



Patterns in research and data sharing for the study of form and function in caviomorph rodents

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The combination of morphometrics, phylogenetic comparative methods, and open data sets has renewed interest in relating morphology to adaptation and ecological opportunities. Focusing on the Caviomorpha, a well-studied mammalian group, we evaluated patterns in research and data sharing in studies relating form and function. Caviomorpha encompasses a radiation of rodents that is diverse both taxonomically and ecologically. We reviewed 41 publications investigating ecomorphology in this group. We recorded the type of data used in each study and whether these data were made available, and we re-digitized all provided data. We tracked two major lines of information: collections material examined and trait data for morphological and ecological traits. Collectively, the studies considered 63% of extant caviomorph species; all extant families and genera were represented. We found that species-level trait data rarely were provided. Specimen-level data were even less common. Morphological and ecological data were too heterogeneous and sparse to aggregate into a single data set, so we created relational tables with the data. Additionally, we concatenated all specimen lists into a single data set and standardized all relevant data for phylogenetic hypotheses and gene sequence accessions to facilitate future morphometric and phylogenetic comparative research. This work highlights the importance and ongoing use of scientific collections, and it allows for the integration of specimen information with species trait data.

Key words: collections, digitization, functional traits, relational, Rodentia

Recientemente ha resurgido el interés por estudiar la relación entre morfología, ecología, y adaptación. Esto se debe al desarrollo de nuevas herramientas morfométricas y filogenéticas, y al acceso a grandes bases de datos para estudios comparados. Revisamos 41 publicaciones sobre ecomorfología de roedores caviomorfos, un grupo diverso y bien estudiado, para evaluar los patrones de investigación y la transparencia para la liberación de datos. Registramos los tipos de datos que se utilizaron para cada estudio y si los datos están disponibles. Cuando estos datos se compartieron, los redigitalizamos. Nos enfocamos en los ejemplares consultados, y en datos que describen rasgos ecológicos y morfológicos para las especies estudiadas. Los estudios que revisamos abarcan el 63% de las especies de caviomorfos que actualmente existen. Encontramos que raramente fueron compartidos los datos que se tomaron para especies, y menos aún para ejemplares. Los datos morfológicos y ecológicos eran demasiado heterogéneos e exigüos para consolidar en un solo banco de datos; debido a esta circunstancia, creamos tablas relacionales con los datos. Además, enlazamos todas las listas individuales de especímenes para crear un solo banco de datos y estandarizamos todos los datos pertinentes a hipótesis filogenéticas, así como los números de acceso de secuencias genéticas, para así facilitar eventuales estudios comparados de morfometría y filogenia. Este trabajo resalta la importancia de las colecciones científicas y documenta su uso, además permitiendo la futura integración de datos derivados de ejemplares con datos sobre rasgos ecomorfológicos a nivel de especie.

Palabras clave: base de datos relacional, colecciones, digitalización, rasgos funcionales, Rodentia

New World hystricognath rodents represent approximately 10% of all extant species of Rodentia. This group, also known as the Caviomorpha, underwent an impressive radiation resulting in four extinct and 10 extant families (D'Elía et al. 2019; Defler 2019) since invading South America in the Middle Eocene (Antoine et al. 2012). In terms of species diversity, occupied habitats, locomotor modes, and range of body sizes, caviomorph rodents are one of the most diverse mammalian clades (Ojeda et al. 2016). The rich taxonomic and ecological diversity in this group is assumed to reflect the diversification of numerous morphological features involved in resource use and the occupation of different adaptive zones (Wainwright and Reilly 1994; Foote 1997). Ecomorphology has been well-studied for certain groups of caviomorphs. For example, a considerable amount of research has examined the relationship between the cranial, dental, and limb morphology of species with fossorial lifestyles and their digging and feeding behaviors (Verzi and Olivares 2006; Steiner-Souza et al. 2010; Echeverría et al. 2017; Morgan et al. 2017).

Research on the ecology, evolution, and ecomorphology of Caviomorpha, as well as of other vertebrate clades, has benefited from recent methodological advances allowing for robust characterization of species morphology. The combination of morphometrics with phylogenetic comparative methods and the advent of large comparative life history data sets has motivated research designed to test if reported patterns are evidence of adaptation to specific ecological strategies (e.g., Arbour et al. 2019), convergent evolution, or the result of phylogenetic inertia (i.e., artifacts of evolutionary history, see Hansen and Orzack 2005).

