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ErythroCite: a database on red blood cell size of fishes

DATA DESCRIPTOR

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Size is a fundamental trait in biology, and cell size plays a key role in cellular functions, influencing physiological adaptations and evolutionary processes in living organisms. For decades, scientists have been fascinated by the considerable variation in cell sizes among animals, yet systematic efforts to compile such data have been scarce. To address this gap, we employed a systematic map approach to create ErythroCite, an open-source database of fish erythrocyte sizes. This comprehensive resource encompasses 1,764 records from 660 species among four major lineages: Actinopterygii, Chondrichthyes, Dipnoi, and Cyclostomata. Our findings reveal a remarkable 414-fold range in cell volume, with most studies on bony fishes and limited data on juveniles and earlier life stages. Life stage and sex were infrequently reported, but available data showed equal representation of adult of females and males. ErythroCite offers valuable insights for studies in macroecology, macrophysiology, comparative physiology, evolutionary biology and cell biology. We anticipate this resource will facilitate comparative approaches and meta-analyses, globally driving further exploration of erythrocyte diversity and function in fish.

Introduction

Size plays a pivotal role in biology due to its profound impact on the functioning of life¹. For centuries, scientists have been fascinated by the causes and consequences of size-related variations among organisms. Although much of this interest has centred on overall body size, the exploration of cellular characteristics can be traced back to 1675, when the description of human red blood cells was provided^{2,3}. Two centuries later, in 1875, George Gulliver's illustrations revealed a remarkable variation in sizes of blood cells across vertebrates⁴. Gulliver's work enhanced the understanding of erythrocyte diversity within the animal kingdom, particularly regarding characteristics associated with the variation in size of erythrocytes.

In most vertebrates, erythrocytes, or red blood cells (RBCs), represent the predominant blood cell type and the most abundant cellular component, playing a central role in metabolic physiology⁵. Their functionality stems primarily from haemoglobin, a specialised oxygen- and carbon dioxide-binding protein that facilitates the physiological process of oxygen delivery from respiratory organs to tissues^{6,7}. Moreover, erythrocyte characteristics provide insights into how species have physiologically adapted to different environmental conditions^{8–11}. Recent studies have demonstrated that cell size significantly influence ectothermic species' responses to rising ambient temperatures^{12–15}. Additionally, studies indicate intercorrelations between cell sizes across various organs

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and tissues¹⁶. This systemic relationship positions erythrocyte size as a simple yet useful proxy for assessing whole-organism cellular dimensions^{17,18}. However, despite the importance of cell size in monospecific studies and multi-species comparison on other vertebrate groups¹⁹, there is currently no comprehensive, up-to-date database on RBC characteristics across diverse species.

To address this knowledge gap, we developed ErythroCite, the most extensive database of cell size-related traits to date, incorporating data for 660 fish species. ErythroCite goes beyond merely cataloguing blood cell size by integrating phylogenetic relationships, biological traits, and ecological information of four lineages of fishes. We focused on fish as a starting point for several reasons. First, fish account for approximately 50% of all vertebrate species, with over 35,000 described species²⁰. Their erythrocytes are distinctively oval, flattened, and biconvex in shape²¹. Unlike the enucleated red blood cells of mammals, these nucleated cells offer valuable insights into the evolutionary adaptations of other ectothermic vertebrates, such as amphibians and reptiles. Second, while both aquatic organisms and high-altitude terrestrial vertebrates face oxygen limitations, water-breathing species, such as fishes, are more frequently exposed to low and fluctuating oxygen condition. Consequently, their gas transport systems—including the properties of red blood cells—must function efficiently to ensure oxygen delivery to tissues.

Third, the availability of trait databases for fish enables integration of ErythroCite with other datasets, enhancing our understanding of factors influencing variations in cell size. Finally, the establishment of a red blood cell database for fish is necessary to enhance and update existing initiatives, such as the Animal Genome Size Database²², which includes cell size information for several vertebrates groups. This should be achieved through a systematic, multilingual approach to literature review and data collection.

We expect ErythroCite helps researchers to conduct more robust comparative analyses and investigate the adaptive significance of erythrocyte size across a diverse range of fish species, thereby facilitating a deeper understanding of its evolutionary importance. In particular, we anticipate that the creation of this database will strengthen the current theory of optimal cell size⁹, which relates cell size to metabolism of organisms.

