

Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection

Femoral diaphysis and dorsal rib cross sections belonging to 206 and 174 amniote, respectively, were collected through means of microCT scan or thin sectioning (e.g. Spinosaurus, Suchomimus, and Baryonyx), or obtained from the literature. Sections were then imaged to allow quantification of bone compactness and quantitative analyses. See the supplementary data attached to this manuscript for a complete list of data used in this study, origin of the data, and type of data acquisition. Femoral and dorsal rib sections were converted into black and white figures in VGStudio Max 3.4 for data obtained through microCT scan or in Photoshop CS5 for imaged thin sections. Bone density was quantified with the freely available software BoneProfiler 2.0-1 (<https://max2.ese.u-psud.fr/epc/conservation/boneprofiler.html>). The freely available software "Fiji" (<https://imagej.net/software/fiji/>) was used to measure the maximum diameter of the femur diaphyses and rib cross sections.

Data analysis

Phylogenetic analyses were performed in TNT (Tree analysis using New Technology) v. 1.1. In order to build an informal Supertree to test the role of phylogeny on the evolution of bone density, we used the freely available software Mesquite 3.7 (<https://www.mesquiteproject.org/>). The tree was calibrated using "bin_timePaleoPhy" from the R package Paleotree. Bone density, femoral midshaft and rib cross section diameters, and different combinations of 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). To establish explicit predictions of ecology in extinct taxa, we built a phylogenetically-flexible discriminant analysis (pfDA) using the function phylo.fda (sourced from <https://github.com/lSchmitz/phylo.fda>). In order to correct for the bias that phylogenetic structure introduces in form to function relationships, phylo.fda adjusts the phylogeny with the value of phylogenetic signal (Pagel's lambda) which maximizes the log likelihood of the linear fit among variables.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

All data described in this paper, including measurements, provenance information for fossil specimens, phylogenetic datasets, and CT scans collected for this study, are available in the Extended Data Figures, Supplementary Materials, and in Morphosource

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|--------------------------|---|
| Study description | In this study, we conduct phylogenetic comparative analyses of osteohistological and bone density data in a broad sample of amniotes, including dinosaurs, (n=380) to assess the presence and extent of aquatic adaptations in non-avian dinosaurs. First, we use comparative analysis to validate bone compactness as a proxy for subaqueous foraging capabilities in amniotes. We then use this proxy to provide evidence that a clade of medium- to giant-bodied predatory dinosaurs, Spinosauridae, was ecologically adapted to life in water, representing the first known aquatic radiation among non-avian dinosaurs. Disparate ecological niches are herein recognized among spinosaurids: whereas Baryonyx and Spinosaurus are strongly predicted as subaqueous foraging species, Suchomimus is inferred as a more terrestrial, potentially wading animal, although sharing morphological similarities with Baryonyx. Our findings greatly expand the ecological disparity of non-avian dinosaurs. |
| Research sample | This study collected bone compactness values from the femora (n=206) and dorsal ribs (n=174) of extant and extinct amniote taxa. The data collected aimed to cover the broadest taxonomic and ecological diversity possible among amniotes. While part of the data were available from the literature, our team collected data for 79 modern and extinct taxa. |
| Sampling strategy | We sampled 374 amniote taxa (380 individuals) spanning the entire tree of life, body size variation, and ecological diversity of this clade, in order to verify the influence of phylogeny, allometry and ecology on bone density, and to infer ecological adaptations among non-avian dinosaurs. The dataset here published is the largest ever built for bone density in amniotes. Because this includes extant and extinct clades and captures a broad ecological variability within each major amniote clade, we believe that the analyzed dataset is a consistent representation of ecological evolution in Amniota. |
| Data collection | Data collected for this study were acquired through thin sectioning or microCT scan. These were collected in the respective Institutions housing the specimens. MicroCT scans were collected for the diaphyses of femora and then imported in VGStudio Max 3.4 where a section of the diaphysis was extracted. Thin sections were imaged through petrographic microscopes and then transformed in Photoshop in a black and white image (black for bone). See the supplementary dataset attached to this study for the list of taxa examined. In order to expand the dataset and cover a broader range of taxa and ecologies, we obtained data from the literature. In this case, thin sections were directly transformed in black and white figures in Photoshop. In few cases, quantification of bone density was already undertaken in literature: in these cases, the values for bone density and maximum diameter were simply collected. While all authors contributed with specimens, M.F. transformed the sections in black and white figures and quantified bone density and maximum diameter of the sections. |
| Timing and spatial scale | Data were collected from FMNH, YPM at Yale, AMNH, NHMUK, UMZC, SMNS, UUVF, IGWH, NMQR, NMW, BSP, MPEF, AODF, IVPP, UM, MBC, MOR, OUMNH, MWU, MLP, STIPB, CAV, GPIT, UMMZ, OUMNH-J, LACM, SMNS, IPS, LO, RR, TMM, ROM, Wijk, SIPB R, ZMNH, CRILAR, UA, IPB, GAD, FSAC-KK, BPI, UF, ML, and MACN-PV. Data collection started in 2015 and was constantly conducted until 2019. |
| Data exclusions | No data were excluded |
| Reproducibility | Quantification of bone density was performed three times for each taxon to confidently replicate density measurements. Analyses of ecological inference were run over 100 trees generated for all amniotes to evaluate the effects of stratigraphic uncertainty on our analyses; the results were summarized thereafter. All data and coding required to replicate our results are available as supplementary material to this study. Replication of the results were successful. |
| Randomization | Randomization was applied to the alternative 100 phylogenies obtained for the PGLS analyses aimed at finding potential correlations between bone density, ecology and allometry. All other analyses do not require randomization. |
| Blinding | Not applicable because experiments do not require blinding |

