nature portfolio

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# Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

## 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<br>*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<br>*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

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| Data collection | Scan volumes were reconstructed in Phoenix Datos\|x 3.1 (RRID:SCR_017996) with an in-line median filter and an ROI-CT filter. Segmentation, quantification, and 3D visualisation were performed in VGSTUDIO MAX 2025.4 (RRID:SCR_017997). Fusion projections were posterised in GIMP 2.10 (RRID:SCR_003182) and scaled in FIJI 2.16 (RRID:SCR_002285). Aridity Index values and geocoordinates were retrieved in QGIS 3.40.12 (RRID:SCR_018507). Directional trait profiles were extracted from exported image stacks in R 4.4.0 (RRID:SCR_001905) using the imager package. No custom software was used for data collection beyond the R code provided in Supplementary File 3. |
| Data analysis | All statistical analyses were performed in R 4.4.0 (RRID:SCR_001905) using the packages ape 5.8, car 3.1-3, geomorph 4.0.8, ggplot2 3.5.1, imager 1.0.8, nlme 3.1-164, phangorn 2.12.1, phytools 2.3-0, RRPP 2.0.3, sf 1.0-18, and strap 1.6-1. Discrete model comparison was performed in BayesTraits 5.0. Custom R code for profile processing, phylogenetic comparative analyses, modularity search, and ancestral state reconstruction is provided in Supplementary File 3 (Analysis.R). Code for Aridity Index computation and for extraction of profile data from VGSTUDIO MAX-exported cross sections is available at www.Ebelosaurus.com/Resources. |

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

Supplementary Notes, Figures, and Tables are provided in Supplementary File 1. All raw data underlying this article are provided in Supplementary File 2, and all analysis code and input files in Supplementary File 3. Code for Aridity Index computation and for extraction of profile data from VGSTUDIO MAX-exported cross sections, together with all input data (approximately 6 GB), is available at www.Ebelosaurus.com/Resources. All µCT scan volumes used for the quantifications will be made available at www.MorphoSource.org on expiry of the embargo (project identifier to be determined; embargo lift in 05/2027).

## Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

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| Reporting on sex and gender | *Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design; whether sex and/or gender was determined based on self-reporting or assigned and methods used.*<br>*Provide in the source data disaggregated sex and gender data, where this information has been collected, and if consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected.*<br>*Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.* |
| Reporting on race, ethnicity, or other socially relevant groupings | *Please specify the socially constructed or socially relevant categorization variable(s) used in your manuscript and explain why they were used. Please note that such variables should not be used as proxies for other socially constructed/relevant variables (for example, race or ethnicity should not be used as a proxy for socioeconomic status).*<br>*Provide clear definitions of the relevant terms used, how they were provided (by the participants/respondents, the researchers, or third parties), and the method(s) used to classify people into the different categories (e.g. self-report, census or administrative data, social media data, etc.)*<br>*Please provide details about how you controlled for confounding variables in your analyses.* |
| Population characteristics | *Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."* |
| Recruitment | *Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.* |
| Ethics oversight | *Identify the organization(s) that approved the study protocol.* |

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

# 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

# Ecological, evolutionary & environmental sciences study design

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

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| Study description | This is a quantitative comparative study. We used µCT scanning to quantify the microanatomy of the cephalic and cervical osteoderm cover in preserved museum specimens of Egernia-group skinks. Nine continuous structural traits were measured per specimen, describing thickness, compactness, structural complexity, anisotropy, and fusion with the skull roof. Three binary lifestyle states served as predictors. These are dry tolerance, fossoriality, and arboreality, and they are non-mutually-exclusive. There was no experimental treatment and no manipulation of organisms. The design is observational, with specimens nested within taxa and taxon means used as the unit of analysis. Comparative models were fitted under a phylogenetic covariance structure derived from a published timetree, with body size and the two non-focal lifestyles included as covariates. |
| Research sample | The sample comprises 80 ethanol-preserved specimens held in the Museums Victoria collection, representing 38 Egernia-group taxa. Coverage per taxon has a median of 2 specimens, a range of 1 to 4, and a mean of 2.1. Snout-vent length ranges from 70 to 334 mm, with a mean of 159 mm and a standard deviation of 81 mm. Sex was recorded on the museum registration for 40 of the 80 |