Methods

We follow MeRIT guidelines established by Nakagawa *et al.*²³ to ensure better clarity and transparency in our reporting and description of methods. These guidelines use author initials in the methods section to attribute specific tasks to individual contributors, complementing the Contributor Roles Taxonomy system (CRediT, <https://credit.niso.org/>).

Literature searches. Our objective was to compile comprehensive data on the cytomorphology of red blood cells in fish species. Specifically, we identified studies that quantified parameters such as cell area and volume, as well as nuclear area and volume. Additionally, we collected associated geographical, biological, and ecological metadata for each entry and species. Furthermore, we gathered bibliometric information for each study for literature mapping on this subject.

The search for information was conducted by FPLeiva using three search engines: ISI Web of Science (core collection), Scopus, and Google Scholar (Fig. 1). The first two search engines were used exclusively for searches in English on 12 July 2024, utilising Radboud University's subscription to these services. The combination of Boolean search terms employed was: (red blood cell* OR erythrocyte OR RBC OR haematids OR red corpuscle* OR erythroid) AND (area OR size OR dimension OR volume OR diameter OR morpho*) AND (fish OR teleost OR shark* OR ray* OR skate OR ratfish OR ghostshark OR spookfish OR aquatic vertebrate OR elasmobranchii OR chondrichthyes OR osteichthyes OR ray-finned fish* OR bony fish*). From these searches, the full records were downloaded, including abstracts, keywords, and all relevant information, across all years and editions, and document types. Using ISI Web of Science, a total of 4,341 records were identified, whilst in Scopus, 1,039 records were found.

The search using Google Scholar was conducted on 22–24 July 2024, targeting studies published in Spanish, Italian, Portuguese, German, French, and Polish. To facilitate this multilingual search, we translated the English keywords into these six languages. For all languages except Spanish (the native language of FPLeiva), we used DeepL (www.deepl.com/) for initial translations. Native speakers then verified the accuracy of these translations: CAFreire for Portuguese, MShokri for Italian, KAlter for German, LSerre-Fredj for French, and AHermaniuk for Polish. We chose these languages to optimize the inclusion of non-English studies that could be read by at least one of the manuscript's authors. The software Publish or Perish²⁴ was used to search and extract records for each language. To accommodate Google Scholar's 256-character search string limit, we modified our initial Boolean terms for each language. We condensed the search strings while preserving the essential concepts of our research question, ensuring comprehensive searches across all target languages despite Google Scholar's constraints. Table 1 provides detailed translations of these modified search strings.

The Google Scholar searches conducted across various languages yielded a total of 3,599 studies. In total, our multi-engine, multilingual search produced 8,979 records. Subsequently, we screened these records to eliminate duplicates and evaluated their relevance based on titles, abstracts, and keywords.

In addition to our systematic searches, we employed complementary strategies to improve our literature search. For backward searches, we used a subset of the Animal Genome Size database²² (<http://www.genomesize.com/cellsize/fish.htm>) as a starting point. On the 10 of June 2024, FPLeiva accessed the latest version of this database and identified eleven relevant studies. Furthermore, FPLeiva has been compiling information on cell sizes of various ectotherm clades, including fish, through non-systematic searches. This ongoing effort added nine more studies to our review (Fig. 1).

To streamline the screening process, we utilized Rayyan²⁵, an artificial intelligence-based platform designed to expedite systematic reviews by reducing the time required for each screening step. The screening was

