A systematic map and comprehensive database of animal organ sizes

Félix P. Leiva, Luke Ockhuijsen, Jasmijn Polinder, Louise J. Schreyers, Jie Xiong and A. Jan Hendriks

Department of Environmental Science, Radboud Institute for Biological and Environmental Sciences, Radboud University Nijmegen, 6500 GL Nijmegen, The Netherlands.

E-MAIL OF CORRESPONDING AUTHOR (*)

Félix P. Leiva: felixpleiva@gmail.com

AUTHOR'S CONTACT (EMAIL; ORCID):

Félix P. Leiva: felixpleiva@gmail.com; 0000-0003-0249-9274

Luke Ockhuijsen: luke.ockhuijsen@ru.nl; ORCID ID: 0009-0000-0598-8968

Jasmijn Polinder: jasmijn.polinder@ru.nl; ORCID ID: 0009-0003-4572-9778

Louise J. Schreyers: louise.schreyers@ru.nl; ORCID ID: 0000-0002-2607-1494

Jie Xiong: jie.xiong@ru.nl; ORCID ID: 0009-0008-4595-7187

A. Jan Hendriks: jan.hendriks@ru.nl; ORCID ID: 0000-0002-8348-4084

ABSTRACT

The relationship between individual organ size and overall body size in animals is a fundamental biological phenomenon that spans multiple disciplines. However, a comprehensive synthesis of the sources of variation in organ-specific scaling remains lacking, even among mammals, the most extensively studied vertebrate group. We developed a systematic map and compiled a large database of paired organ and body size measurements. This database includes over 10,000 records from 366 species across eight animal classes. Our database provides size estimates for 53 organ types, categorised into 10 physiological systems, with most data derived from digestive, circulatory and excretory systems. In addition, we include extensive metadata to contextualise the original studies, which highlights gaps—such as the season of animal collection and life stage, both of which were among the least frequently reported. We anticipate this comprehensive and reproducible resource will offer a robust foundation for improving the parameterisation and cross-species applicability of simulation models based on physiological and kinetic principles, thereby advancing our understanding of organ size scaling across diverse taxa.

Keywords: scaling, interspecific, intraspecific, metadata, sex, life stage

INTRODUCTION

The manner in which individual organ dimensions change relative to overall body size is termed organ size scaling—a phenomenon fundamental to numerous biological disciplines[1]. Understanding how organ size scaling varies across taxa is essential for addressing key questions in comparative physiology and evolutionary biology, as well as ecotoxicology. This knowledge not only reveals broad patterns of anatomical organisation, but also provides a robust foundation in several research fields, including, but not limited to, physiology, developmental biology, functional morphology, and environmental sciences[2–4].

In developmental biology, elucidating organ size scaling improves our understanding of how organisms maintain cellular function during growth, particularly as shifts in tissue proportions influence organ dimensions[5]. In physiology, organ size scaling is closely linked to metabolic rates and body size, thereby shaping critical processes including oxygen delivery, circulatory dynamics, thermoregulation, and consequently, organisms' responses to environmental changes[1]. From an evolutionary perspective, studies on organ scaling—particularly brain size—have stimulated debates surrounding long-standing evolutionary hypotheses[6,7]. These examples, alongside extensive research dating from Huxley's seminal studies[8,9] to contemporary research[7,10–12], emphasise that scaling relationships lack universality. No single exponent characterises all patterns of organ scaling, as empirical data frequently reveal considerable intra and inter-specific variation and deviations from theoretical models[13,14]. Recognising this variation, within its biological and methodological context, is also important for identifying factors beyond body mass that explain these deviations. Such insights can ultimately help refine the parameterisation of simulation models based on physiological and kinetic principles[15–18].

While the scaling of organ size is a widely studied phenomenon, most analyses have focused on limited range of taxonomic groups (e.g., birds and mammals) and specific organs (e.g., brain size). It is also important to recognise that much of the debate surrounding broader hypotheses, such as the *energy trade-off hypothesis*[19] and the *expensive tissue hypothesis*[6], has driven the compilation of datasets for multiple organs, mainly in mammals[7], or for single organs across various vertebrates and invertebrates groups[20]. However, to our knowledge, no existing databases provide the necessary methodological context to better explain the variation and deviations from theoretical expectations observed in organ size scaling across different taxonomic groups.

This gap highlights the need to investigate whether organ-specific scaling occurs consistently among functionally similar organs, or whether incorporating ecological and other biological traits and methodological context can better explain observed patterns. Addressing these questions is crucial to uncover fundamental principles governing the design and evolution of biological systems across diverse taxa[21]. Nonetheless, the continued absence of centralised, standardised organ size datasets spanning a wide range of species hampers model parameterisation and limits our ability to generalise findings across taxa.

To address limitations in both taxonomic and organ coverage, we have developed a comprehensive database comprising paired data on organ and body size across a diverse range of invertebrate and vertebrate animals. The data, curated through a systematic review of the literature, encompass species from marine, freshwater, and terrestrial environments. Each entry includes biological details such as sex, age, life stage, and body size. The database also contains supplementary metadata outlining the methodological context of each study. Collectively, this resource is designed to support meta-analyses and comparative approaches on organ scaling at both inter- and intra-specific levels, and to enhance understanding of their physiological and evolutionary significance.

MATERIAL AND METHODS

We adhere to the Method Reporting with Initials for Transparency (MeRIT, https://www.merit.help/) guidelines developed by Nakagawa et al.[22] to enhance the clarity and transparency of our reporting and methodological descriptions. These guidelines employ authors' initials within the methods section to attribute specific tasks to individual contributors, thereby complementing the Contributor Roles Taxonomy (CRediT, https://credit.niso.org/) system.

Literature search

We searched the literature using ISI Web of Science (Core Collection, https://www.webofscience.com/) and Scopus (https://www.scopus.com/) to identify studies reporting paired data on organ dimensions and body size. The search was conducted on 23 January 2025, using Radboud University's institutional subscriptions. We included organs common to all vertebrates, as well as functionally similar organs in invertebrates[23]. Search terms were selected to cover specific lineages and categories based on diet, habitat, locomotion, and other relevant groups (e.g., ruminants).