Did the study involve field work? Yes No

Field work, collection and transport

| | |
|------------------------|---|
| Field conditions | Desert escarpment close to Moroccan-Algerian border |
| Location | In- and ex-situ on the slopes of a south-east facing escarpment (Zrigat, southeastern Morocco; 31° 37' N, 4° 16' W) fringing the Aferdou Zrigat plateau (Tafilalt basin, Akrabou Formation, Kem Kem beds). |
| Access & import/export | Permits for fieldwork were obtained from Ministère de l'Energie, des Mines, et de l'Environnement. Permits: 4581/DE/2019 (issued on 17/07/2019) and 4118/DE/2018/DG (issued on 06.06.2018). The work was performed in close collaboration with researchers in Morocco (FSAC, Casablanca). The specimens collected are deposited at the Departement de Géologie/Laboratoire de Biodiversité et Santé, Faculté des Sciences Ain Chock, Hassan II University, Casablanca, Morocco. |
| Disturbance | No disturbance |

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

| n/a | Involvement in the study |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Human research participants |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern |

Methods

| n/a | Involvement in the study |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |

Palaeontology and Archaeology

| | |
|--|--|
| Specimen provenance | The 380 specimens used in the study range from Europe, Mongolia, Africa, North and South America. |
| Specimen deposition | The specimens used in this study are housed in public museum collections and are freely accessible. The Institutions where the investigated specimens are housed are listed in the supplementary data attached to this manuscript. Data were collected from FMNH, YPM at Yale, AMNH, NHMUK, UMZC, SMNS, UUV, IGWH, NMQR, NMW, BSP, MPEF, AODF, IVPP, UM, MBC, MOR, OUMNH, MWU, MLP, STIPB, CAV, GPIT, UMMZ, OUMNH-J, LACM, SMNS, IPS, LO, RR, TMM, ROM, Wijk, SIPB R, ZMNH, CRILAR, UA, IPB, GAD, FSAC-KK, BPI, UF, ML, and MACN-PV. |
| Dating methods | No new dates were provided |
| <input checked="" type="checkbox"/> Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information. | |
| Ethics oversight | No ethical oversight was needed for this study, because based on Museum specimens |

Note that full information on the approval of the study protocol must also be provided in the manuscript.