure 1, Extended Data Figures 1-7,10),

All other investigated non-avian dinosaur clades (ornithomimosaurs[6,8], halszkaraptorine dromaeosaurids[10], and ornithopods[3,4,7]), also show open medullary cavities and a weak or absent probability of subaqueous foraging (see Supplementary Tables 7-10). In contrast, the inference of subaqueous foraging in some spinosaurids is especially convincing because osteosclerosis is observed across multiple skeletal elements in both the holotype of *Baryonyx* (dorsal ribs, scapula, pubis, ischium, femur, and fibula) and the neotype of *Spinosaurus* (dorsal ribs, dorsal and caudal neural spines, femur, tibia, fibula, and manual phalanx) (Figure 1, Extended Data

Figure 10, and Supplementary Figures 2,3), rendering previous biomechanical models inaccurate[12].

Phylogenetic optimization of bone density and the presence of osteosclerosis tentatively suggests that subaqueous foraging, is ancestral for Spinosauridae (Figure 2c, Extended Data Figures 8,9) and that the absence of osteosclerosis in *Suchomimus* results from secondary loss rather than primitive absence. The absence of osteosclerosis does not rule out a dependency on aquatic habitats for predation in *Suchomimus*: anatomical traits are consistent with a largely piscivorous diet, including an elongate snout and conical dentition. One possibility is that *Suchomimus* was a wading predator hunting from riverbanks, as previously hypothesised for other spinosaurids[12,13,24,38,39,40]. Different ecological adaptations (subaqueous foraging and non-diving habits) are recovered between the anatomically-similar sister taxa *Baryonyx* and *Suchomimus*, a pattern not unique to Baryonychinae and also observed in other amniote groups, including Phalacrocoracidae (this study) and Hippopotamoidea[35]. It is possible that environmental factors, such as a sparser distribution of aquatic settings (rivers, lakes)[41] led to less specialized foraging in *Suchomimus*.

Our results suggest the first anatomical adaptations for an aquatic lifestyle appeared in concert with osteosclerosis in spinosaurids. Craniofacial modifications preceded postcranial alterations (Figure 1). The premaxilla gradually became more elongate, while the external naris diminished in size and migrated posterodorsally[9,11], a pattern comparable to the telescoping process observed in the skull evolution of cetaceans[14] and ichthyosaurs[16]. The braincase rotated ventrally and the dentition became conical. These modifications are functionally advantageous for a diet based on slippery, aquatic prey[42]. Postcranial modifications linked to subaqueous foraging, such as elongation of the caudal neural spines to form a propulsive structure, have been reported for *Spinosaurus*[9,11] and the baryonychine *Riparovenator*[40]. Additionally, spinosaurids are characterized by the lowest degree of postcranial pneumatization (restricted to the cervical region and dorsal–sacral neural arches) among large-bodied Cretaceous tetanurans[43], consistent with elevated body density and advantageous for buoyancy control. Although reduction in hind limb length and widening of the pes have only been described in *Spinosaurus*[9,11], many spinosaurids are only known from fragmentary remains (Figure 1), limiting our understanding of their skeletal adaptations. Because of their unique anatomy, spinosaurids may have had ecologies with no modern equivalent, limiting direct autecological interpretations based on modern taxa.

We demonstrate that Spinosauridae, a geographically widespread clade of predatory dinosaurs, was ecomorphologically adapted to life in water, but that aquatic adaptation was otherwise absent among non-avian dinosaurs studied so far. Nonetheless, this finding challenges the hypothesis that non-avian dinosaurs were restricted to terrestrial environments. Spinosaurids were part of the rapid radiation of Tetanurae during the late stages of the Early Jurassic[17]. Increased diversification appeared in concert with morphological innovation and high rates of homoplasy across tetanurans[17]. This ecomorphological radiation may be linked to adaptation to previously under-exploited environments, including multiple independent appearances of aerial capabilities [33]. Our study demonstrates that ecomorphological radiations among non-avian dinosaurs also included the invasion of freshwater ecosystems.

Materials and methods

Osteohistological analyses and assessment of skeletal maturity of spinosaurid specimens

We sampled and investigated postcranial elements of the holotype of *Baryonyx* (NHM R 9951), two individuals of *Suchomimus* (G51, G94), and the neotype of *Spinosaurus* (FSAC-KK 11888) to evaluate their somatic maturity and quantify bone density. The dorsal rib of *Baryonyx* was previously sectioned by Reid[44] and this was here studied for estimation of somatic maturity of the holotype. To quantify bone compactness, the femur of *Baryonyx* was CT scanned at the Natural History Museum, London. Breaks of additional postcranial bones (scapula, pubis, ischium, and fibula) were considered for comparative purposes with the goal of assessing the skeletal extent of osteosclerosis. Skeletal maturity and bone compactness of *Suchomimus* were estimated through sampling and thin sectioning of the femora of the two individuals (briefly described in Ibrahim et al.[9]). A dorsal neural spine, dorsal rib, femur, and fibula were sampled for thin sectioning and inference of ontogenetic stage of the *Spinosaurus* neotype. Moreover, a manual phalanx, caudal neural spines, and tibia of this specimen were also available for bone compactness quantification, because of breaks along the diaphysis. Long bones were cut transversely at the diaphysis, whereas samples of dorsal ribs and the dorsal neural spine of *Spinosaurus* were taken proximally and apically, respectively. The thin sectioning was performed following the protocol by Chinsamy & Rath[45]. The thin sections have a thickness of 50–70 microns and were analyzed with a Leica DM 2500 P petrographic microscope. Photographs of the bone tissue were taken with a ProgRes Cfscan camera. The CT scanned femur of *Baryonyx* was analyzed in VGStudio Max 3.4. Inference of skeletal maturity follows recently proposed nomenclature by Griffin et al.[46]

Phylogenetic analyses

The discovery, description, and completeness of the *Spinosaurus* neotype provides an opportunity to revisit the phylogenetic relationships of spinosaurids. We coded the neotype of *Spinosaurus* in two recent datasets, published by Malafaia et al.[37] and Rauhut and Pol[17], respectively. These two datasets differ in terms of operational taxonomic units (OTUs): whereas Malafaia et al.[37] includes a specimen-level assessment of phylogenetic relationships among spinosaurids, Rauhut and Pol[17] remains the most comprehensive and latest iteration of the original dataset of tetanuran phylogenetic relationships[47]. These two datasets are therefore needed to infer phylogenetic relationships within Spinosauridae and the placement of this clade among tetanurans. The neotype of *Spinosaurus* was coded as a separate OTU in the dataset of Malafaia et al.[37]. Based on the results of this analysis, and given the presence of several apomorphies shared between the *Spinosaurus* neotype and holotype, coding of the neotype specimen based on our anatomical observations was added to the OTU of *Spinosaurus* in the dataset of Rauhut and Pol[17]. The recently described spinosaurine *Vallibonavenatrix*[37] was also added to the dataset published by Rauhut and Pol[17]. We followed the most recent, comprehensive taxonomic and systematic revision of spinosaurid taxa[48,49], therefore excluding *Sigilmassasaurus* and *Oxalaia* (which are regarded as junior synonyms of *Spinosaurus*) from this dataset. Both datasets[17,37] were analyzed under equally weighted parsimony in TNT (Tree analysis using New Technology) v. 1.1[50]. No characters were ordered. We conducted a heuristic search using 1,000 replicates of Wagner trees (with random addition sequence) followed by tree bisection and reconnection (TBR) branch swapping. We calculated decay indices (i.e., Bremer support) and absolute bootstrap frequencies with 10,000 pseudoreplicates to quantify node support.

Bone density

Bone density was used as a proxy for ecological inference. Because different postcranial skeletal elements show contrasting compactness profiles due to allometry during growth[15,27,51,52,53,54], we focused on the femur and dorsal ribs in order to employ a consistent comparative framework;

these skeletal elements have been previously shown to be reliable skeletal element for confident inference of ecological adaptations[e.g.27]. Femoral and dorsal rib cross sections were mainly obtained from the diaphysis and the proximal region, respectively, through thin sectioning, micro-CT scanning, or data mining from the literature (see Supplementary Dataset for the taxa included and the type of data collected). Among dinosaurs, novel data presented in this study include those for the tetanuran theropods *Baryonyx*, *Suchomimus*, *Spinosaurus*, *Megalosaurus*, *Tyrannotitan*, *Eustreptospondylus*, and *Condorraptor* (see supplementary dataset for novel osteohistological data collected for this study). Our femoral dataset includes 206 individuals, representing 200 taxa. All known spinosaurid taxa that preserve the femur are included therein. The discrepancy between the number of individuals and taxa is due to the inclusion of multiple individuals of the following marine reptiles: *Ichthyosaurus*, *Nothosaurus*, *Simosaurus*, Placodontia, and *Champsosaurus*. Our dorsal rib dataset includes 174 taxa. The taxonomic overlap between the two datasets (femur and dorsal rib) is equal to 83 taxa, including *Baryonyx* and *Spinosaurus*.

