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Review

Jonathan L. Dunnum* and Joseph A. Cook

Gerrit Smith Miller: his influence on the enduring legacy of natural history collections

Abstract: A century after the publication of "Catalogue of the land mammals of western Europe" (1912), Gerrit Smith Miller's contributions to European mammalogy endure. His work was a landmark treatment of the European fauna and laid the groundwork for subsequent mammalogists. Miller's impressive body of specimen-based research underscores the fundamental role natural history collections have played in building our understanding of the natural world. Their relevance to basic discovery endures, as collections have evolved since Miller's time to include new materials (e.g., tissues, cell suspensions, linked host/parasites), and as new tools (e.g., genomic sequencing, stable isotopes, niche envelopes) for extracting information have developed exponentially. While still utilized for systematic and taxonomic questions, museums and associated web-based databases (GBIF, GenBank, GoogleEarth) are now critical to our ability to rigorously address questions related to environmental change (e.g., climate change, habitat conversion, emerging pathogens, pollutants and toxicants, biodiversity loss, introduction of exotics). Specimens are the primary resource that objectively documents diversity and vouchers historic conditions. By representing a particular site and time, georeferenced specimens establish critical baseline conditions against which temporal change can be investigated. As in Miller's day, museums remain centers for research and training as future generations of scientists are introduced to biodiversity studies.

Keywords: catalog; Europe; Miller; museums.

***Corresponding author: Jonathan L. Dunnum,** Division of Mammals, Museum of Southwestern Biology, University of New Mexico Albuquerque, New Mexico, USA, e-mail: jldunnum@unm.edu
Joseph A. Cook: Division of Mammals, Museum of Southwestern Biology, University of New Mexico Albuquerque, New Mexico, USA

Introduction

Museums have long played a role in understanding our natural world, and natural history collections have been integral in introducing new generations of biologists and environmental scientists to complexity on the planet. Historically, natural history collections were predominantly the arena in which taxonomists engaged in the description of biodiversity. Today, the role of these collections has evolved significantly; while still relied upon heavily to address taxonomic questions, they are now essential resources in a broad spectrum of research associated with ecology and evolution, phylogenetics, genomics, public health, and environmental change. Museum collections play critical roles in the study of emerging pathogens and environmental contaminants as the well being at the forefront of work in understanding the world's shifting biodiversity, biological invasions, and global climate change (Suarez and Tsutsui 2004).

From the specimens examined by Linnaeus for his series of Systema Naturae to the development of the seminal ideas of Wallace and Darwin, to Miller's "Catalogue of European Mammals," to today's work in areas such as genomics, emerging pathogens, and Geographic Information Systems, natural history collections have been instrumental in fostering biological understanding by providing critical components for research. Although natural history collections were amassed with particular goals in mind, their use and value has evolved. The magnitude and direction of collection growth is dynamic and driven by different factors (e.g., collaborations, donations, research interests of the scientific staff, general efforts to document biodiversity, and the need to answer specific questions important to society). An essential aspect of all the collections that are preserved in perpetuity, however, is that although the material was often collected for a specific reason or study, these specimens later will form the basis for numerous and diverse investigations. Hence, these materials, maintained as part of a permanent archive but readily available to the scientific community, form a deep temporal and broad spatial record of the Earth's biodiversity that is utilized time and time again as new questions or technologies develop. This critical component of our scientific infrastructure remains at the forefront of science because specimens now represent the only true archive of natural diversity capable of establishing historical baseline conditions. These materials are crucial to addressing questions concerning biotic response to change on the planet (e.g., climatic change, invasive species, emerging pathogens, habitat conversion, and effects of pollutants) (Johnson et al. 2011, Lips 2011, Robbirt et al. 2011, Vo Anh-Thu et al. 2011). Because natural history collections have long been centers of research and hubs of academic endeavors, many great minds and fundamental advances in science arose from the halls of natural history collections.

Gerrit Miller's meticulous specimen-based work expanded our understanding of the world's mammalian fauna and provided key insights into assessing and understanding variation within taxa. In following C.H. Merriam's philosophy, Miller created and utilized the natural history collection material in new ways. A key legacy is how he fundamentally changed systematic mammalogy by formalizing standards of operation and establishing the vital role that natural history collections play in biology by ensuring solid, repeatable science.