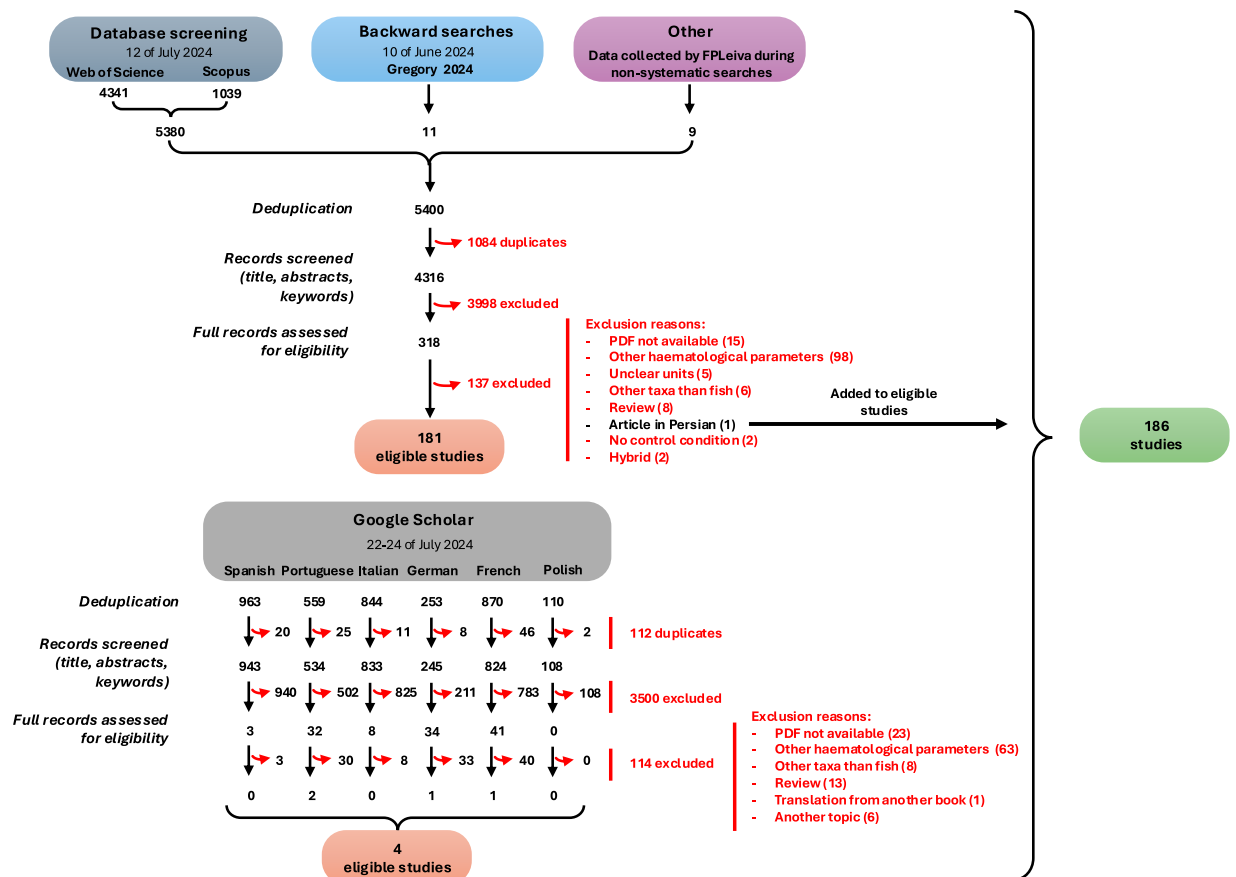


Fig. 1 PRISMA-type diagram showing the systematic literature search for studies reporting cell size measurements in fish red blood cells. For each screening and exclusion stage, the number of studies is detailed. The diagram is based on a previous study by Pottier *et al.*²⁶⁴.

conducted by different team members based on their language expertise: FPLeiva handled the Spanish and English records, while CFreire screened Portuguese studies. MShokri was responsible for Italian, KAlter for German, LSerre-Fredj for French, and AHermaniuk for Polish studies.

Eligibility criteria. We applied the following inclusion criteria: (i) only primary research articles were included, ensuring original data and appropriate credit to primary sources; (ii) we focused on species-specific data for consistency and comparability, excluding genus-level data and hybrid species; only studies measuring mature erythrocytes were considered, avoiding those including immature or developing cells; (iii) we selected studies working with diploid organisms, excluding polyploids due to potential cell size variations from different chromosomal loads²⁶, though we noted as comments when additional data were also available for polyploids; (iv) in cases involving various treatments, only studies that reported experimental control conditions as labelled in the study were considered, to ensure the results were comparable across studies in ErythroCite; (v) for the few instances in which anticoagulants were used during blood collection, we used the mean cell size, as anticoagulants can influence these measurements²⁷; (vi) and when several techniques to obtain cell sizes were employed, we prioritised data obtained from blood smears, as they provide a more consistent measure of cell size compared to live cells, which can vary in size due to their physiological state. Using these inclusion criteria, the number of studies included in ErythroCite across all languages was 186, which were all cited here^{4,28–212}.

Data extraction and metadata. We endeavoured to incorporate the direct estimates of cell area, cell volume, mean corpuscular volume, nucleus area and nucleus volume from the original studies as much as possible. However, in numerous studies, only the lengths of the major and minor axes of the cells and their nuclei were reported. When this was the case, we employed standard formulae to calculate the area and the volume of the cell or its nucleus, assuming that both the cell and its nucleus were shaped like ellipsoids or oblate spheroids^{22,213}.