Archosaurs are represented in the dataset by extant crocodilians, pterosaurs, non-avian dinosaurs, and birds, the latter including both Mesozoic and extant taxa (see supplementary dataset for included taxa). Stem and crown marine mammals, such as cetaceans and seals, and extinct marine reptiles (ichthyosaurs, sauropterygians, and mosasaurs) were included to infer thresholds of bone compactness related to aquatic lifestyle and to calibrate the discriminant analyses aimed to infer ecological adaptations in extinct taxa.

Cross (CT scan) and thin sections of femoral diaphysis and dorsal rib were transformed into black and white figures (black for bone and white for medullary cavity, vascularization, and background) in Adobe Photoshop, following previous protocols[e.g.15,27,36,54]. Images were then imported into the freely available software Bone Profiler[55] (http://134.158.74.46/BoneProfileR/) to quantify bone compactness. In cases where portions of the femoral diaphysis and rib cross sections were missing or deformed, retro-deformation and reconstruction were applied following the methods presented by De Ricqlès et al.[56], in order to minimize the occurrence of taphonomic artifacts in the data. Because the femoral diaphysis of *Baryonyx* is eroded and crushed, the cross section for this taxon was taken from a more intact and better-preserved region closer to the distal portion of the femur (see Supplementary Figure 3). Because the diaphysis of the femur coincides with the highest degree of bone compactness among amniotes[15,27], the quantified degree of osteosclerosis in *Baryonyx* should be regarded as underestimated.

Informal consensus tree

To address the statistical non-independence of interspecific comparisons, we assembled two informal amniote-wide supertrees (see Extended Data Figures 8, 9) using Mesquite v. 3.40[57] on the basis of Upham et al.[58] for Mammalia, Simoes et al.[59] for the backbone of Diapsida, Nesbitt et al.[60] for Archosauria, Langer et al.[61] for Dinosauria, this study for Tetanurae, Brusatte et al.[62] for Coelurosauria, and Prum et al.[63] for Neoaves. We calibrated the resulting tree using the function 'bin_timePaleoPhy' from the R package Paleotree[64], scaling the branches based on genus-level stratigraphic ranges sourced from the Paleobiology Database (www.paleodb.org) and from the specialized literature (see supplementary dataset). We generated 100 trees using this method, which randomly draws first appearance dates and last appearance dates for each taxon from within their stratigraphic ranges. To avoid zero-length branches we set a minimum branch length of one million year.

Ecological inference

We scored extant and extinct taxa whose ecomorphological attributes could confidently be inferred (e.g., ichthyosaurs as being able to dive frequently and not being able to fly) as being able to engage in (a) subaqueous-foraging (0, unable; 1, able but infrequent, e.g., rails; 2, frequent), and (b) flying (0, unable; 1, non-sustained flight, e.g., tinamous, galliforms, *Xenicus longipes*; 2, sustained flight). Extinct taxa with ambiguous ecological inference were scored as unknown. Therefore, the autecology of each taxon is represented by two numerical categories with three states each. Previous studies applied different categorizations for the characterization of aquatic lifestyles among extant and extinct taxa: "aquatic" and "semiaquatic" were used *contra* "subaqueous foraging" applied in this study. Our ecomorphological attribution is focused on a specific behavior linked to an ecology, rather than a categorization of its entirety. We find our categorization to be more accurate: for example, previous studies coded penguins and cetaceans as aquatic, while crocodilians were stated as semiaquatic. While penguins and crocodilians are still ecologically dependent on terrestrial environments (e.g. for laying eggs), cetaceans are completely independent from land. On the other hand, all these clades engage in subaqueous foraging. Therefore, our ecological attribution is in agreement with previously applied ecological categories, but do not exclude dependency to terrestrial environments to satisfy autecological requirements, such as reproductive behavior.

Maximum femoral diaphyseal and dorsal rib cross section diameter was used as a proxy for body size, in order to allow the inclusion of fragmentary fossil remains and to optimize the inclusion of taxa with significantly different body plans. As femoral and rib diameter values range from those of small-bodied modern passerines (*Xenicus*) to very large non-avian theropods (*Tyrannosaurus* and *Spinosaurus*), maximum femoral diameter was log10-transformed.

Bone compactness, femoral midshaft diameter, and different combinations of these ecological traits were used to build 12 linear models upon which phylogenetically-gnostic regressions (PGLS) were performed using the R core function gls (R Core Team). The Akaike information criterion (AICc) was used to establish which linear model best explains variation in bone compactness. Pagel's lambda values were simultaneously calculated to evaluate the degree of phylogenetic signal in each of the relationships. These analyses were run over the 100 trees generated for all amniotes to evaluate the effects of stratigraphic uncertainty on our analyses; the results were summarized thereafter.

To establish explicit predictions of ecology in extinct taxa, we built a phylogenetically-flexible discriminant analysis (pfDA) using the function phylo.fda (Schmitz & Motani[65] sourced from https://github.com/lschmitz/phylo.fda) and following the protocol described in Schmitz and Motani[65], including our two main metric variables (maximum diameter and bone density) and the ecological classifiers from the linear model with the best fit (lowest AICc score). The model in which bone density is explained by subaqueous-foraging exhibits the best fit (see Results, Table 1, and Supplementary Tables 3, 4); therefore, we scored all taxa to a more inclusive category depending on whether or not they are frequent subaqueous-foragers (Supplementary Tables 3, 4). Because our overarching goal is to ascertain aquatic proficiency in large, flightless theropod dinosaurs, we also excluded modern birds that are able to both submerge-forage and fly as this functional trade-off is likely to influence their bone histology and introduce a confounding factor in our predictions. A series of taxa for which aquatic lifestyles have been proposed or fragmentary remains cannot allow a confident scoring were scored as 'unknown' and their ecologies were predicted along with the three spinosaurid target taxa (see supplementary dataset). In order to correct for the bias that phylogenetic structure introduces in form to function relationships, phylo.dfa adjusts the phylogeny with the value of phylogenetic signal (Pagel's lambda) which maximizes the log likelihood of the linear fit among variables[65,66]. Because branch lengths in our phylogenies exhibit some degree of uncertainty, we repeated this analysis with the 100 different trees we generated and summarized the accuracy and predictions across all iterations. This was repeated for both the femora and rib datasets and again excluding graviportals and deep diving taxa in both datasets (see Supplementary Tables 5 & 6 for taxa classified with these ecological traits). In each iteration, the variables (bone compactness and diameter) from the training set of taxa with known ecologies, together with the phylogenetic structure of data, are used to generate the discriminant functions, which are subsequently used to predict the ecologies in extinct taxa with unknown ecologies (including spinosaurids). A said species is predicted as subaqueous forager if the posterior probability is 50% or more, because our inference has only two possible outcomes: subaqueous forager or non-subaqueous forager. We summarised our results by providing the median value of those 100 posterior probabilities and the number of times a particular taxon is predicted as subaqueous forager (median probability of 50% or more). This gives us two proxies of the likelihood of each taxon to be an actual subaqueous forager. For instance, a taxon could be predicted 100 times as subaqueous forager with a median probability of 51% which means the evidence for this extinct species to be an actual subaqueous forager is very weak and this inference has to be considered very unlikely. Median probabilities need to be within the range of 80-100% to be considered as strong evidence of subaqueous forager. Additionally, we considered the presence of an open medullary cavity or osteosclerosis to support our inferences.

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ACKNOWLEDGMENTS We acknowledge P. Barrett and S. Chapman for access to the holotype of *Baryonyx* at the Natural History Museum, London, J. Scannella for access to thin sections of *Tyrannosaurus* housed at the Museum of the Rockies, and M. Fox and J. Gauthier for access to *Poposaurus* at the Yale Peabody Museum. The Moroccan Ministry of Energy, Mines, and the Environment is thanked for providing fieldwork permits to N. I. Members of the 2015-2019 expedition seasons are thanked for their assistance in the field. We thank J. Choiniere, three anonymous reviewers, and the editor for constructive comments that improved the manuscript. Funding: funding was received from the European Union's Horizon 2020 research and innovation program 2014–2018, starting grant (R. B. J. B., 677774); a National Geographic Society grant (N. I., CP-143R-170); a National Geographic Emerging Explorer Grant (N. I.); the Jurassic Foundation (M. F.); the Paleontological Society grant (M. F.), as well as the Explorers Club (grant awarded to M. F.). The Lokschuppen (Rosenheim, Germany) and J. Pfauntsch provided additional financial support for fieldwork led by N. I. in Morocco.

Author contributions: Conceptualization: M.F.; Data collection and curation: all authors; Data quantification: M.F.; Methodology: M.F., G.N., and R.B.; Formal analysis: M.F., G.N., and R.B.; Resources: all authors; Writing – original draft preparation: M.F.; Writing – review and editing: all authors; Visualization: M.F. and G.N.; Supervision: M.F., G.N., R. B., and N.I.; Funding acquisition: M.F., R. B., and N.I.