Miller's biography

We do not attempt to provide a full account of Miller's life and accomplishments. Our aim, instead, is to summarize biographical information from Shamel et al. (1954) within the context of Miller's development as a systematic mammalogist, the advances he brought to European mammalogy, and the role he played in the overall evolution of natural history collections in the past century.

Gerrit was born on December 6, 1869, in Peterboro, New York, to Gerrit Smith Miller and Susan Dixwell Miller. His family was wealthy, affording him the benefits of tutors, private education, and life on a large rural estate. Gerrit was shy and preferred his own company to that of other children, leading him to spend his youth exploring the woods of the family estate. There, at an early age, he developed an interest in the natural world and specifically, the natural history of animals. A key mentor in his early life was his great uncle Greene Smith, a naturalist who lived on the estate, was an avid collector, and who maintained a large ornithological collection. That collection was meticulously prepared and contained representatives of much of the avifauna of the United States. The specimens not only fostered Miller's appreciation for nature but provided his first introduction to collections and museum preparation. As was true for many young zoologists of the time, his first interest was ornithology as mammals were harder to study because traps and collecting methods were not yet well developed. His first paper, "Description of an apparently new Poocaetes from Oregon", (Miller 1888), was published in the Auk, at age 19.

He entered Harvard University in 1890 at the age of 21 and published his first mammal paper, "Description of a new jumping mouse from Nova Scotia and New Brunswick" (Miller 1891), a year later in the "American Naturalist". During his tenure at Harvard, he published 19 papers on birds and mammals. Miller graduated from Harvard with an AB degree in 1894 and took a position with the Biological Survey at the United States Department of Agriculture. There he served under the direction of C. Hart Merriam and was surrounded by many of the prominent mammalogists of the time (e.g., E.W. Nelson, W.H. Osgood, and V.O. Bailey) (Figure 1). This experience was a watershed in terms of Miller's growth as a mammalogist, and his introverted personality was at the heart of his professional success. Because he was asocial, he craved the quiet museum environment where his curious, meticulous, and perfectionist tendencies thrived.

Miller (Figure 2) worked at the Biological Survey until 1898 when he took the position of Assistant Curator at the United States National Museum (USNM). He would become Curator of Mammals in 1909 and continue in that position until 1940 (Figure 3) when he retired from that position to become an Associate in Biology.

He possessed an extremely broad mammalogical knowledge base and described taxa from North and South America, Europe, Africa, and Asia. Like Oldfield Thomas, he utilized the vast resources of the public and private collections to facilitate his systematic work.

Over the course of his lifetime, he published 400 scholarly works, including landmark efforts such as "The Families and Genera of Bats" (Miller 1907a), "List of North American Land Mammals in the United States National Museum" (Miller 1912a), "Systematic results of the study of North American land mammals to the close of the year 1900" (Miller and Rehn 1901), and "List of North American Recent Mammals" (Miller 1924). Over 300 taxa (1 family, 1 tribe, 7 subfamilies, 27 genera, 6 subgenera, 92 species, and 178 subspecies) that he described remain valid (Wilson and Reeder 2005).

His "Catalogue of the Land Mammals of Western Europe in the British Museum" (1912b) was emblematic of his contributions outside North America and solidified his status as a major contributor to modern European mammalogy.

Figure 1 Biological Survey members working at the U.S. National Museum at the turn of the last century. Left to right: A.K. Fisher, E.W. Nelson, W.H. Osgood, and V.O. Bailey (reprinted with permission from USGS-Patuxent Wildlife Research Center's Biological Survey unit).