The keywords combination of Boolean terms used was: ("organ size" OR "organ weight*" OR "organ volume" OR "organ length*" OR "organ surface area" OR "organ exchange area" OR "layer thickness" OR "organ mass" OR "organ scaling" OR "anatomical scaling" OR body proportion) AND ("ileum" OR "gastrointestin*" OR "digestive tract" OR "lung*" OR "pulmonary" OR "brain" OR "kidney*" OR "renal" OR "gut" OR "heart" OR "myocardi*" OR "liver" OR "hepat*" OR "intestin*" OR "stomach" OR "gill*" OR "branchi*" OR "dorsal vessel*" OR "pulsatile organ*" OR "tracheal system*" OR "nephridia" OR "gonad*" OR "gangli*" OR "pancreas" OR "spleen" OR "hepatopancreas" OR "thyroid" OR "pituitary" OR "thymus" OR "bone marrow" OR "muscle" OR "bone*" OR "gland*" OR "adipose depot" OR "visceral") AND ("fish*" OR "reptil*" OR "mammal*" OR "bird*" OR "amphibia*" OR "vertebrate*" OR "annelid*" OR "mollusc*" OR "mollusk*" OR "arthropod*" OR "echinoderm*" OR "cephalopod*" OR "insect*" OR "crustacean*" OR "primate*" OR "rodent*" OR "carnivore*" OR "herbivore*" OR "cetacean*" OR "marsupial*" OR "monotreme*") AND ("body mass" OR "body size" OR "body weight" OR "scaling" OR "scal*" OR "fat-free body mass" OR " fat-free body weight"). The full records were downloaded, including abstracts, keywords, and all relevant information, across all years and editions, and document types. Only references published in English were included in this study, and these were downloaded in BibTeX file format. Using ISI Web of Science, a total of 2,305 records were identified, whilst in Scopus, 2,124 records were found (Figure S1).

Literature screening

To streamline the screening process, we used Rayyan[24], a web-based platform that accelerates systematic reviews by reducing the time required for each screening stage. After removing duplicates (N = 1,061), we implemented a two-step filtering process based on keywords. First, we applied filters to identify terms related to specific organs. Next, we used additional filters to focus on size-related terms. These steps enabled us to detect relevant keywords within the title, abstract, and keyword sections of each reference.

To further refine our selection, we applied filters in Rayyan for both passive (e.g., "were measured", "were analysed") and active expressions (e.g., "we measured", "we analysed") to identify more easily whether an organ had been measured in each study. This approach enabled the identification of 660 relevant studies (Figure S1). Whenever possible, the PDF files of these references were downloaded, and inclusion was determined based on the criteria outlined below, following a full-text screening of each article.

Eligibility criteria

Although our screening of titles and abstracts in the preceding step was as thorough as possible, most studies excluded at the full-text stage were not relevant to the aims of our systematic review. Over 200 studies were excluded because they either lacked relevant data or examined different organ-level traits. A key inclusion criterion was that studies must report paired data on both organ and body size. At this stage, 45 studies were excluded for not reporting body size. An additional 43 studies reported both body size and organ size, but the data were not paired; for example, organ size was reported separately for each sex, whereas body size was provided only as a mean for females and males combined.

Additionally, only primary research articles were included to ensure the use of original data and to give appropriate credit to primary sources, meaning that reviews were excluded from our study (N = 37). We also focused exclusively on extant, species-specific data to maintain consistency and comparability, thereby excluding genus-level data, hybrid species, extinct species, and studies focusing solely on foetuses (only studies including neonates and older life stages individuals were retained). In cases where studies involved various treatments (e.g., exposure to chemical treatments), only those reporting experimental control conditions, as defined in the original publication, were considered, to ensure comparability across studies in our database.

Applying these inclusion criteria, along with the exclusion of studies for which data could not be accessed (e.g., no PDF available or authors did not provide raw data after request), or that were duplicates, the final number of studies included in our database was 235. All primary articles used to construct the database have been referenced[7,25–258]. This practice establishes the most plausible starting point for encouraging the sharing of primary data[259].

Data extraction and metadata

We extracted the mean values where available for paired body size and organ size in both invertebrates and vertebrates, along with their respective sample sizes and measures of dispersion, such as standard deviation, standard error, or confidence intervals. All data extractions were carried out by FPLeiva. Data on organ size and body mass available exclusively in tables or text were extracted directly. For data presented solely in figures, without accompanying text or tables, we used the metaDigitise package[260] to extract means and measures of dispersion. Furthermore, as our database also aims to explore sources of intraspecific (within-species) variation, we extracted raw data from scatter plots using WebPlotDigitizer v5.2[261] via its online platform (https://automeris.io). Additionally, we reviewed archived data from studies and extracted raw data from supplementary materials whenever available.

For each study, we collected a range of methodological information (metadata) related to both organ size and body size. This list was further complemented with the taxonomy of the species. We collected metadata associated with the context in which the studies were conducted. This study context was categorised following the Society of Toxicologic Pathology's classification[262], with an additional category for ecological and evolutionary studies. For wild collected animals, we also gathered metadata concerning the temporal (season of collection) and spatial origin (geographical coordinates) from which organ sizes were measured. When animals originated from wild populations, we extracted geographical coordinates. However, when the collection location was given as a place name (e.g., Calbuco, Chile), we used GeoNames (https://www.geonames.org/) to obtain approximate coordinates.

Where possible, we included all sources of within-species variation reported in the original studies, such as age, life stage, body size, sex, and the side (left or right) of paired organs (e.g., lungs, kidneys, adrenal glands). These metadata not only allow for testing the robustness of conclusions emerging from specific analyses but also enable researchers to filter data based on their requirements or research questions. The latter was infrequently reported; in such cases, we assumed that studies not specifying organ side measured both sides. Regarding organ selection criteria, we only included studies reporting masses of complete organs rather than partial specimens. Although such cases were rare, this ensured rigorous comparability across all studies in our analysis. We aimed to use similar units for expressing organ mass. In a few cases, body sizes reported in length units were converted to wet body mass (grams) for certain fish species, using species-specific length-weight relationships obtained from FishBase[263]. In cases where it was not stated whether masses were measured using fresh or dried organ, we assumed they were weighed fresh, as was the case for most studies.

Taxonomy and phylogeny

Species names were examined for synonyms and any recent updates that could affect their taxonomy. To achieve this, we used a taxonomic harmonisation procedure[264], which was also applied to other traits[265]. This harmonisation involved three automated steps: first, species names were checked against the National Center for Biotechnology Information (NCBI) taxonomy database; second, any unmatched names were verified using the Integrated Taxonomic Information System (ITIS) database; and third, any remaining unmatched names were cross-checked with the Global Biodiversity Information Facility (GBIF) database. If a match was found, the corrected taxonomic name was re-checked through both NCBI and ITIS to ensure accurate classification. Ultimately, only species-level names were retained in the database, with subspecies grouped under their respective species. For species that could not be verified through this process, manual checks were conducted using additional online resources, such as FishBase[263]. We utilised the harmonised species list to retrieve the phylogenetic relationships of the species from Open Tree of Life[266]. All analyses were carried out in R version 4.3.2[267].

Data records

After applying the distinct criteria inclusion, our database contains 10,702 records collected from studies published between 1964 and 2024 (Figure 1A). The most pronounced increase in the number of published studies occurred after 1975. By January 2025, the date of the literature search, the cumulative total had reached 235 articles reporting paired data on organ and body size (Figure 1A); these constitute the total of articles included in this database. These studies were published across 154 different journals. The greatest number of studies appeared in Poultry Science (15 studies), followed by Journal of Experimental Biology (12 studies), with Journal of Anatomy and Aquaculture contributing five studies each. Several other journals—including Physiological and Biochemical Zoology, Journal of Zoology, Journal of Animal Physiology and Animal Nutrition, European Poultry Science, British Poultry Science, and Asian-Australasian Journal of Animal Sciences—contributed four studies each (Figure 1B). The remaining journals published fewer than four articles.