The formula for cell area (A) was:

$$A = \pi \times \left(\frac{a}{2}\right) \times \left(\frac{b}{2}\right)$$

Language	Keywords combination
English	(red blood cell* OR erythrocyte OR RBC OR haematids OR red corpuscle* OR erythroid) AND (area OR size OR dimension OR volume OR diameter OR morfo*) AND (fish OR teleost OR shark* OR ray* OR skate OR ratfish OR ghostshark OR spookfish OR rabbitfish OR aquatic vertebrate OR elasmobranchii OR chondrichthyes OR Osteichthyes OR ray-finned fish* OR bony fish*)
Spanish	(glóbulo rojo* OR eritrocito OR hematíes OR corpúsculo rojo* OR eritroide) AND (área OR tamaño OR dimensión OR volumen OR diámetro OR morfo*) AND (pez OR peces OR teleósteo OR tiburón OR raya* OR quimera OR vertebrado acuático OR elasmobranchios OR chondrichthyes OR osteichthyes OR pez óseo)
Portuguese	(glóbulo vermelho* OR eritrócito OR hematídeos OR corpúsculo vermelho* OR eritroide) AND (área OR tamanho OR dimensão OR volume OR diámetro OR morfo*) AND (peixe OR teleósteo OR tubarão* OR raia* OR quimera OR vertebrado aquático OR elasmobrânquios OR chondrichthyes OR osteichthyes OR peixe ósseo*)
Italian	(globulo rosso OR eritrocita OR ematidi OR corpuscolo rosso OR eritroide) AND (area OR dimensione OR volume OR diametro OR forma) AND (pesce OR teleosteo OR squalo* OR razza OR chimera OR vertebrato acquatico OR elasmobranchi OR chondrichthyes OR osteichthyes OR pesce osseo)
French	(globule rouge OR érythrocyte OR hématides OR globule rouge OR érythroïde) AND (zone OR taille OR dimension OR volume OR diamètre OR morfo) AND (poisson OR téléostéen OR vertèbré aquatique OR élasmobranches OR chondrichthyens OR ostéichthyens OR poisson osseux)
German	(rotes Blutkörperchen* OR Erythrozyt OR rote Blutzellen* OR erythroid) AND (Bereich OR Größe OR Dimension OR Volumen OR Durchmesser OR Morphologie) AND (Fisch OR Teleostei OR aquatisches Wirbeltier OR chondrichthyes OR osteichthyes OR Knochenfische)
Polish	(czerwona krwinka* OR erytrocyt* OR hematyd* OR czerwony krwinek* OR erytroid) AND (obszar OR rozmiar OR wymiar OR objętość OR średnica OR morfo*) AND (ryba OR teleost OR rekin OR płazczka OR kręgowiec wodny OR elasmobranchii OR chondrichthyes OR osteichthyes OR oścista ryba)

Table 1. Keywords combination used to search for references in seven different languages. The non-English searches are not an exact word-to-word translation due to some limitations of Google Scholar.

The formula used for cell volume (V):

$$V = \frac{4}{3} \times \pi \times \left(\frac{a}{2}\right) \times \left(\frac{b}{2}\right)^2$$

Where 'a' and 'b' denote the lengths of the semi-major and semi-minor axes of an ellipse, respectively. These parameters were employed in the preceding equations to calculate the area (A) and volume (V) of erythrocytes modelled as elliptical shapes.

While most methods for measuring cell volume rely on fixed blood smears, alternative approaches exist. Various studies have reported mean corpuscular volume (MCV, measured in μm^3) as a proxy for cell volume. MCV is typically estimated using a standard formula, as reviewed by Witeska *et al.*²¹:

$$MCV = \frac{Ht \times 10}{RBC}$$

Where Ht is the haematocrit and RBC is the red blood cells counts.

In our database, MCV values are presented in a separate column and should be interpreted with caution when compared to cell volume measurements obtained from blood smears, as emphasized by Gregory²². This distinction is important because MCV is derived from haematological parameters, while smear measurements are obtained through direct microscopic observation. Moreover, MCV represents an average value for the entire erythrocyte population, whereas cell volume estimates from smears provide measurements of individual cells.