Contributions to European mammalogy

Miller's impact extended far beyond his scholarly works on systematics and taxonomy. The methods and philosophy of the "American School of Mammalogy", including the systematic study of large series of uniformly prepared small mammal specimens from all available localities, developed under Merriam were not yet in use by European mammalogists. Miller's most important early influence in Europe involved the introduction of these new museum and field methods. The newly developed "Cyclone" small mammal trap and the methods in small mammal collection were demonstrated in 1894 at the British Museum where they were adopted by Oldfield Thomas; these methodologies quickly spread to France, Germany, Russia, and Japan (Miller 1929). Miller's "Directions for preparing study specimens of small mammals" (1899, reissued in six editions) formally brought the new museum techniques to young mammalogists of Europe and helped standardize trapping protocols and specimen preparation. Additionally, his perspective on subspecies and the importance of examination of large series of specimens to understand geographic variation were critical influences on European mammalogy.

Figure 2 Gerrit Smith Miller circa 1897 (reprinted with permission from USGS-Patuxent Wildlife Research Center's Biological Survey unit).

Miller began working on European taxa about the turn of the 20th century. Prior to publication of the "Catalogue", he had published over 25 papers on European mammals including descriptions of over 60 new taxa (Miller 1901a,b,c, 1903, 1907b,c, 1908, 1909, 1910).

Oldfield Thomas, curator at the British Museum at the time, regarded the creation of a catalog on European mammals as essential. Thomas was impressed by Miller's previous work on European mammals, and in an effort to have Miller's work published out of the British Museum, he induced Miller to write a comprehensive catalog for the

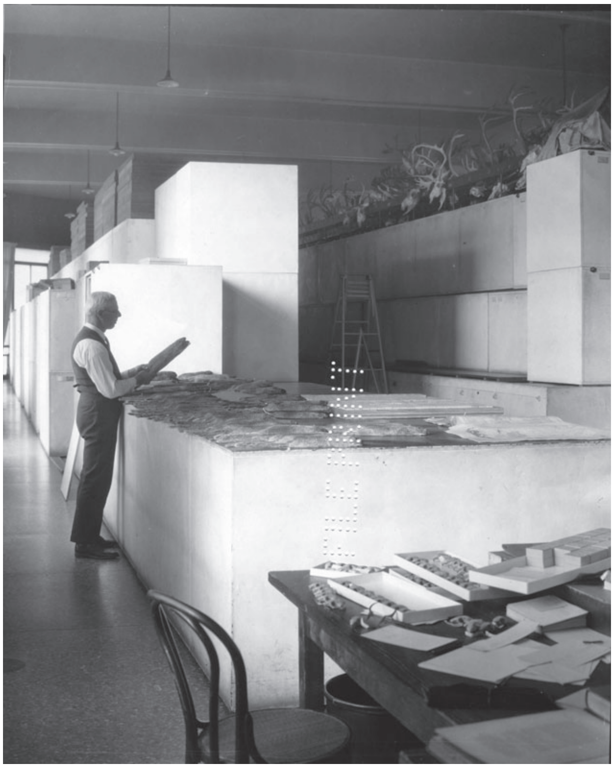

Figure 3 Gerrit Miller comparing ground squirrel skins in the collections of the NMNH (reprinted with permission, Smithsonian Institution Archives - Image MNH-1246).

British Museum. Thomas funded the effort, and in 1905, Miller arranged to devote his entire time to the study of European mammals. In 1908, he was granted a 2 1/2 year furlough from the USNM to spend time in Europe working on the manuscript and collecting specimens (Shamel et al. 1954). In all, the catalog drew upon information derived from 11,500 specimens; 5,000 from the British museum, 4,000 from the USNM, and the remainder from other collections in the US and Europe and targeted field collections made by Miller and others to fill gaps. In addition to the USNM and British Museum collections, Miller utilized material from the museums of Madrid (types of Cabrera), Nimes (types of Crespon), Paris (types of Geoffroy and other historic specimens), Genoa (Italian bats, microtines, and ungulates), Turin (Italian mammals), Naples (type of *Myotis oxygnathus* Monticelli), Geneva (types of Fatio, authentic Swiss specimens of *Lynx*), Lausanne Agricultural School (skull of *Ursus* "formicarius" from the Alps), Munich (type of *Spalax graecus* Nehring), Berlin Agricultural High School (type of *Arvicola ratticeps stimmingi* Nehring), Breslau (skulls of foxes), Leiden (co-types of *Arvicola arenarius* de Selys-Longchamps), Copenhagen (*Mus faeroensis* and small carnivores), Christiania (*Sorex*, *Evotomys*, etc.), Stockholm (Swedish carnivores and rodents), Cambridge (*Mustela erminea ricinae*, *Lemmus lemmus* "crassidens"), and Edinburgh (rodents from northern Scotland) (Miller 1912b).