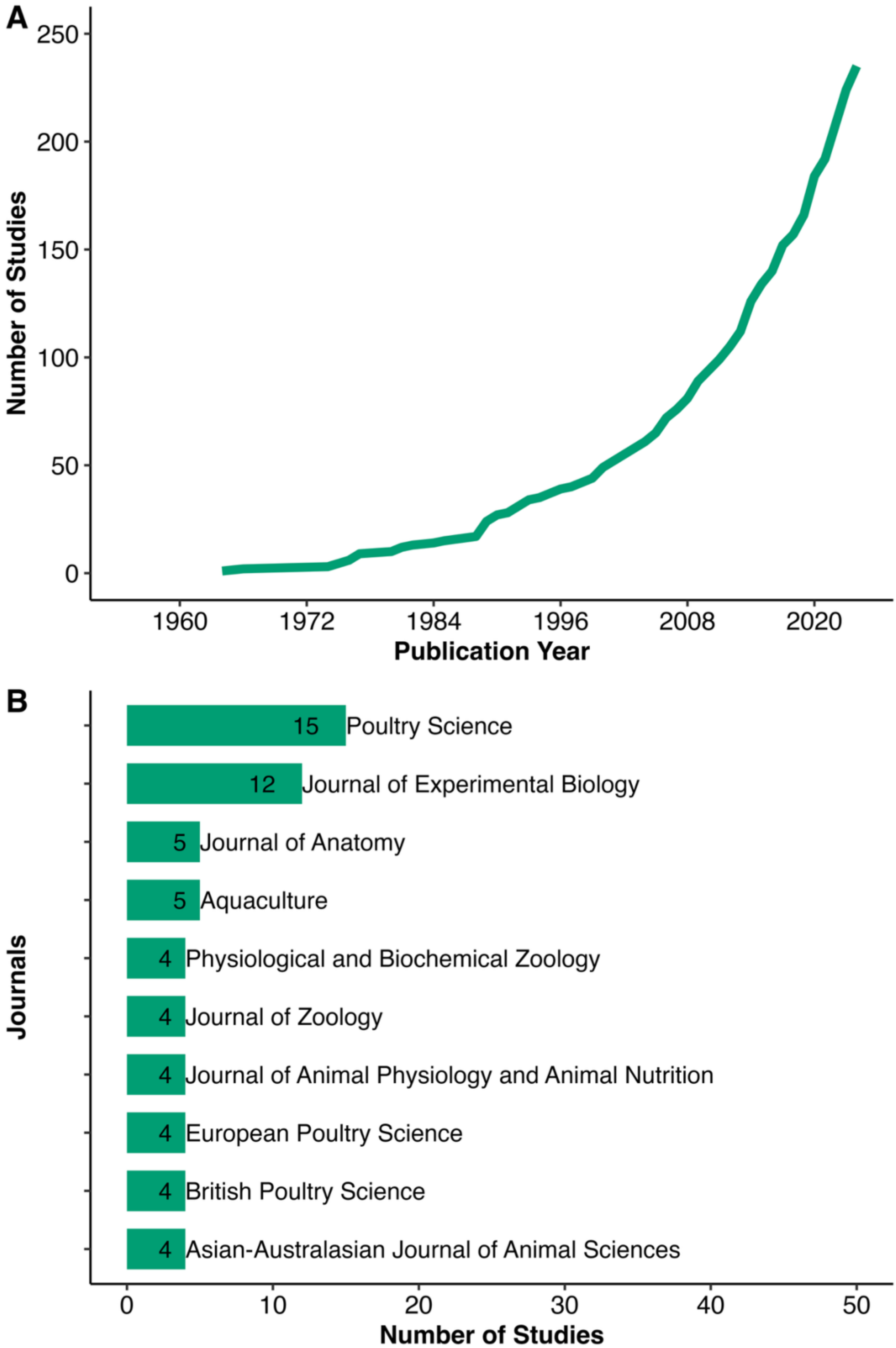


Figure 1. (A) Cumulative number of studies over time and (B) distribution of studies included in the organ size database across the top 10 journals.

Studies included in our database were categorised according to their study context into five groups (Figure 2A). Ecological and evolutionary studies were the most common, with 115 included, followed by those focused on food and nutritional aspects (73 studies), animal health (31 studies), and chemical analyses (21 studies). Studies categorised as consumer products or pharmaceuticals were least represented, with 5 and 3 studies, respectively (Figure 2A).

Regarding the species used to determine organ size, the majority were collected from wild populations (65 studies). Laboratory-reared animals (e.g., mice, rats) and commercially sourced animals (e.g., those purchased from a company) each represented the next largest sources (Figure 2B). Farm and captive animals were used in 32 and 16 studies, respectively, while extant specimens from museum collections were used to a lesser extent. Notably, the source of the animals could not be determined in 45 studies (Figure 2B).

For species collected from the wild, the season of collection was recorded when available. However, this information was not provided in most studies (224 studies) (Figure 2C).