Competing interests: The authors declare no competing interests.

Data availability: All data described and used in this manuscript are freely available. The measurements and provenance information for fossil specimens can be found in the Extended Data Figures and in the Supplementary Dataset. The phylogenetic datasets and the R coding are available as Supplementary Material. The CT scan datasets collected for this study are available in Morphosource (specific links for each taxon can be found in the Supplementary Dataset).

Figures and captions

Femora

Model	AICc	AIC weights	R2	Lambda	Variable	Coefficient	Std.Error	t value	p value
compactness ~ subaqueous foraging	-278.27	0.673	0.172	0.919	**Intercept**	0.63	0.108	5.8585	0.00
					subaqueous foraging	0.164	0.023	7.0225	0.00
compactness ~ subaqueous foraging + sustained flight	-275.35	0.156	0.168	0.915	**Intercept**	0.6315	0.105	6.0075	0.00
					subaqueous foraging	0.163	0.023	7.039	0.00
					sustained flight	-0.056	0.026	-2.151	0.0326
compactness ~ subaqueous foraging + flight	-275.33	0.154	0.168	0.912	**Intercept**	0.633	0.104	6.089	0.00
					subaqueous foraging	0.162	0.023	6.945	0.00
					flight	-0.057	0.027	-2.41	0.03

Dorsal ribs

Model	AICc	AIC weights	R2.	lambda	Variable	Coefficient	Std.Error	t-value	p value
compactness ~ subaqueous foraging	-164.167	0.638	0.108	0.969	**Intercept**	0.648	0.061	10.652	0
					subaqueous foraging	0.154	0.033	4.7195	0
compactness ~ subaqueous foraging + sustained flight	-161.538	0.171	0.104	0.97	**Intercept**	0.651	0.06	10.8315	0
					subaqueous foraging	0.152	0.032	4.735	0
					sustained flight	-0.055	0.024	-2.2595	0.02545
compactness ~ subaqueous foraging + flight	-161.421	0.162	0.104	0.968	**Intercept**	0.655	0.06	10.9355	0
					subaqueous foraging	0.148	0.032	4.575	0
					Flight	-0.056	0.025	-2.234	0.0271

Table 1. Phylogenetic regressions comparing explanations of bone compactness as a function of size and ecological traits among femora and dorsal ribs. Explanatory variables are combined in all possible ways in different linear models. Linear models are ordered from best model to worst. Median values from the 100 phylogenies used for the phylogenetic regressions. Models with negligible AIC weights were trimmed down from this Table but can be found in the supplementary information (Supplementary Tables 3-4). These analyses are two-sided and no adjustments were applied for multiple comparisons.

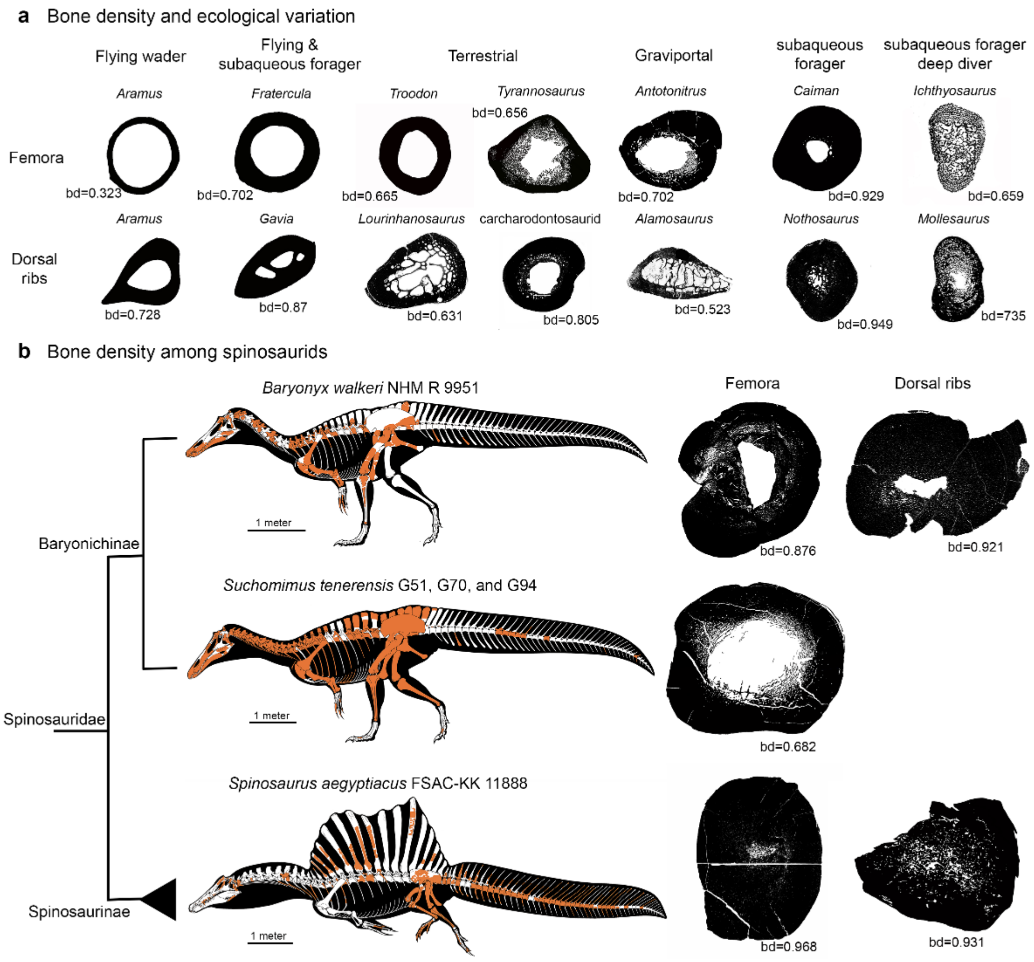


Figure 1 (to be published as ¾ page width, 136 mm). Osteohistology and ecological variation among amniotes, including the analyzed spinosaurid taxa. a) Bipedal, land-dwelling archosaurs, such as theropods show the presence of an open medullary cavity. This condition is furthered in flying archosaurs such as birds. Two osteosclerotic patterns are present among subaqueous foraging animals: (1) increase in thickness of the bone cortex, as observed in crocodilians and penguins, for animals adapted to shallow waters; or (2) substitution of the bony cortex with trabecular networks, usually found in deep divers, e.g., ichthyosaurs, mosasaurs, and cetaceans. Occupation of the medullary cavity by spongiosa is also observed in quadrupedal, graviportal animals, such as sauropods, ornithischians, and large-bodied terrestrial mammals. b) Femur and dorsal rib sections and bone density of the holotype of *Baryonyx*, *Suchomimus*, and the neotype of *Spinosaurus* used for calculation of bone density in this study. Skeletal reconstructions are based on single individuals (holotype of *Baryonyx* and neotype of *Spinosaurus*), exception made for *Suchomimus* (see Supplementary Information for further details); preserved bones are highlighted in orange. The schematic tree is based on the phylogenetic analyses performed in this study (see Supplementary Information for results and discussion of these analyses). Abbreviations: bd=bone density.