Natural history collections are an essential resource for studying form and function in a multispecies comparative and evolutionary context. They constitute the most important source of data needed to characterize species and understand their evolutionary relationships (Funk 2018). However, museum specimens remain largely underused. For instance, the published paleontological literature is based on only a fraction of the fossils housed in collections worldwide (Marshall et al. 2018). In addition, from a digital point of view, most fossil collections represent “dark data” because they are inaccessible through web searches or computer interfaces. These issues also apply to a large fraction of Recent mammal specimens and to a large extent to the data already gathered from them. This is pertinent because approximately one-third of mammal specimens housed in collections in Latin America and the Caribbean, which house a large number of caviomorph specimens, were found to be digitally unavailable by specialized data aggregators (Dunnum et al. 2018).

Even when useful trait data are published, most are not readily accessible or formatted for immediate reuse, and are thus digitally “gray” data because of file format, complex structure, and because there is often no general way to aggregate the outputs from multiple studies (see Verde Arregoitia et al. 2018). In addition, these data are often not made public, an issue certainly not limited to mammalogy and related to multiple facets of research culture. Habit, sense of competition, fear of adverse use of shared data, as well as a lack of awareness of the different sharing platforms are compounded with unclear mandates for

making data available. These issues are gradually being recognized as barriers to data sharing (Parr and Cummings 2005; Fecher et al. 2015).

Here, we focus on ecomorphological studies of caviomorph rodents, a diverse group that has been the subject of a large body of research, with the aim of reviewing the published literature and aggregating ecomorphological resources relevant for studying the ecology and evolution of the group. First, we list and define morphological and ecological traits examined for each reviewed study; second, we list all examined museum material and where it is housed; lastly, we standardize available data on gene sequence accessions to facilitate future phylogenetic reconstructions or requests for tissue samples.

After re-digitizing and standardizing all available data from a set of relevant publications, we produced the following data products: 1) data definitions for the traits and measurements studied; 2) a directory of sources for trait data (morphology and ecology); 3) re-digitized trait data (whenever possible); 4) a Master Specimen list (collection and specimen IDs); and 5) a Master Accession list for gene sequences.

This synthesis helps us highlight the importance of natural history collections and provides a snapshot of existing patterns and practices for sharing data derived from these types of studies. By identifying taxonomic and spatial gaps in research efforts, we can also recognize and highlight opportunities for future study. We expect that this list of resources will be of use to those wishing to work with caviomorphs, either as a guide for designing morphometric protocols, or planning collection visits, requests, and loans. We also hope that this study serves as an example that can be emulated with other taxonomic groups.

MATERIALS AND METHODS

Literature data.—We searched for articles published up to October 2019, using the following search terms in the Google Scholar search engine (<https://scholar.google.com/>): [(caviomorph) AND (“eco-morphology” OR “ecomorphology” OR “morphometric”)]. We did not use word truncation or wildcards because Google Scholar uses automatic word stemming. We also examined the literature cited in the chapters relevant to ecomorphology in a specialized compilation on caviomorph diversity and evolution (Vassallo and Antenucci 2015). We considered only those studies that analyzed morphology or morphological diversification in relation to ecology in a multispecies comparative context. Under these criteria that emphasize research into form and function across multiple extant taxa, we did not include various studies that also focus on caviomorphs and use morphological data such as descriptions of new species, or studies focusing on species delimitation, geographic variation, or phylogeography. To characterize ecology, we focused on habitat types, diet, and locomotor strategies because these traits are widely used and relevant to species’ ecosystem function.

Digitization.—For the majority of the studies in our sample, we relied on the data provided in the online (HTML) or binary (PDF) versions of the files, which were often presented as appendices or tables in the main text. A small proportion of

studies provided supplementary material or uploaded data to specialized repositories. We followed a set of technical recommendations for sharing data in mammalogy (Verde Arregoitia et al. 2018) to restructure all relevant data, specimen lists, and supplementary files into analysis-ready tables, defined here as data in a rectangular layout with rows and columns, a single header row, and a minimal set of variables shared between these tables that allowed us to manage our data as a collection of linked tables. The relationships between our re-digitized data products are summarized in Fig. 1.

We aimed to follow a reproducible digitization workflow that would minimize the amount of manual data entry, to avoid modifying the original values through typing mistakes, omissions, and inadvertent reshuffling. In this way, any errors would be reproducible and traceable when comparing the re-digitized data with the original version as a last step in the process. For re-digitizing the data, we relied on *pdftools* (Ooms 2018) and the *tidyverse* (Wickham et al. 2019) suite of R packages.