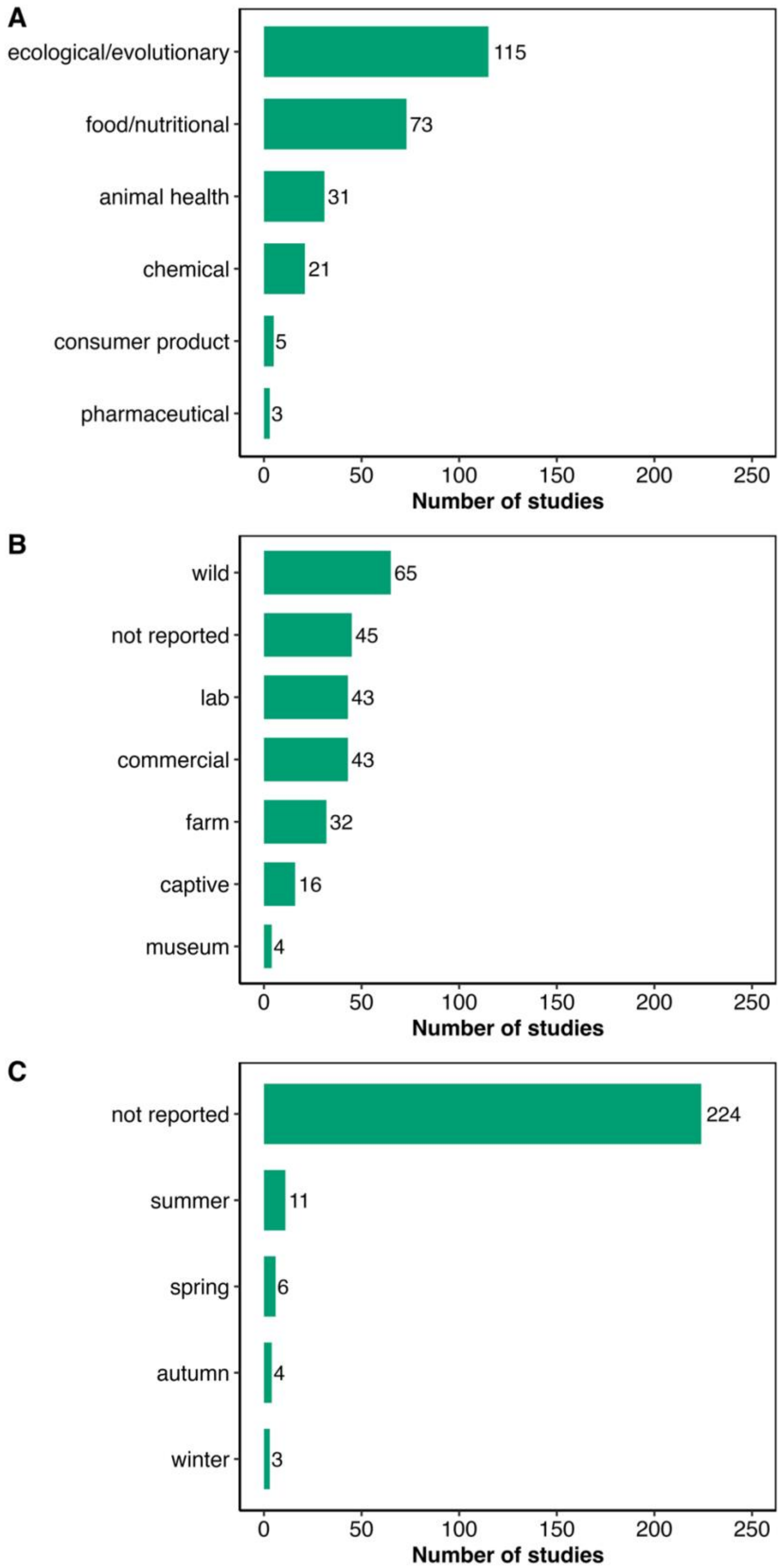


Figure 2. Number of studies reporting organ size measurements according to study context (A), source of specimens (B), and season of collection (C). Note: The sum of studies exceeds the total studies in our database (235) because individual studies may report multiple categories (e.g., a single study using both wild/lab animals), with each combination counted separately.

Most studies included in our database correspond to terrestrial species (Figure 3A), with a smaller proportion involving aquatic species. Among the aquatic studies, freshwater species were more commonly represented (38 studies) than marine species (25 studies). Much of the information related to sex or life stage was largely absent from the published articles. This was especially true for life stage, which could not be determined in 156 studies. Adults and juveniles were the most frequently examined life stages, while earlier life stages were less studied, with fewer than 10 studies for each (Figure 3B).

With respect to sex (Figure 3C), males were used in slightly more studies than females: 110 studies used only males, 91 studies used only females, and 27 studies included both sexes (Figure 3C).

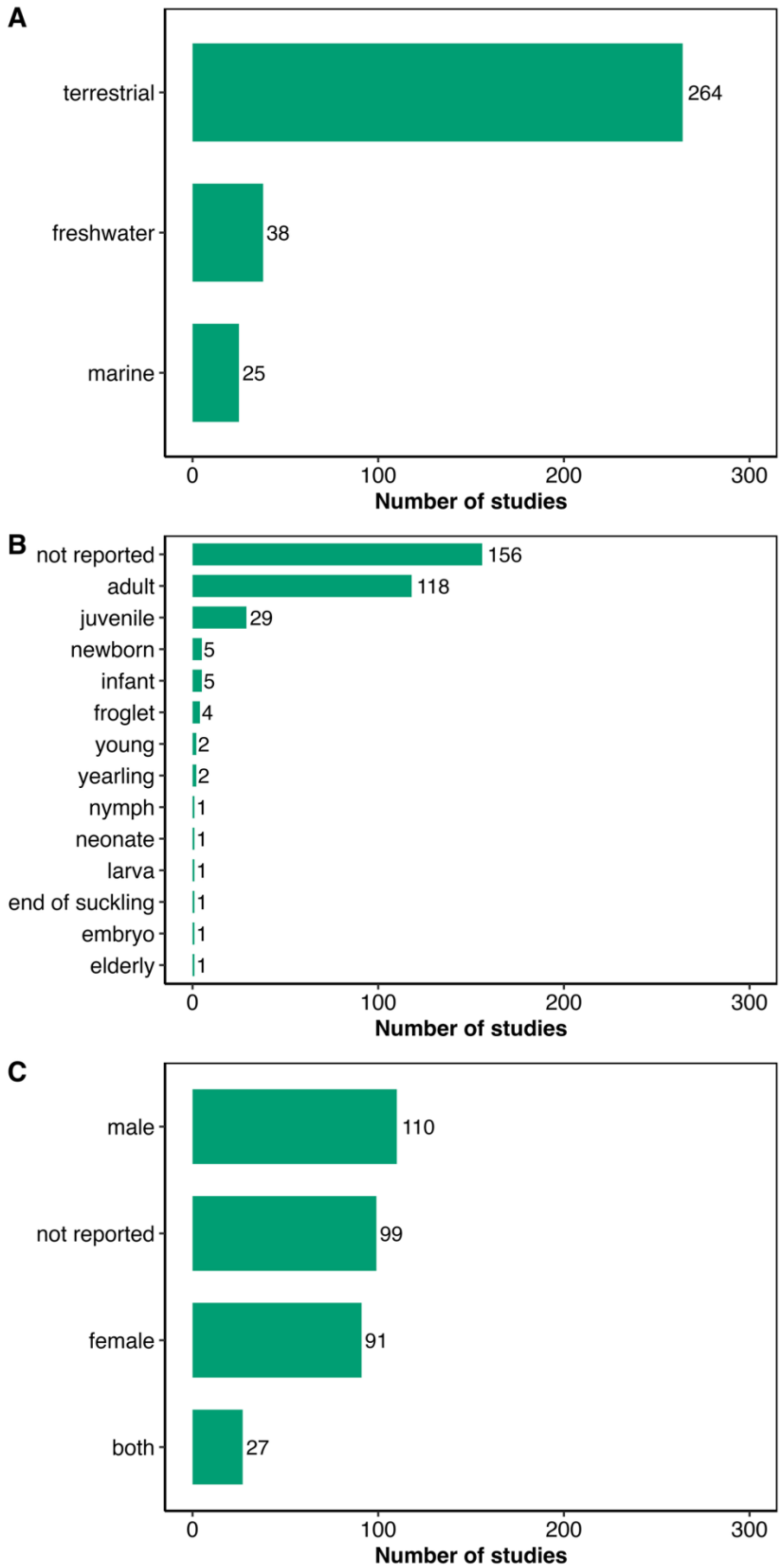


Figure 3. Number of studies reporting organ size measurements according to habitat (A), life stage (B) and sex (C). Note: The sum of studies exceeds the total studies in our database (235) because individual studies may report multiple categories (e.g., a single study covering both freshwater /marine habitat), with each combination counted separately.