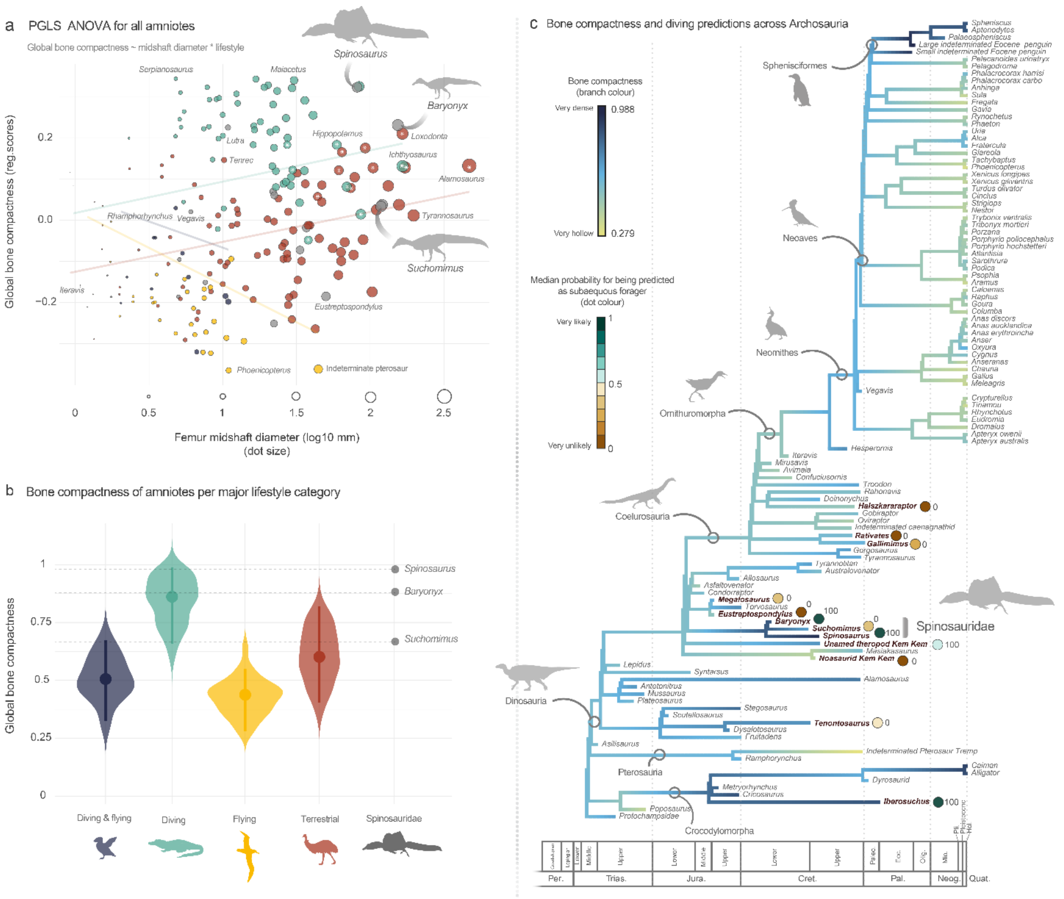


Figure 2 (to be published as ¾ page width, 136 mm). Relationship between midshaft density of femur, diameter and major lifestyle among amniotes including Spinosauridae. a) PGLS linear model (n=206 independent observations, n=200 taxa) of bone density as a function of log10 femur midshaft diameter values for our dataset of amniotes with main lifestyle category as a factor using a randomly draw phylogeny from the 100 phylogenies generated (same topology, variable branch lengths). Solid lines represent linear fits for the four categories. Dashed line represents linear fit for aquatic taxa without deep diving and graviportal taxa (white asterisks inside the dot symbol). b) Violin plots depicting distribution of values of bone density per category. Large dot represents medians, lines are 95% confidence intervals. The values of bone density of the three spinosaurid taxa studied are included. c) Bone density distribution in a time calibrated archosaur consensus tree showing an ancestrally osteosclerotic Spinosauridae and rapid radiation of tetanuran clades during the Early Jurassic (see Extended Figure 8 for bone density distribution across amniotes).

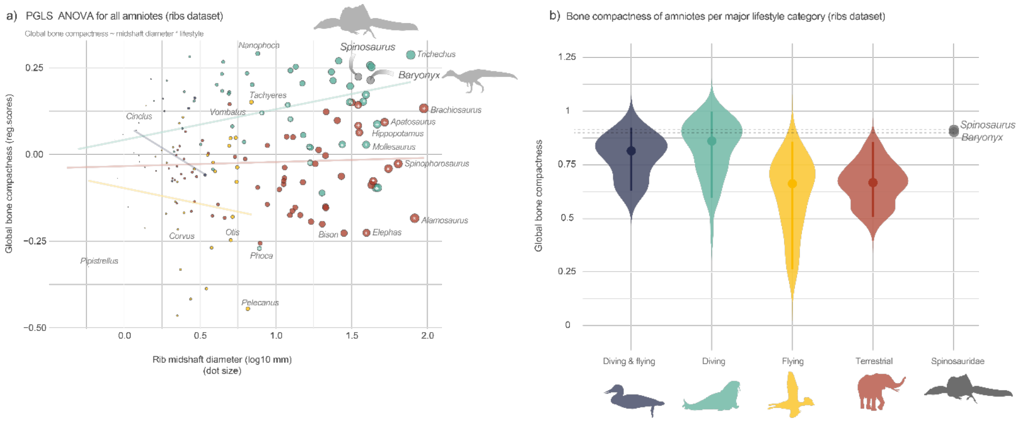
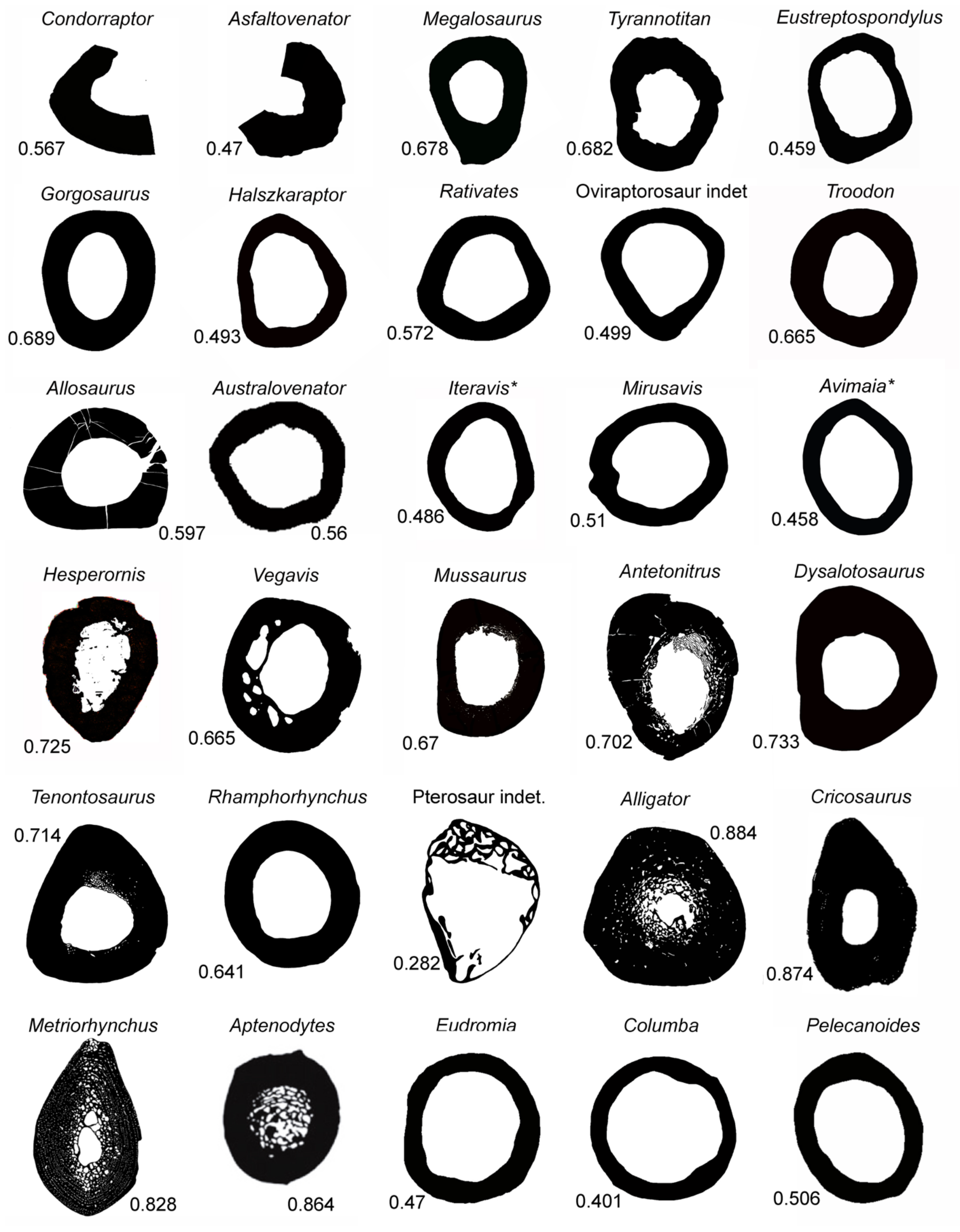
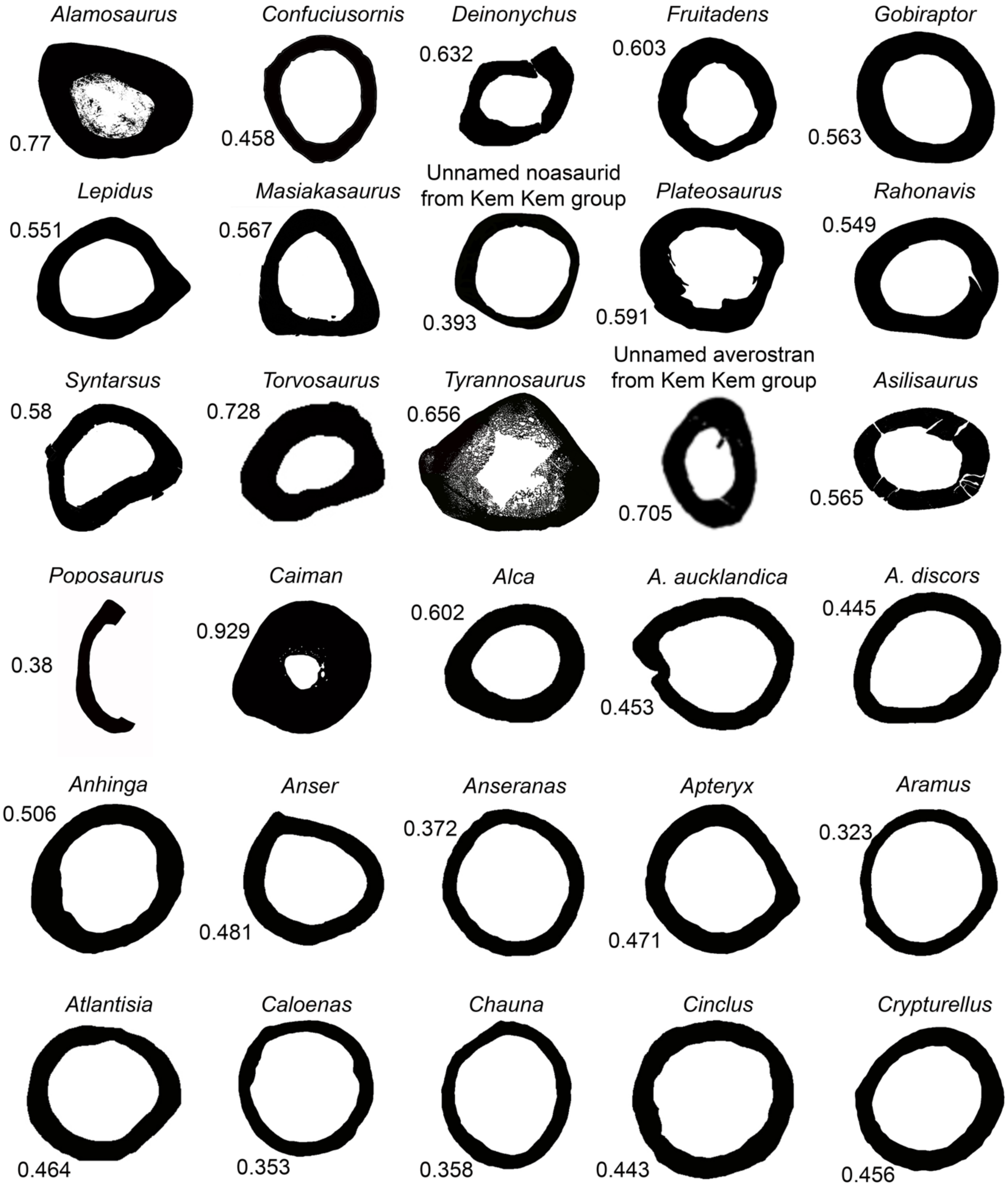