We did not attempt to interpret or correct a small number of duplicated records or possible errors in the original data sets. These possible errors included inconsistencies in the abbreviations used for morphological measurements, or two or more specimens from different species or localities reported with the same collection ID. To avoid issues with file encoding, we replaced special characters in author surnames (e.g., ã with a, and é with e) that we used in file names and as identifying variables in the flat tables. We also removed notes, units, superscript notations, and footnotes from table values, leaving only one value per cell.

Collections.—Given the importance of voucher specimens, we standardized collection names and acronyms reported in all lists of specimens examined. We used the register of Mammal Collections in the Western Hemisphere recognized by the American Society of Mammalogists (Dunnum et al. 2018) as the main source of formal institutional names and acronyms. For collections not present in this list, we used the WikiSpecies institutional data summaries (<https://species.wikimedia.org/wiki/Category:Repositories>), the glossary in Patton et al. (2015), and the Global Registry of Biodiversity Repositories (May 2018 version, <https://www.gbif.org/grscicoll>).

RESULTS

We identified 41 relevant studies, published between 1999 and 2019. These may not include all existing works on such a

well-studied group, but we consider our sample to be representative in terms of taxonomic focus and topics addressed. Some studies in our sample also included fossil material and Old World representatives of Hystricomorpha. Brief statements summarizing each of the studies reviewed are listed in Appendix I, and metadata on each study (taxonomic focus, sample size, and morphometric approach) are provided in Supplementary Data SD1.

Our re-digitization of tables, appendices, and supplements yielded 120 separate files, corresponding to 28 specimen lists, ecology trait data from 30 studies, morphology data from 23 studies, trait definitions from 21 studies, gene sequence accession lists from seven studies, and landmark configurations from 11 studies. All of these tables are available as separate delimited text files in the Supplementary Material of Verde Arregoitia et al. (2019). We then aggregated each data type (e.g., morphology, diet, ecology, gene sequences) into separate “master lists,” also provided as .csv files, which can be explored through an interactive web application (https://luisdva.shinyapps.io/caviomorph_ecomorphology_resources_app/) built using the Shiny web application framework for R (Chang et al. 2019) that can also be downloaded and run locally (Verde Arregoitia 2019).

Importance of specimens.—The majority of the studies we reviewed (37 of 41) examined or sampled collection specimens. However, of these, only 28 provided lists of examined specimens. Most specimens were examined for morphological trait data. Cranial, mandibular, and dental characters were assessed most often, while postcranial and external characters were sampled less frequently. In parallel, genetic data were gathered from some of the specimens assessed morphologically.

In total, 4,646 specimens housed in 44 collections across 12 countries were examined for morphological data or sampled for genetic material. Although reporting of unique specimen identifiers varied among authors and studies (e.g., through subtle differences in notation, prefixes, or letter case), we found that approximately one-third of all specimens were examined for at least two distinct studies. In our compilation, the most “popular” voucher was a specimen of the southern tuco-tuco, *Ctenomys australis* (MLP7.XI.95.6), housed at Museo de la Plata in Argentina, which was examined in seven studies. Most of the specimens examined were located in South American collections, but collections in the United States and Europe also housed specimens that were examined.

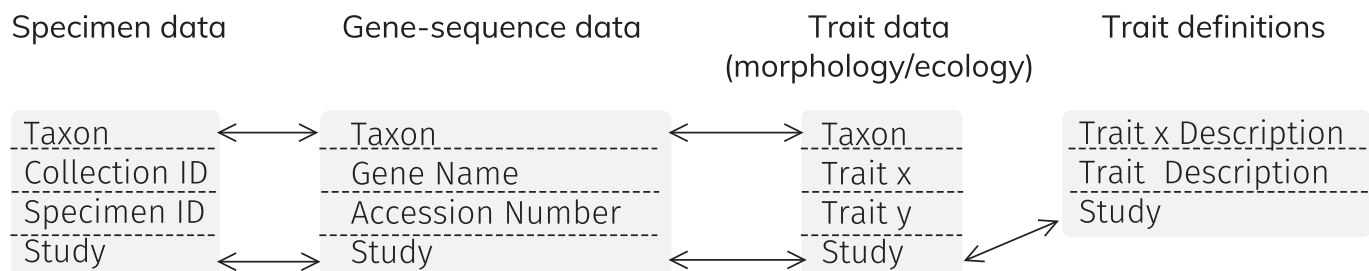


Fig. 1.—Schematic representation (Entity Relational Diagram) of the relational data structure used to aggregate and query the re-digitized data products. All the data collected from the literature were assigned into one of the four categories shown, and each separate file contained at least one of the two variables used to link tables together (taxon or study).

