



INVITED PAPER

## How many species of mammals are there?

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Accurate taxonomy is central to the study of biological diversity, as it provides the needed evolutionary framework for taxon sampling and interpreting results. While the number of recognized species in the class Mammalia has increased through time, tabulation of those increases has relied on the sporadic release of revisionary compendia like the *Mammal Species of the World* (MSW) series. Here, we present the Mammal Diversity Database (MDD), a digital, publically accessible, and updateable list of all mammalian species, now available online: <https://mammaldiversity.org>. The MDD will continue to be updated as manuscripts describing new species and higher taxonomic changes are released. Starting from the baseline of the 3rd edition of MSW (MSW3), we performed a review of taxonomic changes published since 2004 and digitally linked species names to their original descriptions and subsequent revisionary articles in an interactive, hierarchical database. We found 6,495 species of currently recognized mammals (96 recently extinct, 6,399 extant), compared to 5,416 in MSW3 (75 extinct, 5,341 extant)—an increase of 1,079 species in about 13 years, including 11 species newly described as having gone extinct in the last 500 years. We tabulate 1,251 new species recognitions, at least 172 unions, and multiple major, higher-level changes, including an additional 88 genera (1,314 now, compared to 1,226 in MSW3) and 14 newly recognized families (167 compared to 153). Analyses of the description of new species through time and across biogeographic regions show a long-term global rate of ~25 species recognized per year, with the Neotropics as the overall most species-dense biogeographic region for mammals, followed closely by the Afrotropics. The MDD provides the mammalogical community with an updateable online database of taxonomic changes, joining digital efforts already established for amphibians (AmphibiaWeb, AMNH's Amphibian Species of the World), birds (e.g., Avibase, IOC World Bird List, HBW Alive), non-avian reptiles (The Reptile Database), and fish (e.g., FishBase, Catalog of Fishes).

Una taxonomía que precisamente refleje la realidad biológica es fundamental para el estudio de la diversidad de la vida, ya que proporciona el armazón evolutivo necesario para el muestreo de taxones e interpretación de resultados del mismo. Si bien el número de especies reconocidas en la clase Mammalia ha aumentado con el tiempo, la tabulación de esos aumentos se ha basado en las esporádicas publicaciones de compendios de revisiones taxonómicas, tales como la serie *Especies de mamíferos del mundo* (MSW por sus siglas en inglés). En este trabajo presentamos la Base de Datos de Diversidad de Mamíferos (MDD por sus siglas en inglés): una lista digital de todas las especies de mamíferos, actualizable y accesible públicamente, disponible en la dirección URL <https://mammaldiversity.org>. El MDD se actualizará con regularidad a medida que se publiquen artículos que describan nuevas especies o que introduzcan cambios de diferentes categorías taxonómicas. Con la tercera edición de MSW (MSW3) como punto de partida, realizamos una revisión en profundidad de los cambios taxonómicos publicados a partir del 2004. Los nombres de las especies nuevamente descritas (o ascendidas a partir de subespecies) fueron conectadas digitalmente en una base de datos interactiva y jerárquica con sus

descripciones originales y con artículos de revisión posteriores. Los datos indican que existen actualmente 6,495 especies de mamíferos (96 extintas, 6,399 vivientes), en comparación con las 5,416 reconocidas en MSW3 (75 extintas, 5,341 vivientes): un aumento de 1,079 especies en aproximadamente 13 años, incluyendo 11 nuevas especies consideradas extintas en los últimos 500 años. Señalamos 1,251 nuevos reconocimientos de especies, al menos 172 uniones y varios cambios a mayor nivel taxonómico, incluyendo 88 géneros adicionales (1,314 reconocidos, comparados con 1,226 en MSW3) y 14 familias recién reconocidas (167 en comparación con 153 en MSW3). Los análisis témporo-geográficos de descripciones de nuevas especies (en las principales regiones del mundo) sugieren un promedio mundial de descripciones a largo plazo de aproximadamente 25 especies reconocidas por año, siendo el Neotrópico la región con mayor densidad de especies de mamíferos en el mundo, seguida de cerca por la región Afrotropical. El MDD proporciona a la comunidad de mastozoólogos una base de datos de cambios taxonómicos conectada y actualizable, que se suma a los esfuerzos digitales ya establecidos para anfibios (AmphibiaWeb, Amphibian Species of the World), aves (p. ej., Avibase, IOC World Bird List, HBW Alive), reptiles “no voladores” (The Reptile Database), y peces (p. ej., FishBase, Catalog of Fishes).