Supplementing the material from the public museums, Miller accessed a large number of private collections, including those of Charles Mottaz in Geneva (3000 French, Swiss, and Italian specimens), C.H. Merriam (numerous European specimens received from de Selys-Longchamps), Angel Cabrera of Madrid (Spanish mammals, including several types), Enrico Festa of Turin (Italian mammals), Angelo Ghidini of Geneva (Swiss and north Italian mammals), and Fernand Lataste of Cadillac-sur-Garonne, France (carnivores and microtines) (Miller 1912b). In short, no other monograph, to date, had utilized the breadth of materials that Miller incorporated or, for that matter, relied so heavily on the holdings of natural history collections. The breadth of collections required for Miller's work illustrated the inherent value of voucher material but also demonstrated the role that both small regional collections and large scale national museums have in documenting diversity.

The "Catalogue" built upon the monographic works of Blasius (1857) and Trouessart (1910), laid the taxonomic foundation used by subsequent mammalogists working in Europe, and represented the first comprehensive treatment to assess variation within the European fauna. Miller recognized 197 species from 69 genera, excluding the marine or partially marine taxa. Although difficult to compare precisely due to variations in geographic coverage and inclusion of exotics, the most current taxonomic treatment of European taxa covered about 164 species from 75 genera (Mitchell-Jones et al. 1999).

The format included extensive information that we now accept as standard in current systematic works. In questions of nomenclature, Miller followed the International Code and the rulings of the Commission strictly and consistently. For each taxon, synonymies, type localities, and distributional information were presented. The accounts were comprehensive, including extensive diagnoses, external, cranial, and dentition character descriptions and illustrations. Tables of external and cranial measurements illustrated the sexual and geographic variation within taxa.

Miller passed away on February 24, 1956 and was widely regarded as one of the most outstanding American mammalogists of his generation (Figure 4). The significance of the "Catalogue" (and Miller's other specimen-based work) extended beyond its utility as a taxonomic foundation for further mammalogical work in that the inclusion of the lists of specimens examined provided the essential link between the publication and the museum voucher specimens. This simple connection is fundamental

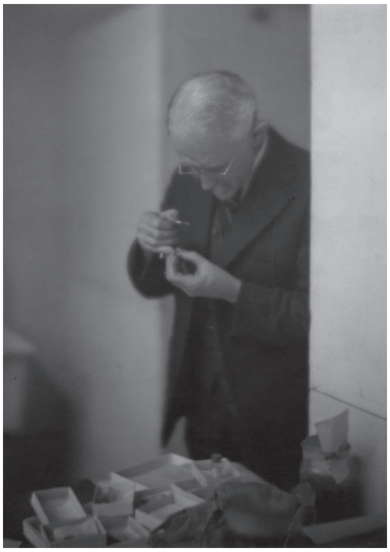

Figure 4 Gerrit Miller examining skeletal material during his later years at the NMNH (reprinted with permission, Smithsonian Institution Archives - Image SIA2012-10006).

in establishing repeatability in science by allowing future investigators to return to the precise materials that form the basis for the research. The voucher model demonstrates how properly archived and cited specimens play a critical role in facilitating future tests of conclusions reported in publications or even data available in the ethersphere. This connection between data and specimens is a vital legacy from Miller and others at that time that museums strive to ensure endures into the future. A vivid example of the importance of repeatability is the growing genomic databases such as GenBank that are rife with errors (Longo et al. 2011). Accuracy of these online mega-databases can be verified only for those genetic accessions that are tied to permanent samples (e.g., museum voucher specimens) (Ruedas et al. 2000, Pleijel et al. 2008). Only in these cases, can future scientists test, retest, and build upon previous genomic research.