Figure 3 (to be published as ¾ page width, 136 mm). Relationship between dorsal ribs density, diameter and major lifestyle among amniotes including Spinosauridae. a) PGLS linear model (n=174 taxa) of bone density as a function of log10 rib cross section diameter values for our dataset of amniotes with main lifestyle category as a factor using a randomly draw phylogeny from the 100 phylogenies generated (same topology, variable branch lengths). Solid lines represent linear fits for the four categories. Dashed line represents linear fit for aquatic taxa without pelagic and graviportal taxa (white asterisks inside the dot symbol). b) Violin plots depicting distribution of values of bone compactness per category. Large dot represents medians, lines are 95% confidence intervals. The values of bone density of *Baryonyx* and *Spinosaurus* are included (see Extended Figure 9 for bone density distribution across amniotes).

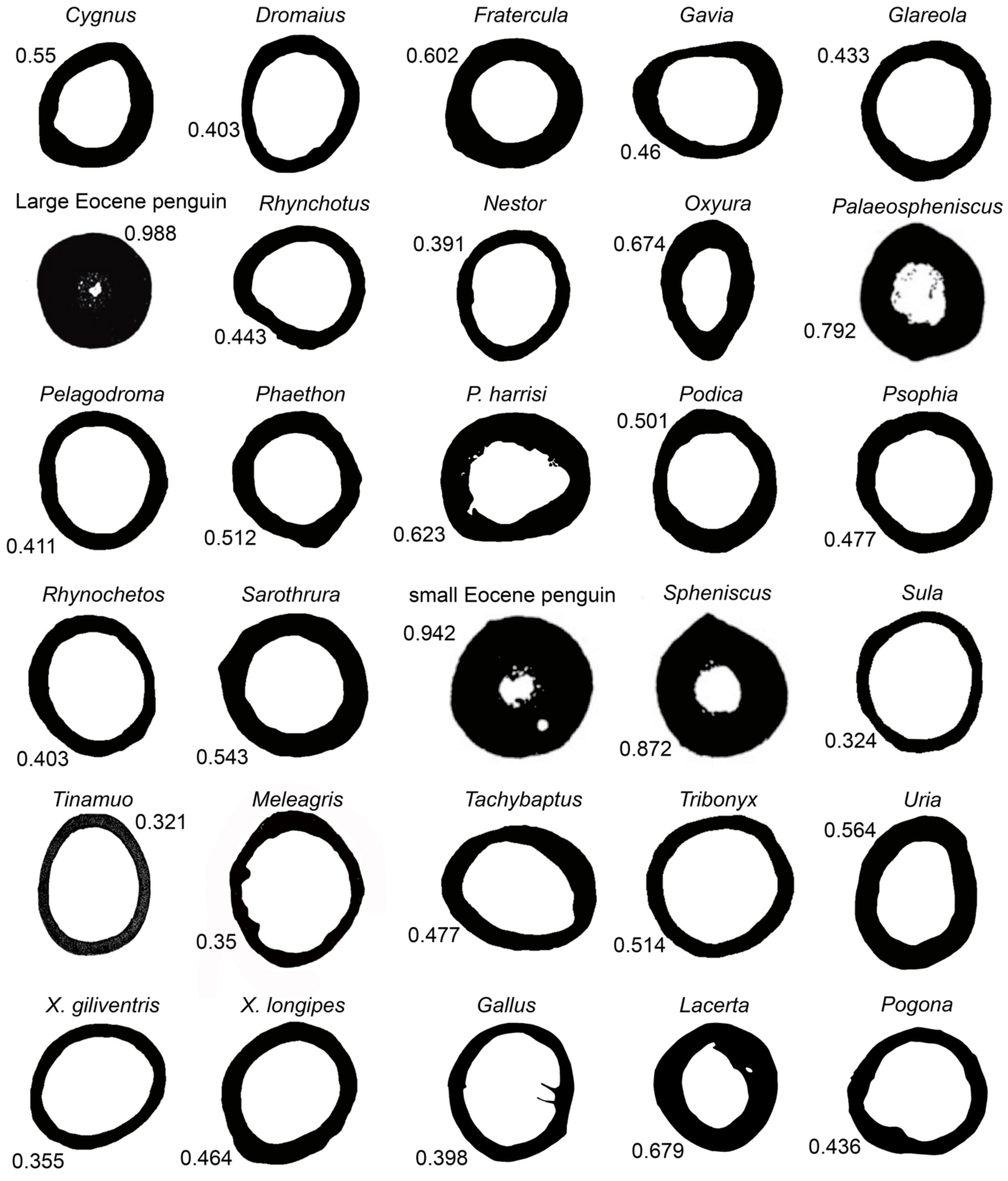
Extended Data Figures



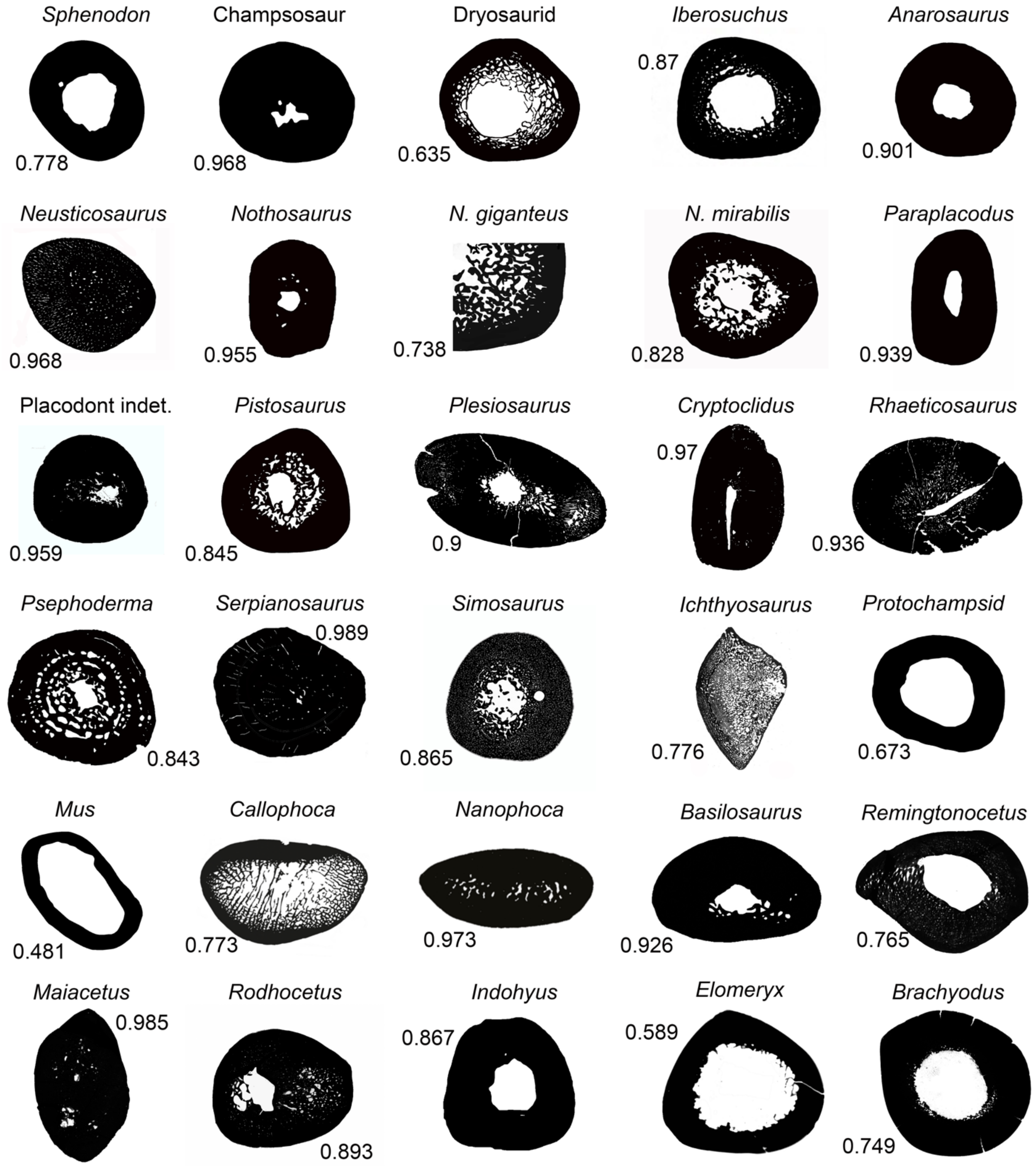
Extended data Figure 1. Comparative array of archosaurian femoral diaphysis included in the dataset. Numerical values represent the bone density quantified for each taxon. Asterisks indicate femoral diaphysis that were retro-deformed before quantification of bone density due to taphonomic deformation and/or fragmentation present in the fossil.



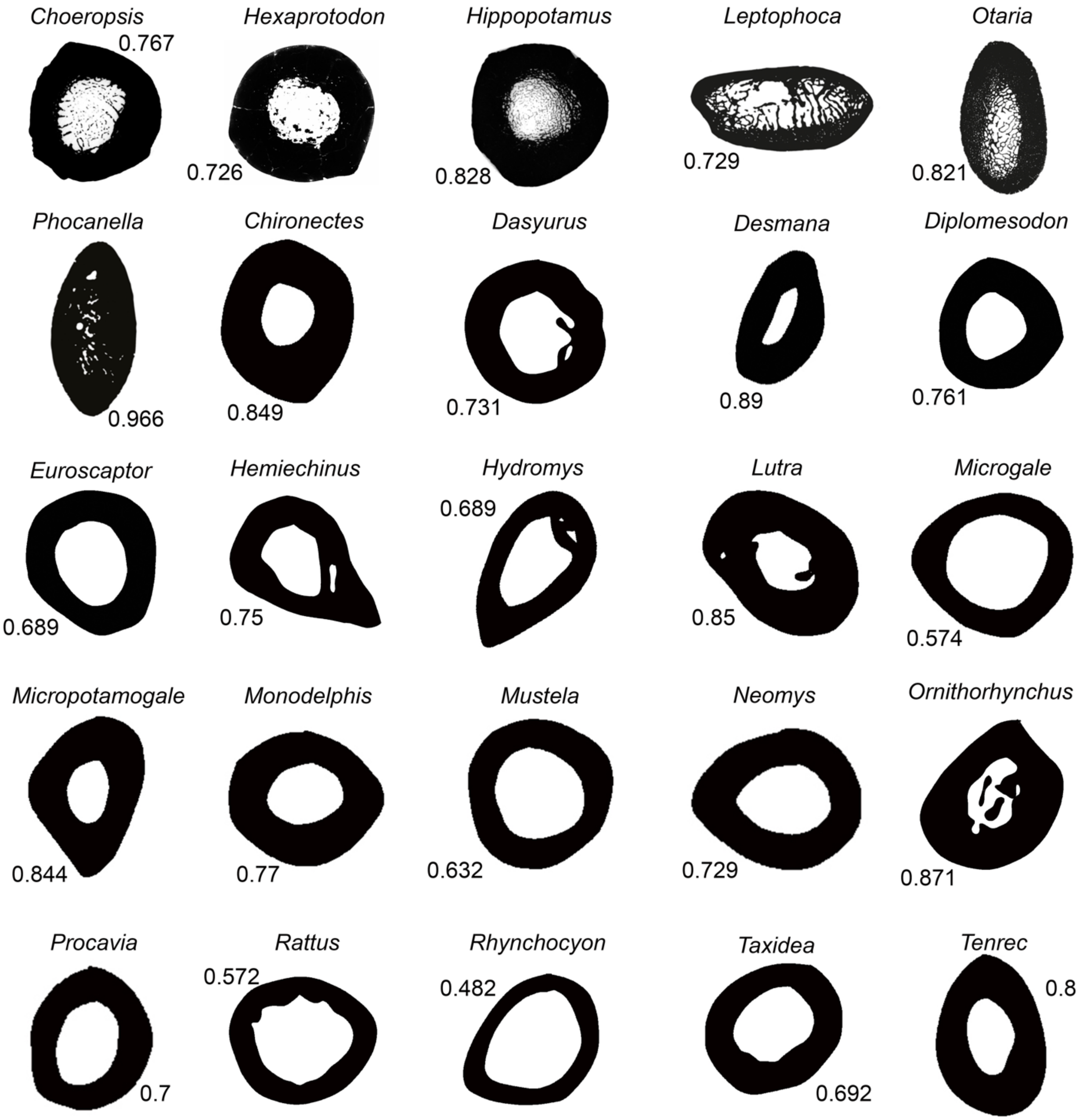
Extended data Figure 2. Comparative array of non-avian and avian femoral diaphysis included in the dataset. Numerical values represent the bone density quantified for each taxon.



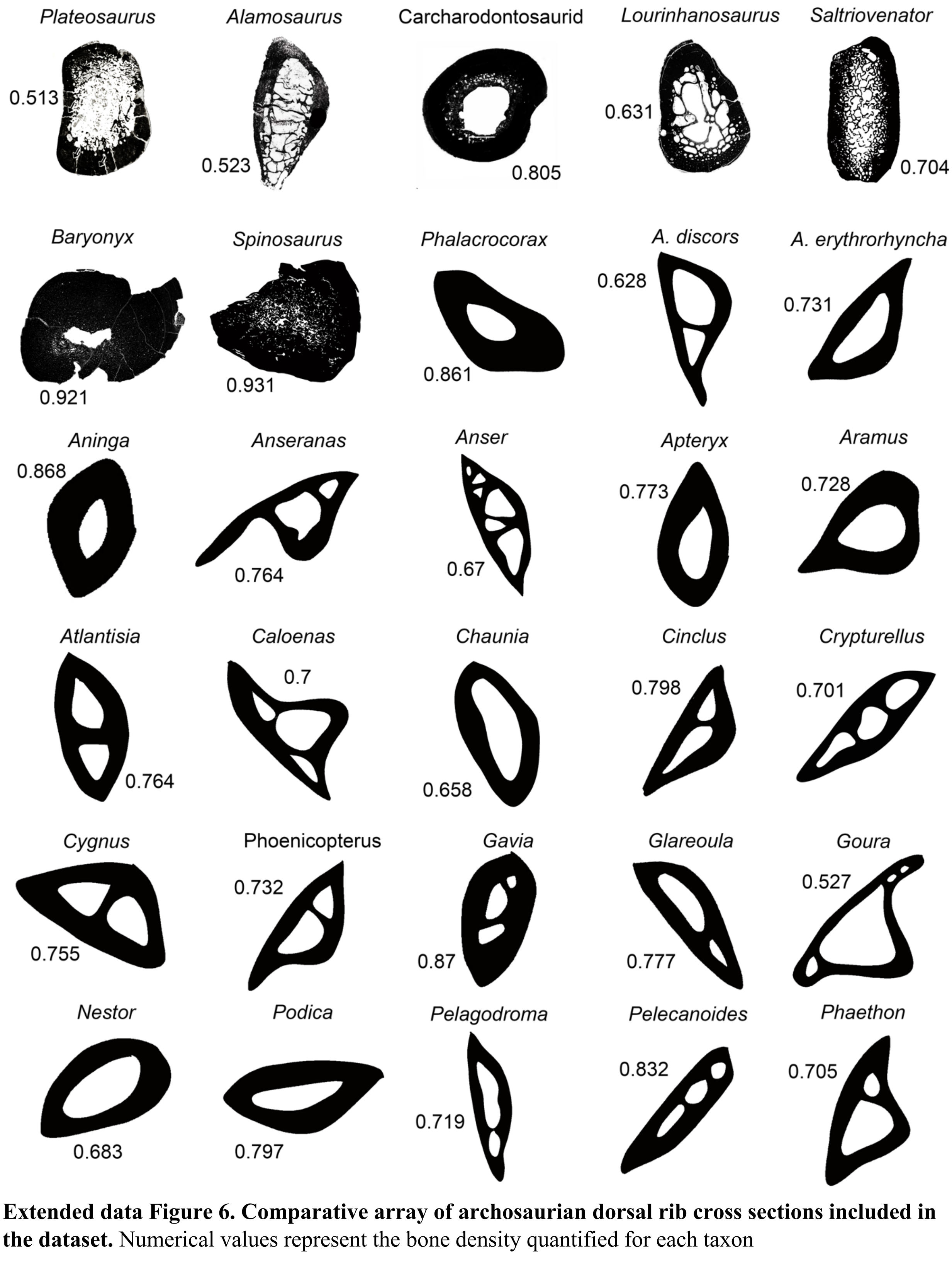
Extended data Figure 3. Comparative array of avian and lepidosaur femoral diaphysis included in the dataset. Numerical values represent the bone density quantified for each taxon