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| | specimens, comprising 21 males and 19 females, and was not recorded for the remaining 40. Juveniles and visibly damaged specimens were excluded before scanning. The sample was chosen to represent the taxonomic breadth of the Egernia group as resolved in the reference timetree, and it spans the full range of body sizes and the three lifestyle states present in the group. |
| Sampling strategy | No statistical procedure was used to predetermine sample size. Sample size was set by specimen availability in the Museums Victoria collection, under a target of at least two adult specimens per taxon and, where the collection allowed, one specimen of each sex and two specimens per subspecies. This is sufficient because inference operates at taxon level against a fixed phylogeny of 38 tips. Taxonomic coverage therefore determines statistical resolution, and within-taxon replication serves to stabilise the taxon mean rather than to contribute independent observations. Group-level diagnostics reported in Supplementary File 2 confirm that the smallest lifestyle group contains 9 taxa, and analytical methods robust to this imbalance were selected accordingly. |
| Data collection | µCT scans were acquired by R.E., J.R.B., R.A., and J.M. on a Phoenix Nanotom M at the Trace Analysis for Chemical, Earth and Environmental Sciences (TrACEES) Platform, University of Melbourne. Snout-vent length was recorded before scanning, and linear head dimensions were measured digitally from the reconstructed volumes. Segmentation, microanatomical quantification, and trait extraction were performed by R.E. in VGSTUDIO MAX 2025.4. Fusion between the skull roof and the cephalic osteoderms was quantified by R.E. from posterised top-view parallel-projection renders. Lifestyle states were coded by R.E. from the published literature. Aridity Index values were derived from the Global Aridity Index database and matched to occurrence records from the Atlas of Living Australia. |
| Timing and spatial scale | Scanning was carried out between 15 and 20 February 2024. The specimens themselves are historical museum accessions. A collection date is recorded for 46 of the 80 specimens, spanning 1897 to 2017, and no date is recorded for the remaining 34. Georeferenced localities are available for 52 of the 80 specimens and span latitudes 42.95° S to 6.57° S and longitudes 115.87° E to 155.35° E. This covers continental Australia from Western Australia to the east coast, Tasmania, and Melanesia. Sampling was not periodic, because each specimen contributes a single set of measurements and no individual was measured more than once. |
| Data exclusions | Exclusions were applied at three points, and all criteria were established before the relevant analyses. First, juveniles and visibly damaged specimens were excluded before scanning. Second, occurrence records were filtered before the Aridity Index computation to remove localities outside the distribution reported in the literature, unconfirmed human observations, and duplicate reports falling within the same Aridity Index grid cell. Third, four quantified traits were excluded from the comparative analysis as redundant or technically unsuitable, these being Tb.Th_hull, Tb.Sp_hull, V_OD/V_ES, and asym, with the assessment given in Supplementary Note 19. Directional profile data for fus were subset to exclude the anterior 41% of the profile on the basis of model fit, and BS/TV_hull and Tb.N_hull were replaced by their first principal component after a PCA showed near-perfect collinearity. |
| Reproducibility | No experiments were repeated in the sense of independent replication, because each specimen yields a single scan and a single set of measurements. Reproducibility was addressed instead through protocol standardisation and full computational transparency. Scan settings and workflow were held as constant as possible across the dataset, and all scan and thresholding parameters are reported per specimen in Supplementary Table 5. Advanced surface determination was used for all region-of-interest definitions, which places boundary localisation at sub-voxel precision and reduces operator dependence. All raw trait data, lifestyle coding, the phylogeny, and the complete analysis code are provided in Supplementary Files 2 and 3, so every reported result can be regenerated from the supplied inputs. |
| Randomization | Randomization is not applicable to this study. Specimens were not allocated to groups by the investigators. Lifestyle states are intrinsic properties of the taxa and were coded from published natural history accounts. Potential confounding was handled statistically rather than by allocation. Body size and the two non-focal lifestyle states were included as covariates in every model, collinearity among predictors was screened using Variance Inflation Factors, and all inference was conducted under a phylogenetic covariance structure to account for shared ancestry. |
| Blinding | Blinding was not relevant to this study. Segmentation and quantification were performed on specimens whose taxonomic identity is inseparable from the specimen itself, so the operator could not be blinded to group membership. The risk of operator bias is limited because trait extraction was threshold-driven and automated within VGSTUDIO MAX rather than based on subjective scoring. Lifestyle coding was carried out from the published literature independently of the microanatomical measurements. |