Key words: biodiversity, conservation, extinction, taxonomy

Species are a fundamental unit of study in mammalogy. Yet species limits are subject to change with improved understanding of geographic distributions, field behaviors, and genetic relationships, among other advances. These changes are recorded in a vast taxonomic literature of monographs, books, and periodicals, many of which are difficult to access. As a consequence, a unified tabulation of changes to species and higher taxa has become essential to mammalogical research and conservation efforts in mammalogy. Wilson and Reeder's 3rd edition of *Mammal Species of the World* (MSW3), published in November 2005, represents the most comprehensive and up-to-date list of mammalian species, with 5,416 species (75 recently extinct, 5,341 extant), 1,229 genera, 153 families, and 29 orders. That edition relied on expertise solicited from 21 authors to deliver the most comprehensive list of extant mammals then available. However, the episodic release of these massive anthologies (MSW1—Honacki et al. 1982; MSW2—Wilson and Reeder 1993; MSW3—Wilson and Reeder 2005) means that taxonomic changes occurring during or soon after the release of a new edition may not be easily accessible for over a decade. For example, MSW3, compared to MSW2, resulted in the addition of 787 species, 94 genera, and 17 families compared to MSW2 (Solari and Baker 2007). Since the publication of MSW3, there has been a steady flow of taxonomic changes proposed in peer-reviewed journals and books; however, changes proposed more than a decade ago (e.g., Carleton et al. 2006; Woodman et al. 2006) have yet to be incorporated into a Mammalia-wide reference taxonomy. This lag between the publication of taxonomic changes and their integration into the larger field of mammalogy inhibits taxonomic consistency and accuracy in mammalogical research, and—at worst—it can impede the effective conservation of mammals in instances where management decisions depend upon the species-level designation of distinctive evolutionary units.

The genetic era has catalyzed the discovery of morphologically cryptic species and led to myriad intra- and interspecific revisions, either dividing species (splits) or uniting them (lumps). Many groups of mammals are taxonomically complex and in need of further revision, especially those that have received relatively little systematic attention or are morphologically or

behaviorally cryptic (e.g., shrews, burrowing mammals). For example, the phylogenetic placement of tenrecs and golden moles (families: Tenrecidae and Chrysochloridae) has long been a point of taxonomic contention, having variously been included within Insectivora, Eulipotyphla, and Lipotyphla. Taxonomic assignment of this group was only conclusively resolved when genetic data (Madsen et al. 2001; Murphy et al. 2001), as corroborated by morphology (Asher et al. 2003), aligned Tenrecidae and Chrysochloridae in the order Afrosoricida and found it allied to other African radiations in the superorder Afrotheria (Macroscelidea, Tubulidentata, Hyracoidea, Proboscidea, Sirenia). As analytical methods evolve and techniques become more refined, mammalian taxonomy will continue to change, making it desirable to create an adjustable list of accepted species-level designations and their hierarchical placement that can be updated on a regular basis. Such a list is needed to promote consistency and accuracy of communication among mammalogists and other researchers.