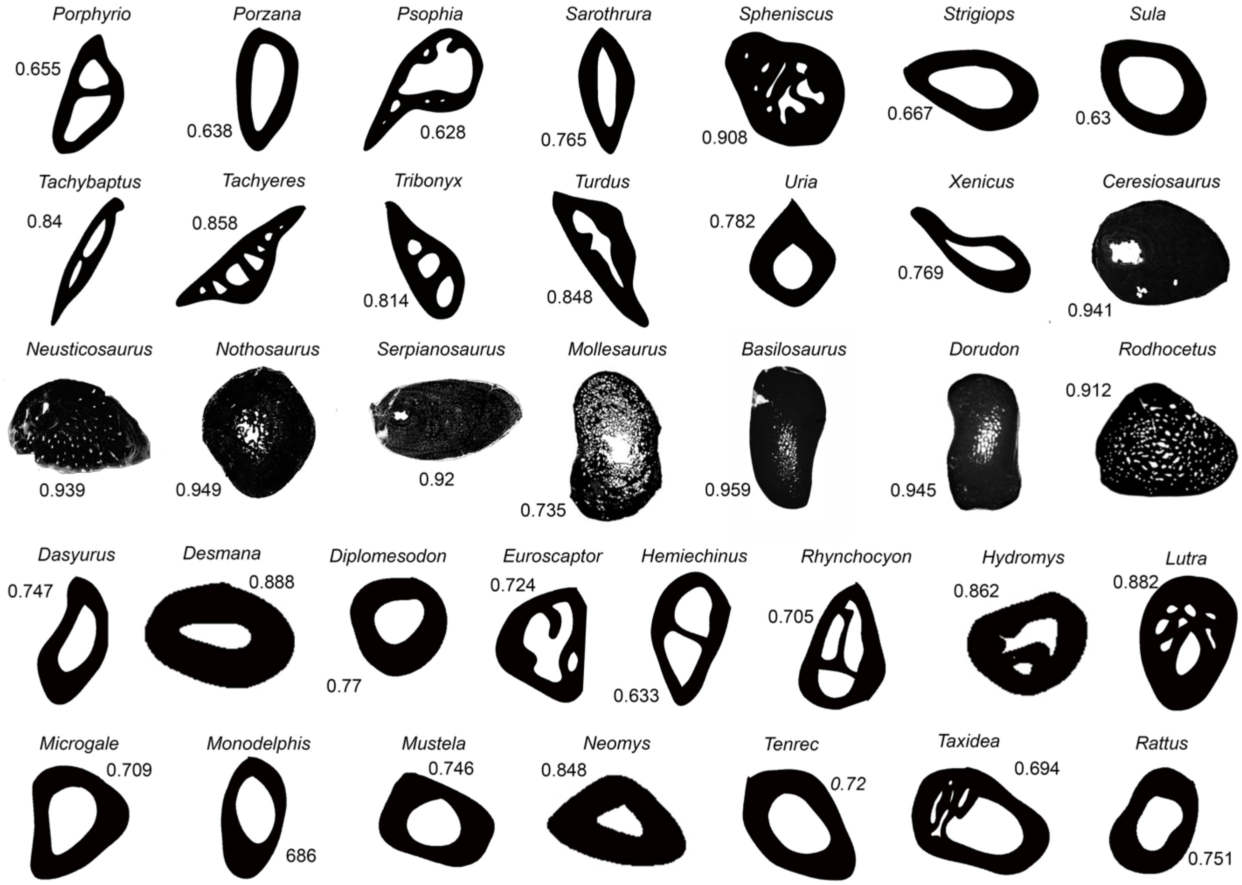
Extended data Figure 4. Comparative array of amniote femoral diaphysis included in the dataset. Numerical values represent the bone density quantified for each taxon



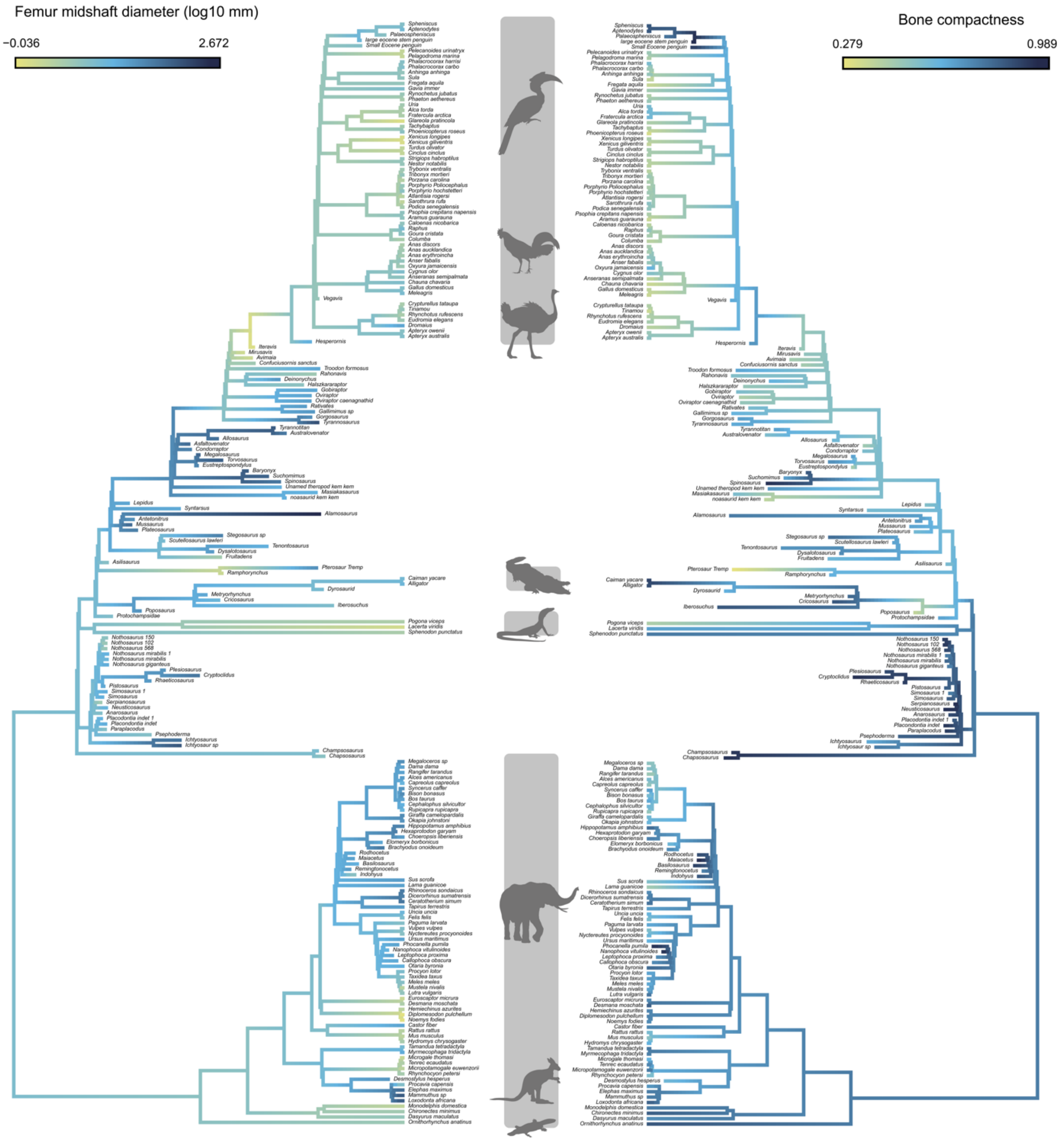
Extended data Figure 5. Comparative array of mammalian femoral diaphysis included in the dataset. Numerical values represent the bone density quantified for each taxon