Despite the extensive number of studies included in this work, the collection of methodological information (metadata) related to cell size estimation was relatively limited. Nevertheless, we gathered metadata associated with collection location where the species were sourced, body size, sex, and life stage studied. When location descriptions were general (e.g., Araucanía Region, Chile), coordinates were obtained from the OpenStreetMap Data Search Engine Nominatim (<http://nominatim.openstreetmap.org>). For more specific locations, such as named hatcheries, institutes, or localities, we utilized Google Maps to determine precise geographical positions. Additionally, we provided, in an additional column, the description of the location from where the animals were sourced, which should be used to filter, for example, wild-collected animals, in case users are interested in testing latitudinal hypotheses of cell size variation. This is because, for instance, an institute location does not necessarily correlate with natural habitat conditions in the same area.

We converted fish body sizes reported in length units to wet body mass (in grams) using species-specific length-weight relationships obtained from FishBase²⁰. There was a single study, Martins *et al.*^{127,214}, providing approximately 3,700 observations for 15 fish species. For this study, we averaged the cell sizes at the specimen level (five individuals per species). For studies presenting cell size data exclusively in figures without accompanying textual or tabular information, we employed Plot Digitizer, a Java-based program designed to extract X-Y coordinates from graphs (<http://plotdigitizer.sourceforge.net>).

Taxonomy and phylogeny. The species names were scrutinised for synonyms and any updates that might influence the taxonomy. To accomplish this, we adopted the taxonomic harmonisation procedure outlined by Lenoir *et al.*²¹⁵ and Leiva *et al.*²¹⁶. This taxonomic harmonization consists of three automated steps: first, we searched for species names in the National Center for Biotechnology Information (NCBI) taxonomy database; second, we verified any unmatched taxonomic entities using the Integrated Taxonomic Information System (ITIS) database; and

third, we cross-checked remaining unmatched entities against the Global Biodiversity Information Facility (GBIF) database. If a match was identified, the corrected taxonomic entity was re-evaluated through the entire verification process in NCBI and ITIS to ensure accurate classification. Ultimately, only names at the species levels were retained in the database, with subspecies aggregated at the species level (e.g., *Catostomus catostomus*). The majority (91%) of species name verifications were sourced from NCBI, with ITIS and GBIF providing additional support. For the remaining species that could not be verified through this process, manual checks were performed using additional resources such as FishBase²⁰ and World Register of Marine Species (WoRMS)²¹⁷. When using ITIS, several species were grouped within the class Teleostei, while GBIF left most species unassigned to any class. In these cases, we manually reassigned these species to the class Actinopterygii. To address potential issues of data interoperability, we have additionally included the taxonomy of the species based on FishBase. This will allow users to more easily combine the cell size data with other fish traits, thereby enhancing interoperability between datasets from different studies²¹⁸.

We retrieved the phylogenetic relationships of the species from Open Tree of Life (OTL)²¹⁹. For *Choerodon albigena*, which lacked information in the OTL, we added it using the phylogenetic position of its sister species, *Choerodon cephalotes*.

We utilised the harmonised species list to obtain the associated realm for each species from FishBase²⁰, accessed through WoRMS on 14 November 2024, using the WoRMS Taxon Match tool²²⁰. In WoRMS, the realms freshwater, brackish, marine, and terrestrial are assigned as a binary variable (1 or 0). In our database, we recorded whether a species occupies more than one aquatic realm throughout their life. This process resulted in five categories: marine, marine-brackish-freshwater, marine-brackish, freshwater-brackish, and freshwater, reflecting the diversity of habitats that species occupy and recognising their ability to adapt to different environmental conditions throughout their life cycle.

All analyses were carried out in R version 4.3.1²²¹. The *rutils* package version 0.0.0.9²²², *readxl* package version 1.4.3²²³, *dplyr* package version 1.1.4²²⁴, *plyr* package²²⁵, *writexl* package version 1.5.0²²⁶, *tibble* package version 3.2.1²²⁷, *sessioninfo* package version 1.2.2²²⁸, *rnaturalearth* package version 1.0.1²²⁹, *tidygeocoder* package version 1.0.5²³⁰, *kableExtra* package version 1.4.0²³¹ and *DataExplorer* package version 0.8.3²³² were used to curate, format, and inspect data. The *RefManageR*^{233,234} was used to manipulate references. The *rgbif* package version 3.7.8^{235,236}, *rfishbase* package²³⁷ and *taxize* package version 0.9.98^{238,239} were used for the taxonomic harmonization. The *rotl* package version 3.1.0²⁴⁰, *ape* package version 5.8²⁴¹, *phytools* package version 2.1-1²⁴² and *ggtree* package²⁴³⁻²⁴⁷ were used to create and manipulate phylogenetic trees. The *ggplot2* package version 3.5.1²⁴⁸, *ggpubr* package version 0.6.0²⁴⁹, *fishualize* package version 0.2.3²⁵⁰, *cowplot* package version 1.1.3²⁵¹ and *ggthemes* package version 5.0.0²⁵² were used to produce figures.