Ecomorphological traits.—Thirty-seven studies considered morphological traits, but only 23 of the studies provided morphological trait data, often averaged for species or genera. Specimen-level raw data were rarely provided (Table 1). Two noteworthy examples (Elissamburu and Vizcaíno 2004; Candela and Picasso 2008) provided detailed specimen-level data. To aid future research that considers morphology and specimens, we digitized trait definitions or morphometric protocols (landmark configuration tables) of all listed studies (Verde Arregoitia et al. 2019). To interpret morphology in an ecological dimension, ecological traits were considered in 30 studies (Table 2). The most commonly used traits pertained to locomotor or substrate-use strategies (e.g., arboreal, burrowing), followed by descriptors of habitat preferences and distribution (e.g., preferred vegetation communities or soil types), and finally feeding or dietary habits.

Genetic and phylogenetic data.—Thirty-one of the studies assessed aspects of ecology, morphology, or diversification in a phylogenetic context, either using published phylogenetic hypotheses or by inferring new phylogenies based on morphology or DNA sequences. Eight of the studies used gene sequences to reconstruct the evolutionary relationships among taxa and provided accession data, other studies modified existing topologies. After disambiguating accession IDs and sequence versions referring to the same entry (e.g., AF007040 and AF007040.1 both referred to the same sequence), we identified nine genes and 414 unique sequences, including complete mitogenomes for 44 species. For the studies that used previously published phylogenies, the sources of phylogenetic data are provided in Supplementary Data SD1.

Taxonomic patterns.—We standardized the overall list of taxa considered across all studies using the package “taxize” (Chamberlain and Szöcs 2013) to resolve spelling variations before checking synonyms and taxonomic changes. For this part

of the analysis, we focused on species and only considered extant taxa. We aligned the taxonomy with the Mammal Diversity database (Burgin et al. 2018), but followed the classification reviewed in D’Elía et al. (2019) and included capromyids in the highly diverse Echimyidae. Across all studies, we identified 196 species of rodents, of which 169 correspond to Caviomorpha. The remaining 27 are Old World hystricognaths or muroids used for comparisons. Collectively, the studies we reviewed considered 63% of extant caviomorph species in an ecomorphological context.

We assigned each study a taxonomic scope on the basis of its focal taxa. Studies could have a wide scope (spanning multiple families), or they could focus on particular families or genera. Twenty studies were wide in scope, focusing on caviomorphs in general. Eight studies focused on Ctenomyidae (a diverse family represented by a single living genus), seven on Echimyidae, two on the superfamily Cavoidea, two on Octodontidae, and one on Erethizontidae. Two studies worked with a single genus each (*Trinomys* and *Tympanoctomys*).

Across the lists of specimens examined, all extant caviomorph families and genera were represented in at least one study and by at least one specimen per genus. This excludes the five genera of Caribbean echimyids (*Boromys*, *Brotomys*, *Heteropsomys*, *Hexolobodon*, and *Isolobodon*) that went extinct in the Holocene (cf. Mooers et al. 2009). The two most species-rich families in the clade (Echimyidae and Ctenomyidae) were represented in more studies, while the monospecific Dinomyidae appeared in the fewest studies (Table 3).

DISCUSSION

The extraordinary species richness of caviomorph rodents is accompanied by considerable ecological diversity

Table 1.—Studies of caviomorph rodents that used and provided morphological trait data, with the respective number of observations, the type(s) of structure examined, and the level of resolution of the data provided.

Study	Number of observations	Structures examined	Data resolution
Álvarez and Pérez (2019)	16	Mandibular, dental	Species
Álvarez et al. (2011b)	19	Mandibular	Species
Álvarez et al. (2013)	26	Cranial	Genus
Becerra et al. (2012)	33	Cranial	Species
Candela and Picasso (2008)	23	Postcranial	Specimen
Echeverría et al. (2017)	24	Cranial, mandibular	Species
Elissamburu and Vizcaíno (2004)	51	Postcranial	Specimen
Fernández et al. (2000)	5	Cranial, postcranial	Species
Lessa et al. (2008)	15	Cranial, mandibular, postcranial	Species
Mora et al. (2003)	10	Cranial, mandibular	Species
Morgan and Verzi (2006)	28	Postcranial	Species
Morgan (2009)	23	Postcranial	Species
Morgan et al. (2017)	3	Cranial, postcranial	Species
Ojeda et al. (1999)	9	Cranial, renal	Species
Olivares et al. (2004)	14	Cranial	Species
Perez et al. (2009)	5	Postcranial	Species
Tavares et al. (2018)	67	External	Species
Tavares et al. (2019b)	8	Postcranial	Species
Tavares et al. (2019b)	6	Cranial	Species
Vassallo and Echeverría (2009)	53	Cranial	Species
Vassallo and Verzi (2001)	23	Cranial	Species
Verzi (2008)	9	Cranial, mandibular	Genus
Verzi and Olivares (2006)	16	Cranial, mandibular	Species