The concept of what constitutes a voucher specimen and associated data has also evolved through time. What was the standard of the day has changed and hopefully improved through time. Miller was the conscience of this evolution in the concept of a voucher specimens as he wrote of the collections of the British Museum, "The older material, though not extensive, includes much that is of historic interest, such as the numerous specimens received from the late Baron E. de Selys-Longchamps, the types of various species described by Gray and Bonaparte, and Darwin's Porto Santo rabbits. It is, however, from the recently obtained material that the collection derives its true value. These specimens are almost without exception carefully prepared skins accompanied by skulls and measurements, together with full records of sex, date, and exact locality" (Miller 1912:v).

Today, we reemphasize Miller's sentiment that our challenge as museum scientists is to ensure that today's collections are as relevant as possible for current research, but also broad and varied enough that unanticipated uses in the future can be addressed. The well-documented material Miller utilized still serves as an irreplaceable baseline for those species and their environment; however, the utility of Miller's specimens for answering many of today's questions is also limited. As the tools used for extracting information from specimens improved, and the questions asked about the specimens expanded, so has the need for new preservation techniques, a wider array of specimen parts, and more integrated approaches (e.g., parasites and viruses) to the original field collections. While the traditional skin and skeletal preservation types remain as important aspects of scientific vouchers of mammals, the collection of material such as frozen tissues, cell suspensions, and parasites is now considered standard procedure. Kageyama et al. (2007) suggest a new, broader definition of voucher "A specimen, a sample, or product thereof, and its associated data, that documents the existence of an organism at a given place and time in a manner consistent with disciplinary standards, to ensure the repeatability of research which otherwise could not be adequately reviewed or reassessed." and proposed the terms "primary voucher" to describe a voucher that physically and visually documents the existence of an organism and "secondary vouchers" to denote the derived products that provide supplemental information about an organism.

Given our current tools for extracting and analyzing genetic information, in many instances, "secondary vouchers" such as cryogenic tissues can provide more insight into the questions related to the evolutionary history, feeding habits, and coevolved viruses and parasites of an organism, than the "primary voucher". Thus, the voucher concept has evolved significantly, with the value of each component changing depending on the technological advances and the focus of research questions. An overriding principle that remains constant is that the specimen value depends on the quality of associated temporal and spatial data.

Individual specimens have the potential to contribute to science for as long as they exist. For example, in 1984, a specimen of *Andalgalomys pearsoni* was collected from Santa Cruz department, Bolivia, and deposited in the Museum of Southwestern Biology (MSB 55245). Three years later, this specimen was designated the holotype of *Andalgalomys pearsoni dorbignyi* by Olds et al. (1987). Over the course of the next 25 years, this specimen represented

A. p. dorbignyi in at least six major taxonomic works, and the specimen was further utilized in nine other publications (Figure 5). The majority of these were molecular phylogenetic studies utilizing genetic sequence data downloaded from GenBank. The deposition of specimen-based sequences in GenBank has had major consequences by expanding the accessibility of museum resources to a wider array of the scientific community (e.g., molecular geneticists). Second, GenBank amplifies the value of individual specimens because the DNA sequences for rare species tend to be used in numerous successive projects. Often, a single specimen then becomes a voucher for many independent scientific studies, and these, in turn, are now highly integrated because all are linked through the same individual. Thus, the value of each specimen increases with time as the number of studies associated with it multiplies.

The challenges for museums today and their role in developing the next generation of scientists

Human impact on the biosphere has increased exponentially over the last century. As a result, we face many critical