Data Records

All materials, including the database, R code, and additional supplementary content are available under the Creative Commons Attribution 4.0 International licence (CC BY 4.0). ErythroCite is archived on GitHub at <https://github.com/felixpleiva/ErythroCite> and preserved on Zenodo²⁵³. This repository contains the data, metadata, and R code (<https://felixpleiva.github.io/ErythroCite/>) used for data curation, as well as for generating the figures and phylogenetic tree. References are also provided as a BibTeX file. ErythroCite will be updated as necessary to incorporate new studies and any identified corrections. In all cases, updates will comply with the standards of the Semantic Versioning Specification (SemVer, <https://semver.org/>).

Data Overview

ErythroCite encompasses over 1,700 records derived from 186 references. After applying the steps of taxonomic harmonization, the final number of unique species included in our database was 660, of which 629 were included in the OTL phylogeny (Fig. 2). In terms of taxonomic diversity, 90.2% were grouped within Actinopterygii (595 species of bony fishes), 8.6% species in Chondrichthyes (57 species of cartilaginous fishes), 0.75% species in Cyclostomata (5 species of jawless fishes) and 0.45% of the species in Dipnoi (3 species of lungfishes) (Fig. 3). To our knowledge, we have compiled the most comprehensive database of erythrocyte (red blood cell) sizes in fish species to date. We anticipate that this database will significantly contribute to understanding the factors influencing cell size variation among fishes and serve as a valuable resource for future research in macroecology, macrophysiology, comparative physiology, and evolutionary biology. However, despite its extensive coverage, our database reveals geographic and taxonomic biases, as well as a lack of reported information in biological metadata. In an ideal scenario, all species included in the current version of ErythroCite would have information on the five traits of interest (Figs. 2, 3), including those from which these traits are derived, such as cellular and nuclear lengths and widths. To address this issue, we foresee the use of phylogenetic imputation methods to fill gaps and to enhance the comprehensiveness of the database^{254,255}. This approach could significantly augment the utility of ErythroCite. Specifically, ErythroCite is expected to facilitate research in two key areas: first, by investigating metabolic theories such as the optimal cell size theory^{9,12,13,18,256-259} and hypotheses related to the development of the cardiovascular system in fishes²⁶⁰; and second, by examining how external factors such as environmental temperature influence variations in fish cell sizes, particularly the observation that species with larger cells tend to inhabit colder regions like the polar areas^{261,262}. These efforts will help identify global-scale variations in cell size by uncovering their underlying causes and analysing their effects. By integrating available metadata, we aim to enhance our understanding of the ecological and evolutionary implications of erythrocyte size diversity in fishes.

Technical Validation

To validate the entries in the ErythroCite database, we employed various approaches. FPLLeiva double-checked all entries resulting from English-language searches. In addition, MShokri and FPLLeiva reviewed a subset of studies representing 38% of the total records. No errors were identified during this stage of verification. We established a procedure to examine inconsistencies in our database, methodically