After completing the steps of taxonomic harmonisation, our database comprised 366 unique species, of which 363 are represented in the Open Tree of Life (OTL) phylogeny (Figure 6). Three species were not included in the OTL: the recently described octopus *Muusoctopus aegir*, which is not yet included in the tree, and two water shrews, *Neomys fodiens* and *Neomys anomalus*, both flagged as *incertae sedis* (i.e., their relationships are unknown or undefined).

From a taxonomic perspective, Aves was the most studied class in our database, represented by 110 studies. This was followed by Mammalia with 78 studies, and Actinopterygii with 29 studies. The remaining classes were less well represented, each with six or fewer studies (Figure 4A). However, this pattern contrasts with the distribution of species in our database. When considering the number and percentage of species per class (Figure S2), Mammalia contains the greatest number of species (227), followed by Aves (71 species), representing 62% and 19.4% of the total species (366), respectively. Bony fishes (Actinopterygii) make up 6.6% of all species (24 species). All other classes each account for less than 4% of the total number of species (Figure S2).

The ten most studied species are shown in Figure 4B. *Gallus gallus* was the most studied species overall, followed by *Rattus norvegicus* (22 studies) and *Mus musculus* (16 studies). These were followed by *Anas platyrhynchos*, *Coturnix japonica*, and *Meleagris gallopavo*. All remaining species appeared in four or fewer studies (Figure 4B).