(Candela et al. 2017). Comparative research has identified traits associated with their locomotor behaviors, substrate-use preferences, and diets. As such, the functional meaning and reconstructed evolutionary histories of cranial, dental, mandibular, postcranial, and external traits are gradually becoming known for several lineages of Caviomorpha. For instance, we now know in great detail about the dental and forelimb specializations for tooth and scratch-digging in lineages within the superfamily Octodontoidea that share belowground lifestyles and herbivorous diets (Lessa et al. 2008; Becerra et al. 2012; Morgan and Álvarez 2013; Echeverría et al. 2017; Pérez et al. 2017), and that echimyids share cranial and appendicular modifications that allow them to access below- or aboveground resources (Tavares et al. 2018, 2019b). However, the reviewed literature hints that a comprehensive understanding of the ecomorphological evolution of the whole caviomorph radiation is lacking. In this sense, we highlight the relevance of our review and of data sharing in general, because comparative approaches rely on data being available so they can be assembled into large data sets of multiple specimens or taxa (Davies et al. 2017). This is a key step toward understanding taxonomic diversity and its corresponding morphological disparity, for caviomorphs or any other mammalian group.

Table 2.—Studies of caviomorph rodents that used and provided data on ecological traits, with the respective number of observations per trait type (i.e., the study provided ecological data on each type of trait for n species or genera).

Study	Substrate use	Habitat and distribution	Diet
Álvarez et al. (2011a)	20		
Álvarez et al. (2011b)	20		
Álvarez et al. (2013)	15	24	
Borges et al. (2017)		24	
Candela et al. (2017)	36		
Echeverría et al. (2017)	11	24	14
Elissamburu and Vizcaíno (2004)	10		
Fabre et al. (2016)	27		
Galewski et al. (2005)	20		
Gomes Rodrigues et al. (2016)	64		
Hautier et al. (2011)		72	72
Hautier et al. (2012)		76	76
Lessa et al. (2008)	12		
Mora et al. (2003)		10	
Morgan (2009)	23		
Morgan and Álvarez (2013)	28		
Ojeda et al. (1999)	9	9	9
Ojeda et al. (2012)	11	11	
Ojeda et al. (2016)	53	53	53
Perez et al. (2009)	15		
Rocha-Barbosa et al. (2015)	9	9	
Rowe and Honeycutt (2002)		11	
Schleich and Vassallo (2003)	28		
Tavares et al. (2016a)		9	
Tavares et al. (2016b)	23		
Tavares et al. (2018)	67		
Tavares et al. (2019b)	8	8	
Tavares et al. (2019a)	6		
Vassallo and Echeverría (2009)	8		
Verzi (2008)	9		

We focused our efforts on cataloguing and “re-digitizing” published data that would otherwise be overlooked by other digitization methods and initiatives that focus on specimens. Concerted efforts, such as the “Integrated Digitized Biocollections project” (iDigBio, <https://www.idigbio.org>) and the open Vertebrate initiative (oVert, <https://www.floridamuseum.ufl.edu/science/overt/>), are now underway to collect, standardize, and make species trait data available (Kissling et al. 2018). Concurrently, specimens are going through mass digitization to provide open access to specimen images, computerized scans, and associated data (Guralnick et al. 2016). The traditional reach of museums and natural history collections has also expanded with contributions such as a recent open-access repository of 3D-scanned skulls of over 300 bat species (Shi et al. 2018). These are all valuable and appreciated efforts that place value on converting specimen data into accessible digital content, putting these materials within reach of underrepresented scientific communities (Drew et al. 2017).

In parallel, our results allowed us to summarize research patterns, and more importantly, to aggregate the relevant data provided in collections-based studies into an accessible and analysis-ready form. The data we digitized here can be queried in a number of ways or combined with new data. The interactive web application exemplifies how the data products we provided can be explored through simple relational queries in any database or programming software to produce automated reports on the studies, taxa, the type of data that have been used, and the data sets themselves, if they were made available.