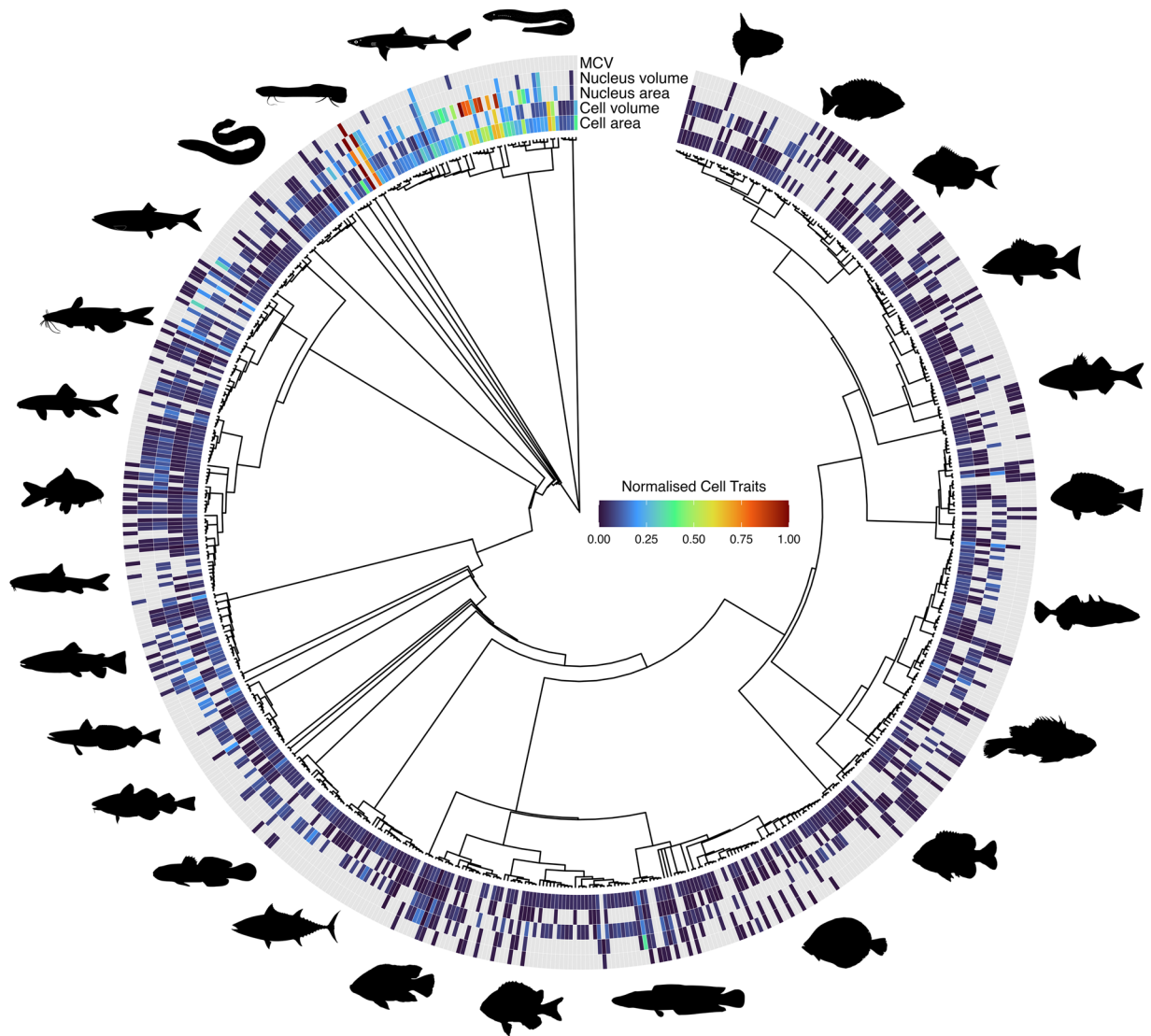


Fig. 2 Phylogenetic relationships and cell size trait distribution among 629 fishes. For illustrative purposes only, the trait values were averaged by species and then normalised by subtracting the minimum and dividing by the range. This standardisation scales all values to a range between 0 and 1. Grey bars indicate missing data for a given species. Silhouettes represent major taxonomic groups (sourced from www.phylopic.org, public domain).

detecting, assessing, and rectifying potential deviations in cell size measurements, and also covering both discrete and other continuous variables. For this purpose, we adopted some of the data verification steps outlined by Pottier *et al.*²⁶³.

We created frequency distribution plots for traits associated with any measure of cell size (cell area, cell volume, nuclear area, nuclear volume, mean corpuscular volume (MCV), cell length, cell width, nuclear length, and nuclear width) to check for outliers. For values in the distribution tails, we conducted checks not only for data entry errors but also for original calculation. Identified errors were corrected in the database. For MCV, we applied the standard formula and verified whether the resulting values closely matched those indicated in the papers. In cases of discrepancy, we considered this calculation as the corrected value, which often proved quite similar and suggested typographical errors in the original article. All these steps and potential corrections were implemented before the release of ErythroCite.

All cellular and nuclear area measurements were expressed in μm^2 , while cell volume, nuclear volume, and MCV were expressed in μm^3 . Both cell and nucleus length and width were measured in μm .

The majority of entries in our database were derived from tables, primarily aggregated as means at the species, sex, or geographical location level. Alongside the mean values, we documented the corresponding sample sizes, the number of specimens analysed, and the associated error of the mean, which can be valuable for meta-analytic approaches. Where possible, all errors associated with each estimate were converted to standard deviation.