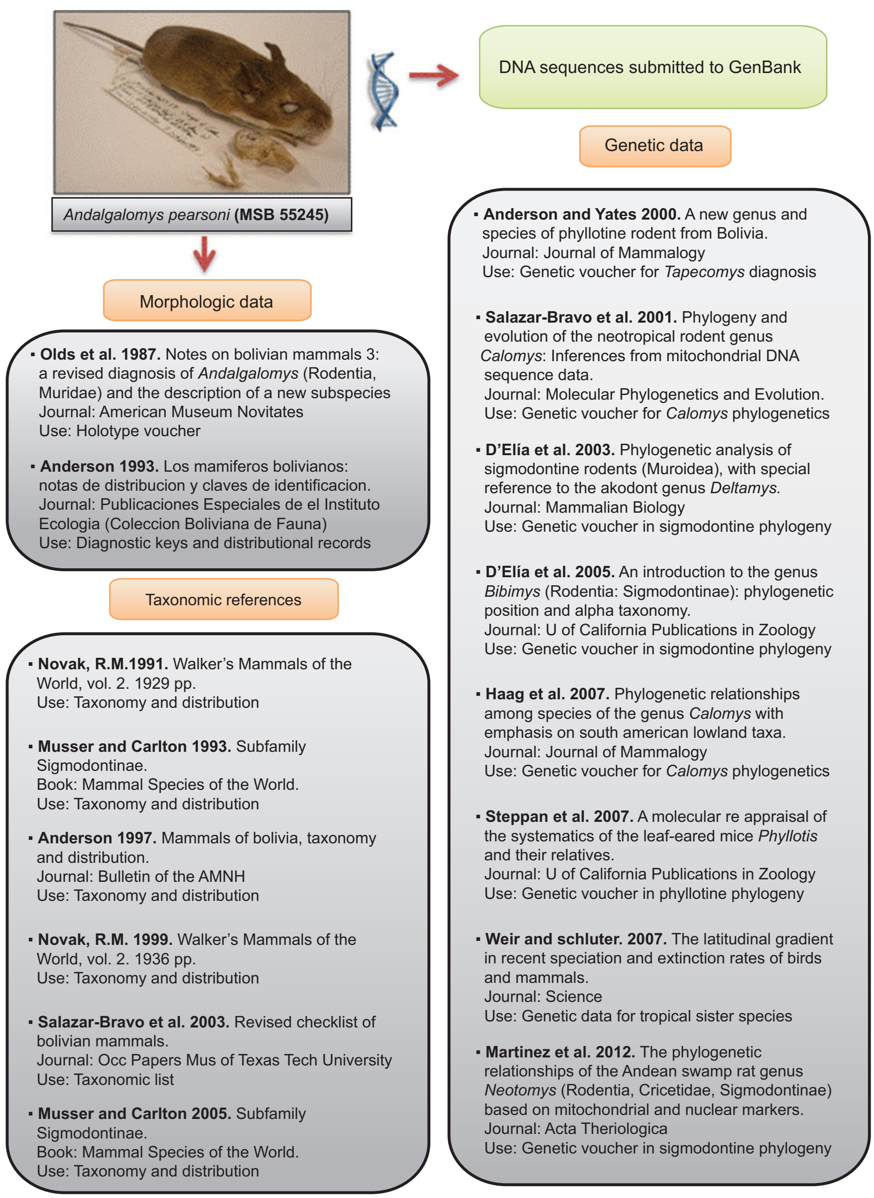

Figure 5 *Andalgalomys pearsoni* dorbignyi (MSB 55245) and array of studies utilizing information from this single specimen.

challenges, including the need to predict and mitigate the consequences of rapid climate change on biodiversity, human health, and ecosystem services. Meeting these challenges will require innovative solutions from a new cohort of scientists who are able to integrate across disciplinary boundaries and make sense of the mega-datasets emerging onto the web. Natural history collections form the nucleus of a dynamic interdisciplinary network necessary for understanding and addressing these challenges (Figure 6).

Natural history museums have a distinguished record of engaging the next cohort of scientists. Many innovative scientists (e.g., Edward O. Wilson) credit early enthusiasm for science to their first-hand exposure to exploring our planet's rich diversity through collecting specimens. Because museum collections are becoming more accessible due to online availability of natural history databases, students, educators, and the general public alike can more easily investigate the natural world through the use of web-based tools (e.g., Google Earth, BerkeleyMapper, GBIF, Tree of Life, Encyclopedia of Life). To date, informatics-based efforts to tap the vast resources of natural history collections have been limited, but models that allow wider entry into these incredible archives are now being developed (e.g., AIM-UP.org). These new approaches to the study of biodiversity, conservation, ecology, climate change, and evolutionary processes will allow real-time exploration of the extensive archives and cyberinfrastructure of natural history museums, which underlie much of our scientific understanding of the diversity of life on earth. Providing students with skill sets that allow them to integrate broadly across disciplines or multiple datasets is essential, but science curricula in most high schools and undergraduate programs are too specialized and generally limit experiential learning. Natural history collections represent a multitude of biodiversity through their specimens, each of which is georeferenced and time stamped. In addition, many specimens now voucher DNA sequences or other genomic information that is available online. These vast storehouses of biodiversity information thus provide key temporal and spatial components to the emerging arena of bioinformatics.