This exercise can be especially useful in light of recent approaches that integrate trait data and gene sequences in novel ways (e.g., Kohli and Rowe 2019; McLean et al. 2019). Morphological trait data collected from specimens and later “rescued” from published literature are often the basis for quantifying multiple dimensions of biodiversity (e.g., functional, taxonomic, and phylogenetic) and ultimately understanding how diversity is maintained, how it varies across space and over time, and how it can be best preserved.

Even when data derived from collections are important, their accessibility often are overlooked. At a time of worrying

Table 3.—Number of extant species per family of Caviomorpha (following the Mammal Diversity reference taxonomy and modified following D’Elia et al. 2019), number of species examined per family, number of different studies that examined specimens from each family, and total of number of specimens examined per family across all studies.

Family	Total number of species	Species studied	Studies	Specimens examined
Abrocomidae	10	3	5	42
Caviidae	21	13	14	269
Chinchillidae	7	7	13	86
Tenomyidae	69	40	20	1,380
Cuniculidae	2	2	8	16
Dasyproctidae	15	8	12	164
Dinomyidae	1	1	3	3
Echimyidae	110	67	21	783
Erethizontidae	17	12	8	116
Octodontidae	14	12	16	130

disconnect between biodiversity data and voucher specimens (Troudet et al. 2018), we document, for a diverse and conspicuous mammalian clade, the ongoing usage of natural history specimens in evolutionary and ecological research. The value and scientific potential of collections increases through time. Their potential is enhanced by new genomics, ancient DNA, and stable isotope methods and technologies (Dunnum et al. 2018). Collection holdings can be queried directly in distributed databases such as VertNet (<http://www.vertnet.org>), while gene sequences can also be searched for in specialized repositories (e.g., GenBank). However, our compiled data set of standardized, usable data can be leveraged to identify the location, the research use given, and in some cases, the data collected for specimens of a given taxon. This synthesis can direct future users of natural history collections data (and data derived from them) to the location of useful physical or digital resources, saving time and avoiding unnecessary replication.

The data we collect reflects what we value, and in this study, we noted that collected data is not always shared as part of publications. In our sample of studies, valuable morphological data for individual specimens or species summaries were shared infrequently or shared in ways that would not facilitate the work of future users. It is possible that specimen-level data are made available more frequently in other types of research. For example, in a monographic description of a new species of tuco-tuco, Gardner et al. (2014) provided morphometric measurements for all specimens examined, while a macroecological study also on *Ctenomys* (Martínez and Bidau 2016) provided body size measurements for every field-caught individual in their study. We note that, in our sample of studies, gene sequence identifiers were reported consistently, related to editorial mandates. Deposition of DNA sequence data in centralized repositories has been a requirement of most journals for several years (see Ruedas et al. 2000); a similar mandate to share raw morphological trait data at useful resolutions (e.g., specimen-level measurements together with sample means), would help close gaps in the accessibility of morphological specimen data. In an era with basically no impediment to large supplementary materials files, enforcing data sharing requirements is feasible.

The morphological and ecological data provided in the studies we reviewed were too heterogeneous and sparse to aggregate into a single data set. Therefore, we created relational tables, listing and describing the data provided by the different studies alongside a web app to explore these data interactively. It would be difficult to arrive at a single data standard for all publications; but this is a laudable goal, where much improvement is needed and indeed, recent developments show promise, such as a standardized vocabulary and structure for decentralized sharing and storage of ecological trait data (Schneider et al. 2019) or a platform for collaborative evolutionary research centered around phenotypic data (MorphoBank, <https://morphobank.org>). Suitable discipline-specific technical recommendations and infrastructure to store and retrieve data can foster policies that encourage data sharing (Davies et al. 2017; Verde Arregoitia et al. 2018), as long as those producing data recognize the benefits of sharing.

We expect this contribution to be useful for future research on caviomorphs and hope it will be replicated in other taxonomic groups. This is a single case study with one taxon, and the patterns of data transparency and availability for other small mammal groups are largely unknown but likely similar to that of caviomorphs. Finally, we call on authors of future ecomorphological work to be explicit when reporting the total number of specimens and study taxa considered in their work, and the resolution of the analysis (species, genera). More importantly, researchers should share their specimen-level data whenever possible, providing human- and machine-readable versions of their data to facilitate future reuse and increase the reach and impact of their research.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Metadata for each study reviewed.

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