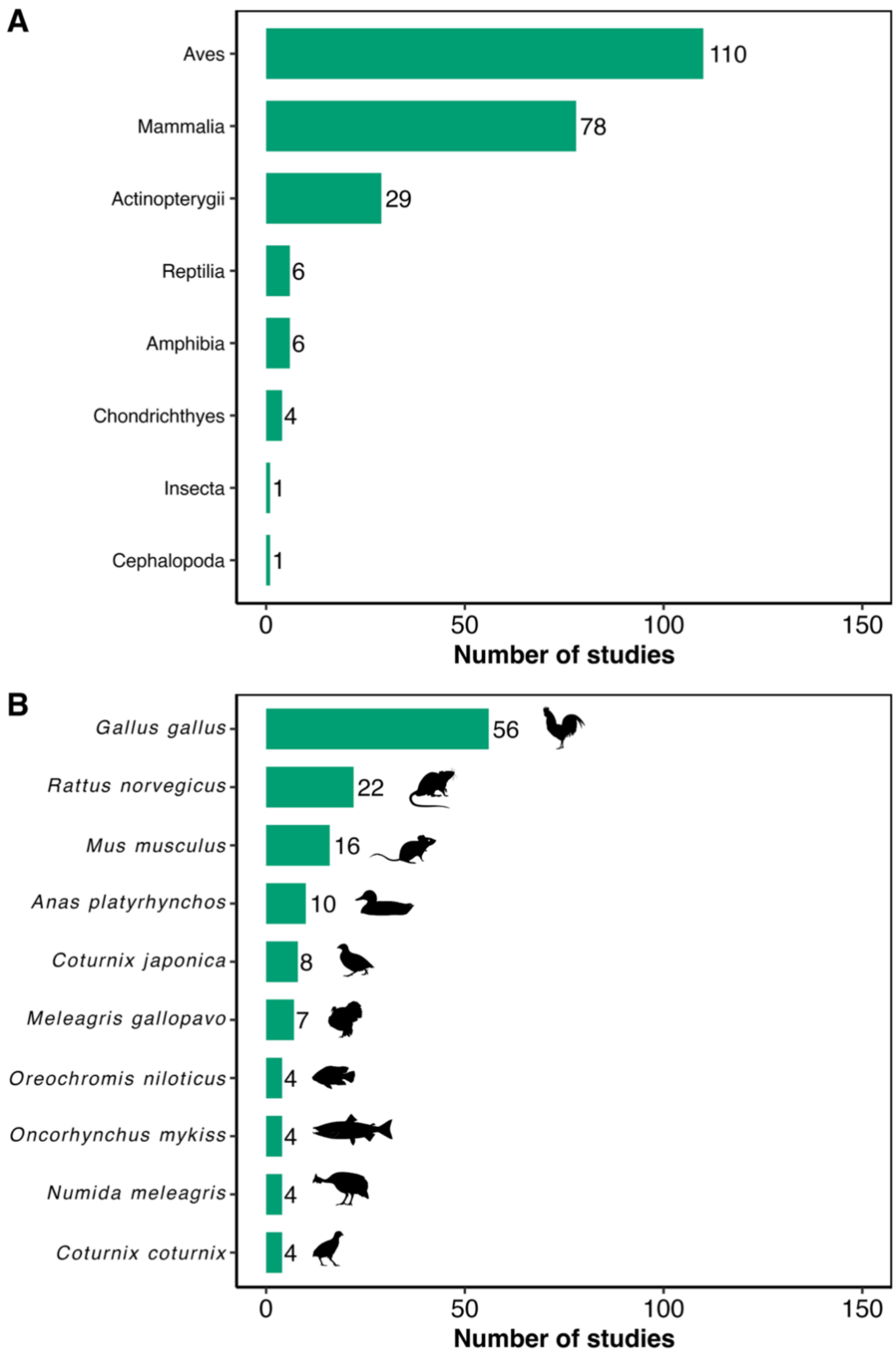


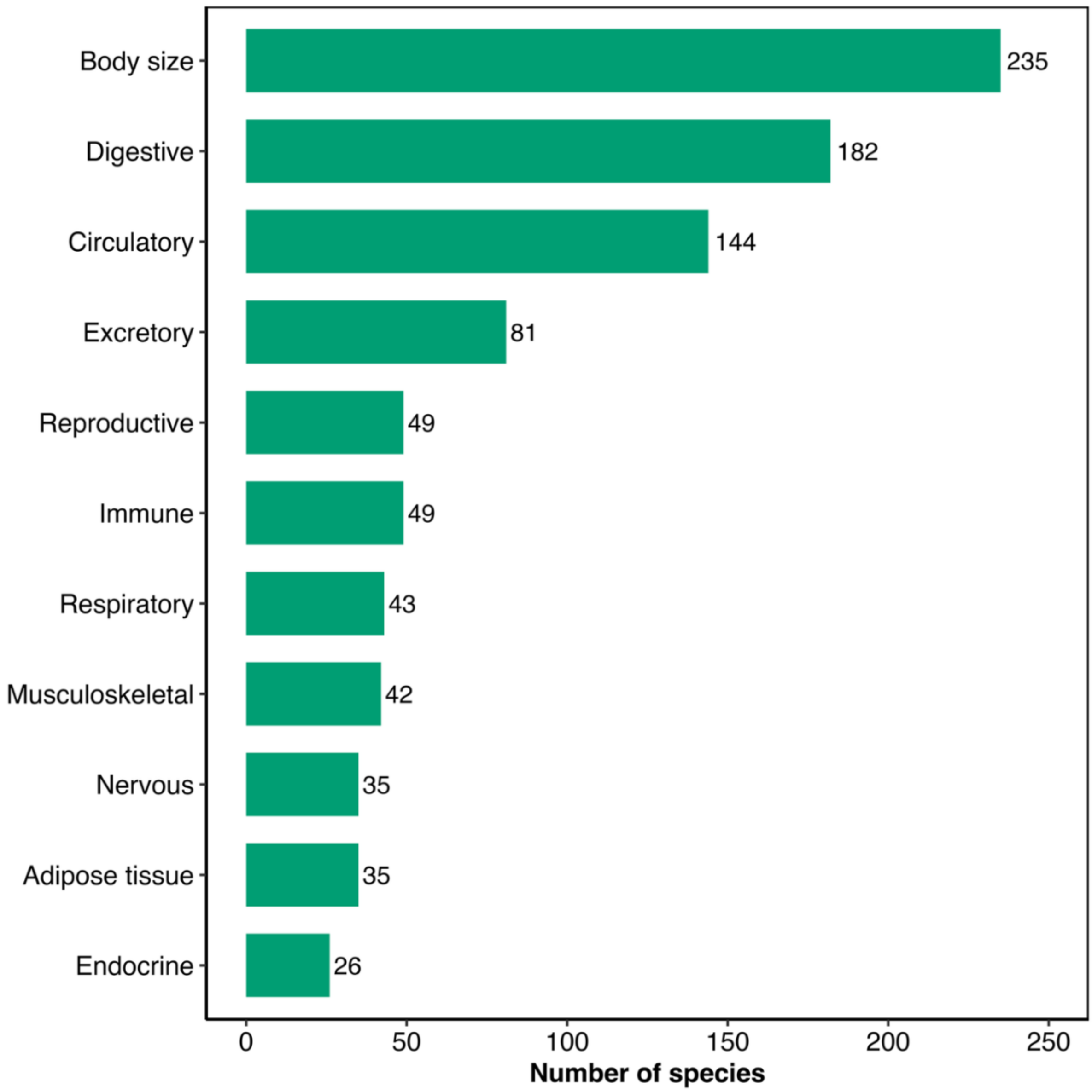
Figure 4. (A) Number of studies included in the organ size database, grouped by taxonomic class. (B) Number of studies for each of the 10 most frequently represented species in the database. Silhouettes depict the same species shown in panel B and were sourced from www.phylopic.org (public domain).

Our initial objective was to consider the widest possible variety of organs across different species of vertebrates and invertebrates. In total, we collected paired data for 53 distinct organs (Table 1 and Figure S3). To facilitate visualisation, we further grouped these organs—guided by expert judgement—into ten systems that collectively capture the functional diversity of the organs included (Figure 5).

Table 1. Systems categories used to classify organs. We have retained the original system names as previously reported. In this instance (*), the relevant system was estimated using 3D modelling.

System category	Examples
Digestive	liver, caecum, intestine, stomach, digestive tract, digestive system, jejunum, duodenum, gizzard, ileum, esophagus, colon, rectum, proventriculus, gut, pancreas
Excretory	kidney, Malpighian tubules, ureter, bladder
Circulatory	heart, ventricle, circulatory system and fat body*, spleen
Immune	thymus, bursa
Nervous	brain, central nervous system, pituitary gland
Endocrine	thyroid/parathyroid glands, adrenal glands, Harderian gland, salt gland
Respiratory	lung, gill
Reproductive	ovary, testes, gonad, uterus, prostate gland, oviduct, epididymides, reproductive system
Musculoskeletal	skeleton, bone, hind limb, fore limb, muscle, musculature
Adipose/fat storage	adipose depot, fat

Of the ten system types included in our database, the digestive system (182 studies), circulatory system (144), and excretory system (81) are the most extensively studied (Figure 5). Most of the remaining systems are each represented by between 35 and 49 studies. The endocrine system is the least studied system, with only 26 studies (Figure 5). Across all organs included in the database, the liver is the most frequently studied, featuring in 68.5% of studies and measured in 171 species (Figures S3 and 6, and supplementary information). The spleen, heart, and kidneys follow, having been measured in 94, 93, and 80 studies, respectively (Figure S3). Only one species, the rat (*Rattus norvegicus*), is represented across all system categories (Figure 6).



325
326 **Figure 5.** Number of studies included in the organ size database, grouped by system.

Figure 6. Phylogenetic relationships and system distribution among 363 species. Green bars represent the systems that were measured in each species, while grey bars indicate missing data for a given species. From the centre outwards: digestive, adipose tissue, circulatory, excretory, nervous, musculoskeletal, reproductive, respiratory, endocrine, and immune systems. Silhouettes indicate major taxonomic groups (sourced from www.phylopic.org, public domain).

To our knowledge, we have compiled the most comprehensive database of paired organ size and body size data to date. We anticipate that this resource will make a significant contribution to understanding the factors influencing organ size scaling and will serve as a valuable foundation for future research into the physiological and evolutionary significance of these relationships. By systematically collecting paired data on organ and body size for both invertebrates and vertebrates, our database provides a robust basis for improving the parameterisation and cross-species applicability of simulation models grounded in physiological and kinetic principles[15–18]. In turn, this enhances predictive accuracy and ecological relevance, supports more rigorous risk assessments, and facilitates simulations of chemical accumulation across a wide range of animal taxa.

Technical validation

As one researcher (FPLeiva) was responsible for extracting 100% of the data (10,604 records), there is a potential risk of data entry errors. To ensure accuracy, minimise the risk of bias, and improve the reliability of the database, we conducted a double-check of approximately 28% of the entries (3,051 records). This double-checking process was performed by FPLeiva (8.05% of records, 863 records), LOckhuijsen (4.02%, 431 records), JPolinder (4.00%, 428 records), LJSchreyers (4.08%, 438 records), JXiong (4.10%, 440 records), and AJHendriks (4.21%, 451 records). Any errors identified during the double-checking stage were corrected by FPLeiva, and corrections were incorporated prior to the release of the database. Additional steps included verifying the accuracy of the names of discrete variables and their units.

Usage notes

We have provided this database along with several metadata that thoroughly describe the context in which each paired measurement of organ size and body size was collected. This enables users to incorporate this methodological information, allowing them to assess the robustness of outputs from various analyses. Special attention should be paid to how filters are applied to select subsets of the data, depending on the specific analysis being conducted and research questions. For example, to evaluate the effect of sex on the scaling of different organs with body size, the available metadata should allow for filtering to include only those studies in which both male and female specimens are present.

All materials, including the database, R code, and additional supplementary content, are provided under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International licence (CC BY-NC-ND 4.0). Users are requested to cite this publication when utilising these resources, and are encouraged, where possible, to cite the original contributing articles to ensure appropriate attribution[259]. We have provided a file containing all references included in the database (.bib) to facilitate their inclusion in future research employing this database.