Miller's vast array of specimen-based work and the tens of thousands of publications that have subsequently utilized museum material, demonstrates the relevance of collections to basic discovery, underscoring the fundamental role that natural history collections have played in building our understanding of the natural world. In this

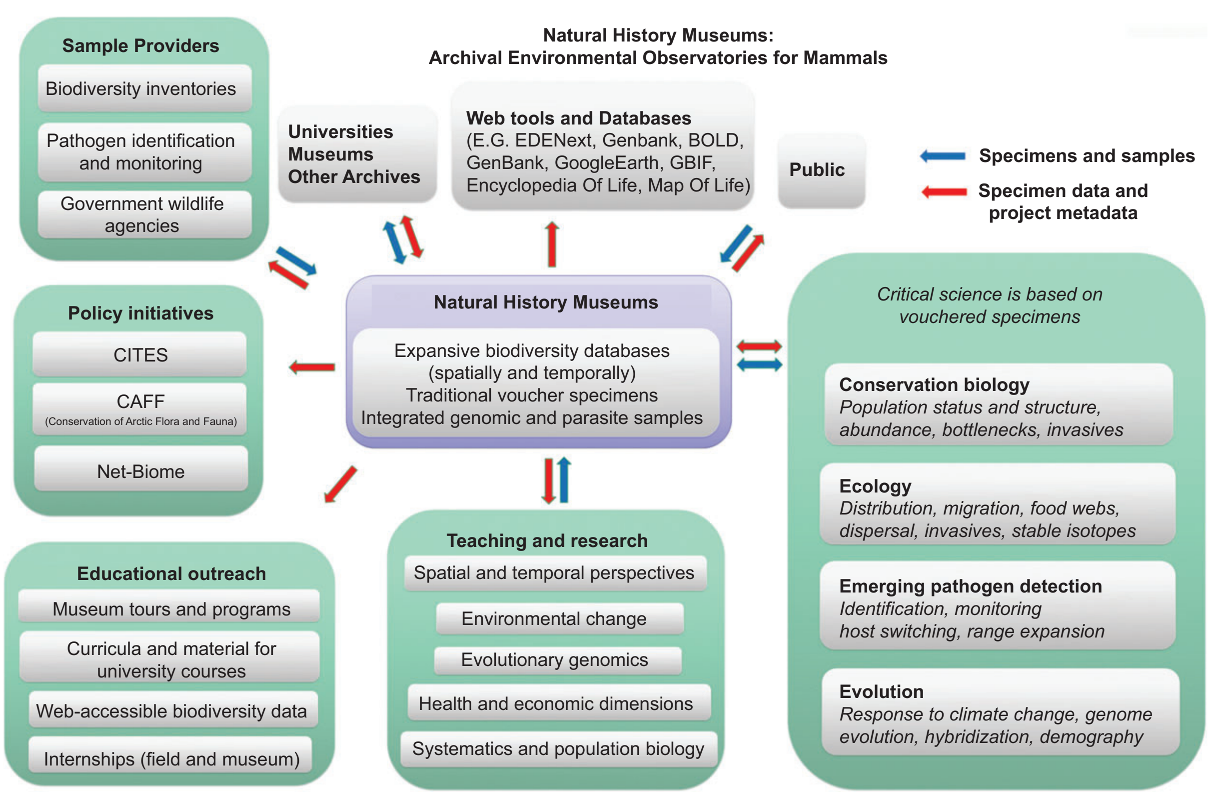

Figure 6 Natural history collections: archival environmental observatories for mammals.

time of unprecedented biodiversity loss, the significance of natural history collections and their value for future environmental science cannot be understated.

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