Did the study involve field work? ☐ Yes ☒ No

# 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 | Involved in the study |
|---|---|
| ☒ | ☐ Antibodies |
| ☒ | ☐ Eukaryotic cell lines |
| ☒ | ☐ Palaeontology and archaeology |
| ☐ | ☒ Animals and other organisms |
| ☒ | ☐ Clinical data |
| ☒ | ☐ Dual use research of concern |
| ☒ | ☐ Plants |

## Methods

| n/a | Involved in the study |
|---|---|
| ☒ | ☐ ChIP-seq |
| ☒ | ☐ Flow cytometry |
| ☒ | ☐ MRI-based neuroimaging |

## Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

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| Laboratory animals | The study did not involve laboratory animals. |
| Wild animals | The study did not involve live wild animals. All material consists of ethanol-preserved specimens already held in the Museums Victoria collection, accessioned over more than a century of prior collecting. No animal was captured, handled alive, transported, or killed for this study. Specimens were scanned intact and returned to the collection. |
| Reporting on sex | Findings apply to both sexes. Sex was considered in the sampling design, in that each species was represented by specimens of both sexes wherever the collection allowed. Sex was taken from the museum registration data rather than assigned by the investigators, and it is recorded for 40 of the 80 specimens, comprising 21 males and 19 females. It is not recorded for the remaining 40. Sex-disaggregated data are provided per specimen in Supplementary File 2. No sex-based analysis was performed. The reason is that sex is unrecorded for half the sample, and that inference operates on taxon means rather than on individual specimens, so the design has no power to resolve within-taxon sex effects. |
| Field-collected samples | The study did not involve samples collected from the field. All specimens were existing museum accessions, held in ethanol under standard collection conditions, and no laboratory work was performed on freshly collected material. |
| Ethics oversight | No ethical approval or guidance was required. The study involved no live animals and no procedures on animals. It used only preserved specimens already held in the Museums Victoria collection, accessed under the institution's standard internal loan and collection-access procedures. |

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

## Plants

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| Seed stocks | *Report on the source of all seed stocks or other plant material used. If applicable, state the seed stock centre and catalogue number. If plant specimens were collected from the field, describe the collection location, date and sampling procedures.* |
| Novel plant genotypes | *Describe the methods by which all novel plant genotypes were produced. This includes those generated by transgenic approaches, gene editing, chemical/radiation-based mutagenesis and hybridization. For transgenic lines, describe the transformation method, the number of independent lines analyzed and the generation upon which experiments were performed. For gene-edited lines, describe the editor used, the endogenous sequence targeted for editing, the targeting guide RNA sequence (if applicable) and how the editor was applied.* |
| Authentication | *Describe any authentication procedures for each seed stock used or novel genotype generated. Describe any experiments used to assess the effect of a mutation and, where applicable, how potential secondary effects (e.g. second site T-DNA insertions, mosiacism, off-target gene editing) were examined.* |