Code availability

The code used for generating the figures and tables in this study is available at https://felixpleiva.github.io/organ_size_DB/. The data will be archived in Zenodo upon acceptance.

Author contributions

Conceptualization: FPLeiva; data curation: FPLeiva, LOckhuijsen, JPolinder, LJSchreyers, JXiong, AJHendriks; formal analysis: FPLeiva; funding acquisition: AJHendriks; investigation: FPLeiva; methodology: FPLeiva; project administration: FPLeiva, AJHendriks; resources: AJHendriks; software: FPLeiva; supervision: AJHendriks; validation: FPLeiva; visualization: FPLeiva; writing – original draft preparation: FPLeiva; writing – review and editing: FPLeiva, JPolinder, LJSchreyers, JXiong, AJHendriks.

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Competing interests

The authors declare no conflict of interest or competing interests

Supplementary data

Supplementary data to this article can be found in the GitHub repository associated to manuscript: https://github.com/felixpleiva/organ_size_DB

SUPPLEMENTARY INFORMATION

Supplementary methods

We conducted preliminary literature searches to refine our selection process, with the aim of achieving a manageable number of references for screening. These pilot searches took place on 23 January 2025. The initial results yielded 27,113 references from ISI Web of Science and 51,593 from Scopus. By refining our keyword combinations through these pilot tests, we reduced the results to 770 and 4,744 references, respectively. No filters—such as language or publication year—were applied during these searches.

To ensure comprehensive coverage, we also applied the same keyword combinations to ProQuest Dissertation & Theses Global to include grey literature. However, even after refining our search terms, this approach still retrieved over 23,000 references, which was unmanageable for our purposes. Consequently, we limited our final search to the ISI Web of Science and Scopus databases, as these platforms have been shown to index most of articles (e.g., see[268]).

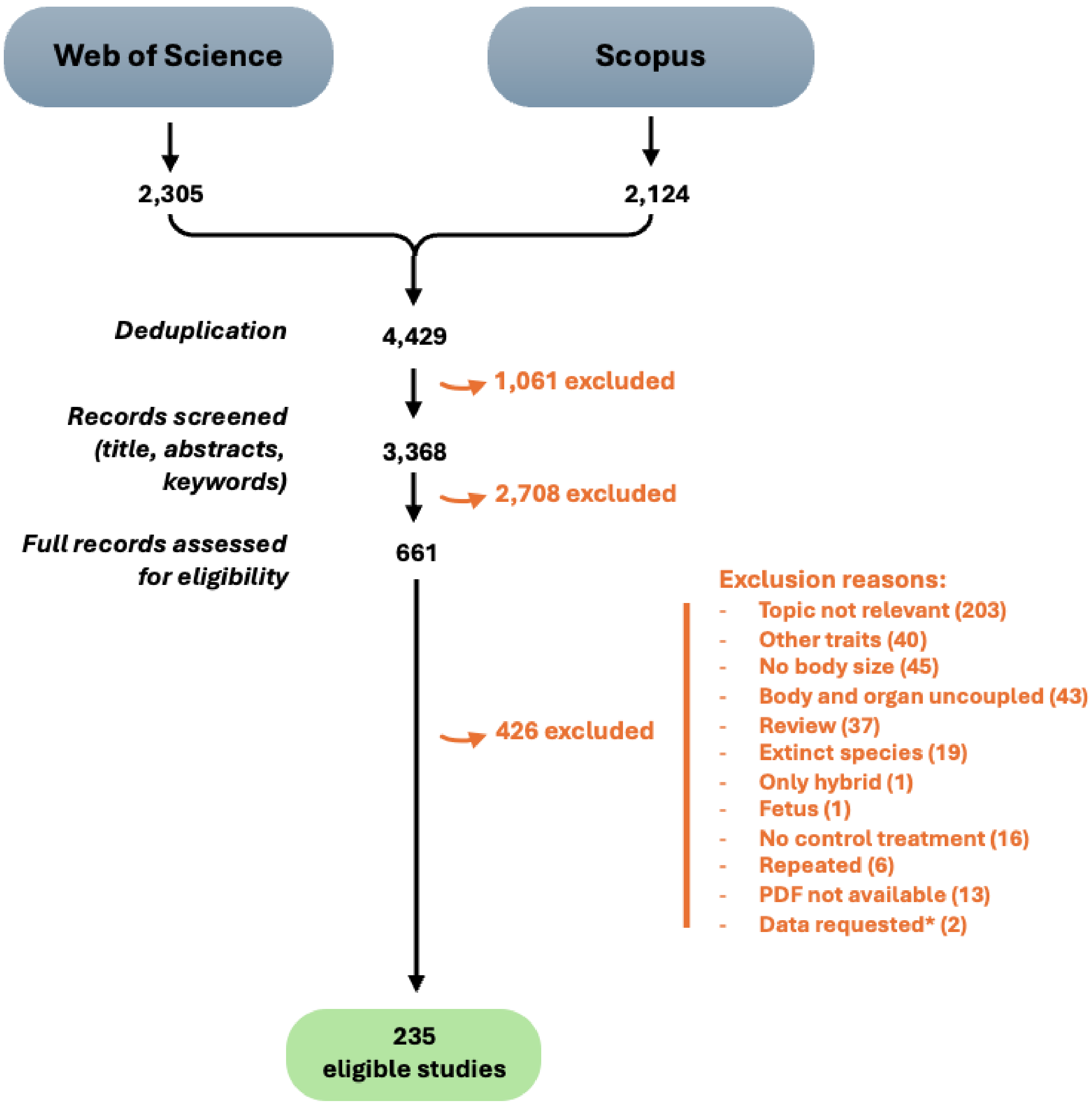

Figure S1. PRISMA-type diagram[269] showing the systematic and non-systematic literature search reporting organ size and body size pairs data. (*) We have not received responses from the corresponding author at the time of the manuscript submission.