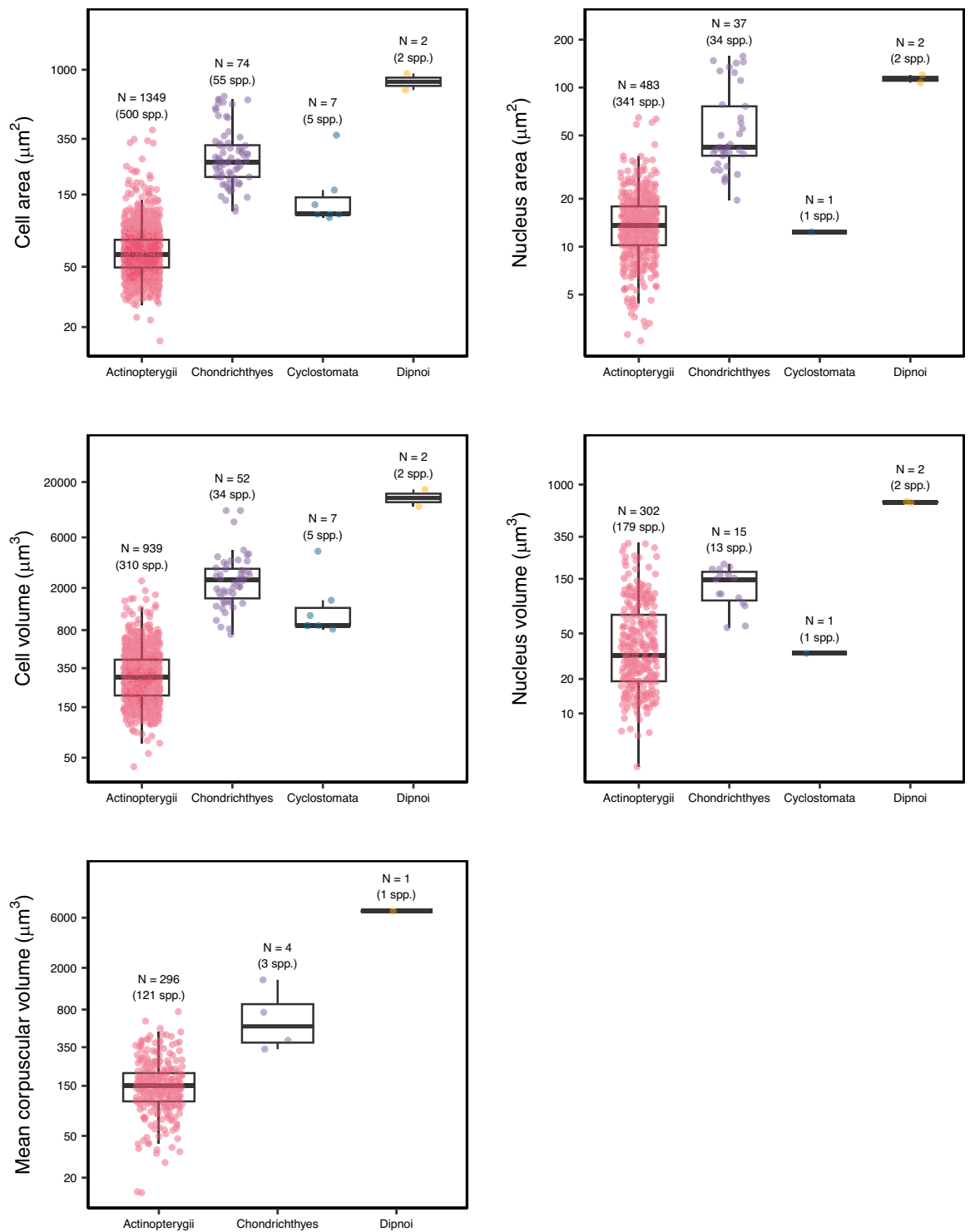


Fig. 3 Cell size of erythrocytes among major lineages of fishes: (A) cell area (μm^2), (B) nucleus area (μm^2), (C) cell volume (μm^3), (D) nucleus volume (μm^3), and (E) mean corpuscular volume (μm^3). The number of species (spp.) and records (N) measured for each of the variables is indicated above each box. No data were available on mean corpuscular volume for Cyclostomata. Boxes show median (horizontal line) \pm 1.5 times the interquartile range (whiskers). Dots represent observations for each trait.

Data availability

The data are archived in <https://github.com/felixpleiva/ErythroCite> and on Zenodo²⁵³ under the <https://doi.org/10.5281/zenodo.18543381>.

Code availability

The code used for generating the figures and tables for this study is available at <https://felixpleiva.github.io/ErythroCite/>.

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