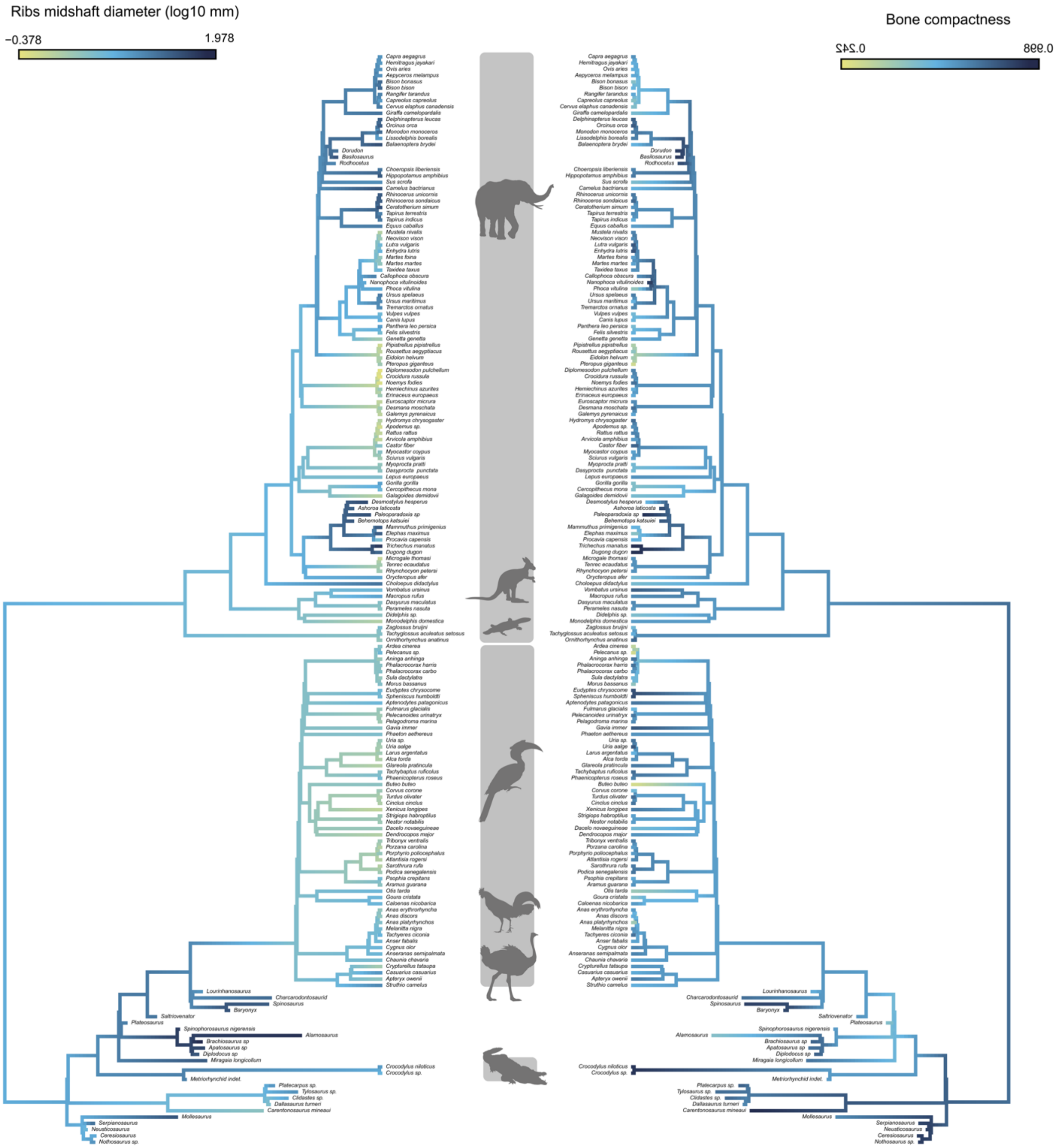
Extended data Figure 6. Comparative array of archosaurian dorsal rib cross sections included in the dataset. Numerical values represent the bone density quantified for each taxon



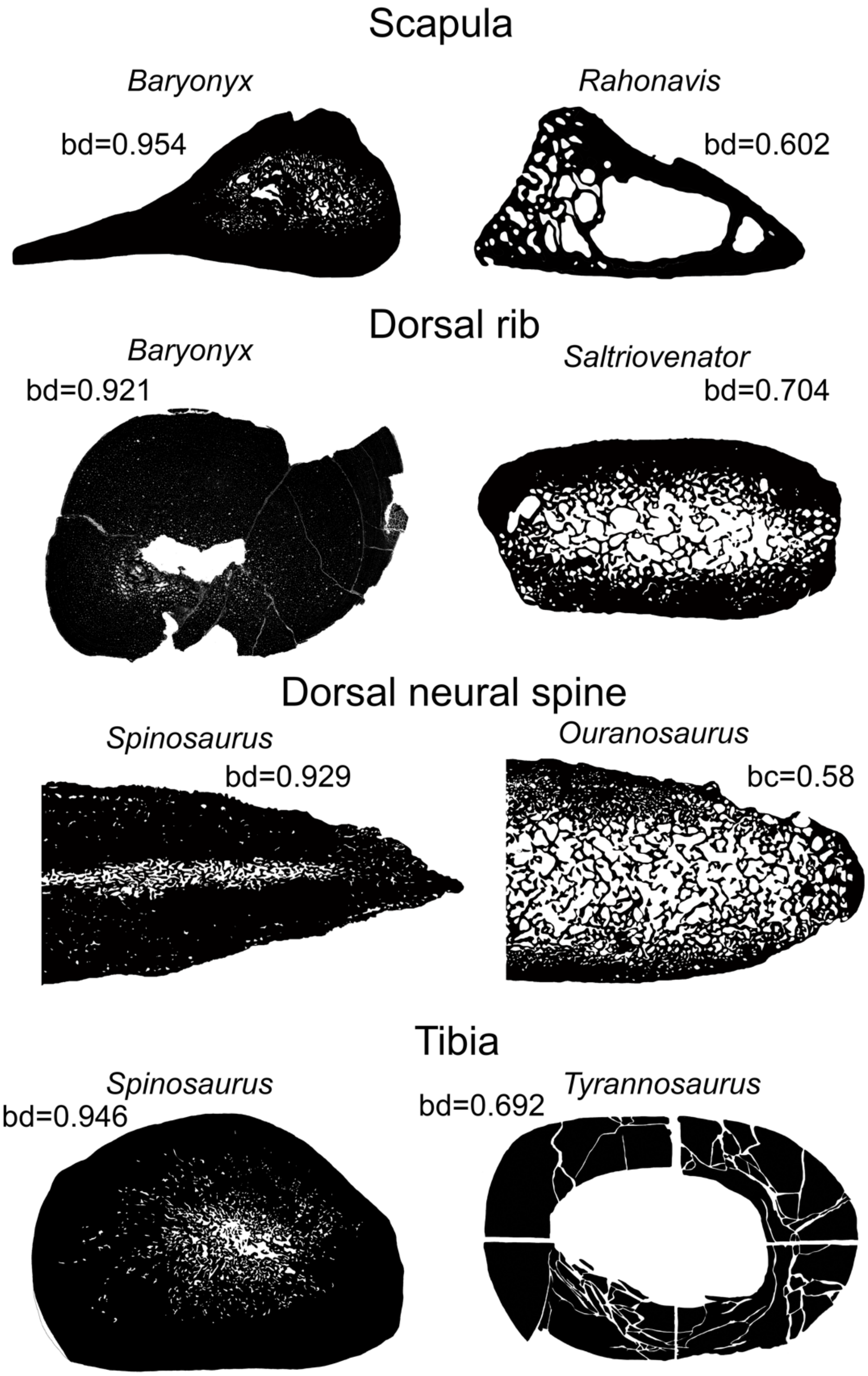
Extended data Figure 7. Comparative array of amniote dorsal rib cross sections included in the dataset. Numerical values represent the bone density quantified for each taxon



Extended Data Figure 8. Bone density and femur diameter phylogenetic distribution plotted on the informal consensus tree used for discriminant analyses representing the phylogenetic relationships of the taxa included in our study.



Extended Data Figure 9. Bone density and dorsal rib diameter phylogenetic distribution plotted on the informal consensus tree used for discriminant analyses representing the phylogenetic relationships of the taxa included in our study.



Extended data Figure 10. Qualitative comparison of bone compactness in selected skeletal elements between osteosclerotic spinosaurids and other non-avian dinosaurs. *Baryonyx* and *Spinosaurus* possess dense, compact bone throughout the postcranial skeleton, namely in the neural spines, ribs, scapula, ilium, pubis, ischium, femur, and fibula. Increased bone density is found in postcranial elements of *Spinosaurus* as well; a reduced medullary cavity is present in the ribs, dorsal and caudal neural spines, manual phalanges, femur, tibia, and fibula. Abbreviations: bd=bone density.