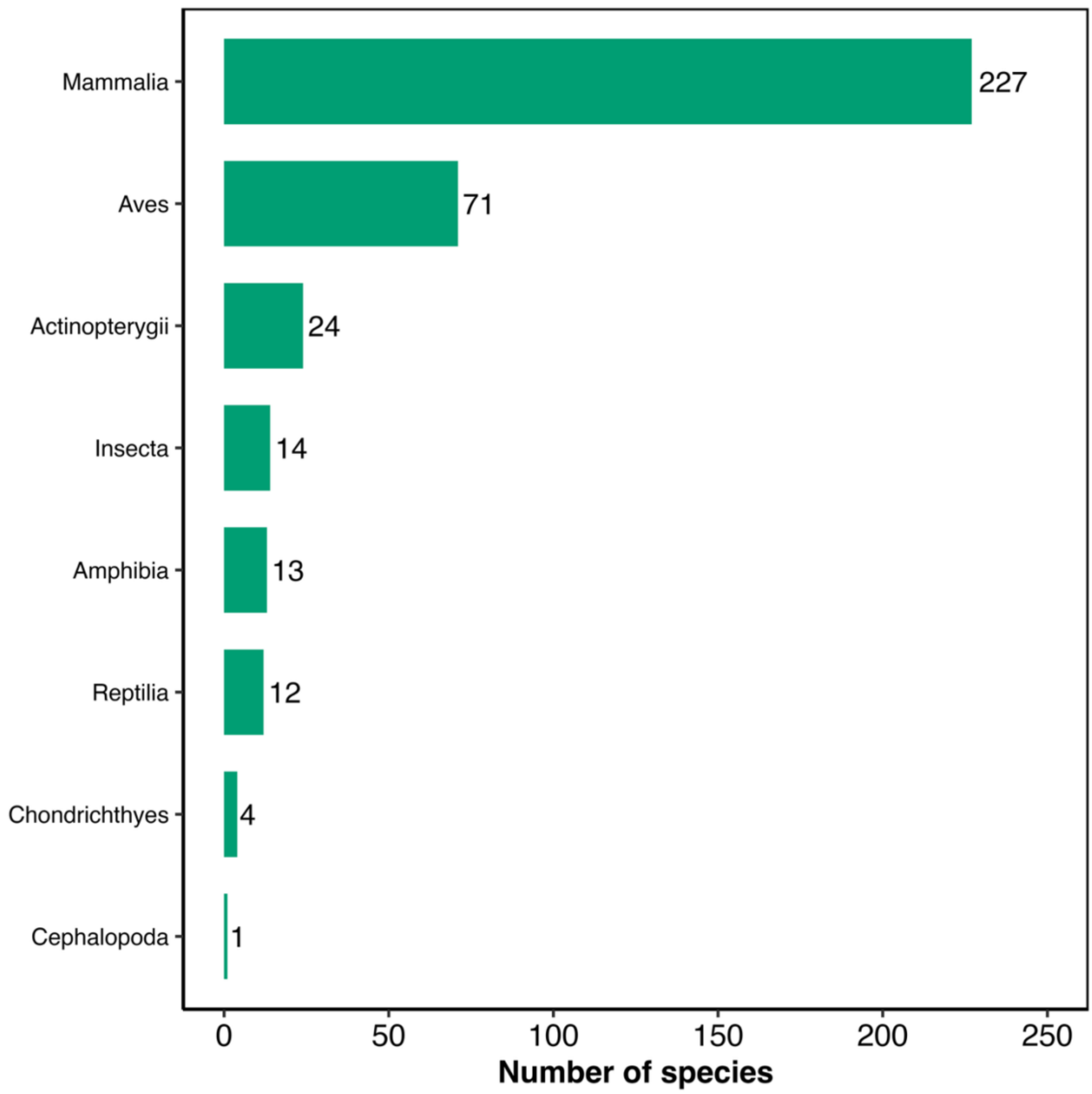

Figure S2. Number of species included in the organ size database, grouped by taxonomic class

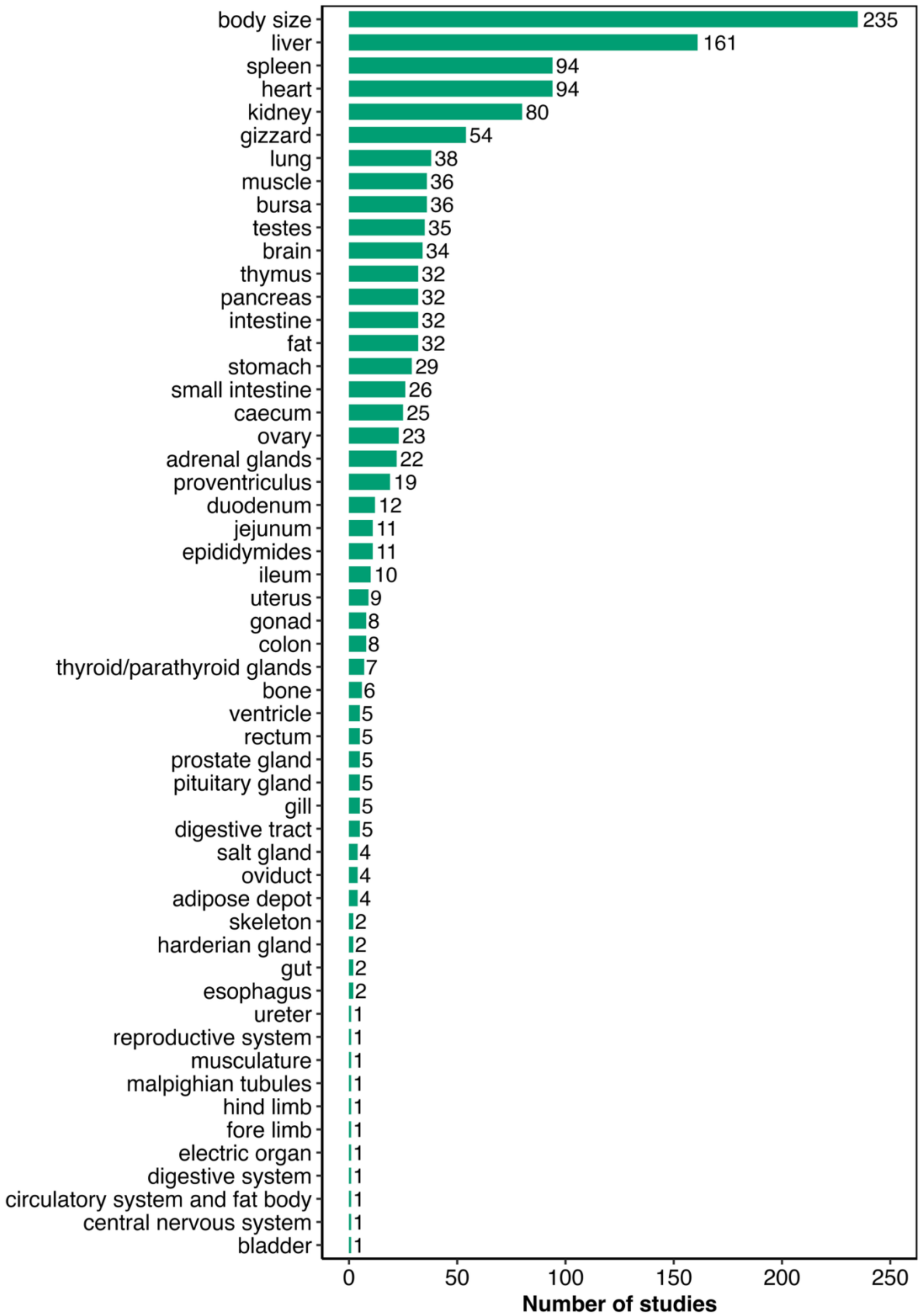

Figure S3. Number of studies included in the organ size database, grouped by type of organ.

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