Here, using MSW3 as a foundation, we provide an up-to-date list of mammal species and introduce access to this species list as an amendable digital archive: the Mammal Diversity Database (MDD), available online at <http://mammaldiversity.org>. We compare our list to that of MSW3 to quantify changes in mammalian taxonomy that have occurred over the last 13 years and evaluate the distribution of species diversity and new species descriptions across both geography and time. We intend the MDD as a community resource for compiling and disseminating published changes to mammalian taxonomy in real time, rather than as a subjective arbiter for the relative strength of revisionary evidence, and hence defer to the peer-reviewed literature for such debates.

## MATERIALS AND METHODS

Starting from those species recognized in MSW3, we reviewed > 1,200 additional taxonomic publications appearing after MSW3's end-2003 cutoff date in order to compile a list of every recognized mammal species. In addition to evaluating peer-reviewed manuscripts, other major references included the *Handbook of the Mammals of the World* volumes 1–6 (Wilson

and Mittermeier 2009, 2011, 2014, 2015; Mittermeier et al. 2013; Wilson et al. 2016), *Mammals of South America* volumes 1 and 2 (Gardner 2007; Patton et al. 2015), *Mammals of Africa* volumes 1–6 (Kingdon et al. 2013), *Rodents of Sub-Saharan Africa* (Monadjem et al. 2015), *Taxonomy of Australian Mammals* (Jackson and Groves 2015), and *Ungulate Taxonomy* (Groves and Grubb 2011). We linked each species to its primary, descriptive publication and if a species was taxonomically revised since 2004, the associated revisionary publications also were linked. The list was curated for spelling errors and compared to the species recognized in MSW3 to determine the total change in the number of recognized species over the interval 1 January 2004 to 15 August 2017; the latter date was our cutoff for reviewing literature. As with MSW3 and the IUCN (2017) RedList, species totals for the MDD include mammalian species that have gone extinct during the last 500 years, an arbitrary period of time used to delimit species “recently extinct”. The IUCN taxonomy was downloaded on 28 June 2017.

We considered “de novo” species descriptions to be those species recognized since MSW3 and named with novel species epithets (post-MSW3 proposal date), whereas “splits” are species established by resurrecting an existing name (i.e., elevated subspecies or synonym, and pre-MSW3 proposal). We based these 2 bins of new species on the epithet authority year to enable downstream analyses of species discovery trends. However, we acknowledge that this categorization is not precise regarding the more complex (and biologically interesting) issue of how many species were derived from new field discoveries of distinctive populations versus the recognition of multiple species within named forms (Patterson 1996). Nevertheless, we expected the de novo category to encompass those field discoveries along with other types of species descriptions, and the splits category to encompass instances where existing names are elevated or validated, both of which are categories warranting future investigation.

In addition to taxonomic ranks (order, family, genus, species) and primary data links, MDD species information includes the year of description, scientific authority, and geographic occurrence by biogeographic region. Here, we approximate the biogeographic realms defined by the World Wildlife Fund (Olson and Dinerstein 1998; Olson et al. 2001), with the exception that we classified countries split across multiple biogeographic realms as belonging exclusively to the realm covering the majority of that country. We defined the Nearctic realm as all of North America, including Florida, Bermuda, and all of Mexico. The Neotropical realm included all of South America, Central America, and the insular Caribbean. The Palearctic realm included all of Europe, northern Asia (including all of China), Japan, and northern Africa (Egypt, Algeria, Tunisia, Morocco, Western Sahara, Canary Islands, and the Azores). The Indomalayan realm included southern and southeastern Asia (Pakistan, India, Nepal, Bhutan, Vietnam, Laos, Myanmar) and all islands west of Sulawesi including the Greater Sunda and Philippines. The Afrotropical realm included all of sub-Saharan Africa and the Arabian Peninsula, plus Madagascar and the nearby Indian Ocean islands (e.g., Comoros, Mauritius,

Seychelles). We grouped the Australasian and Oceanian realms to include a single category for Australia, New Zealand, Sulawesi, and the islands east of Sulawesi, including Melanesia, Polynesia, Micronesia, Hawaii, and Easter Island, but excluding the Palearctic Japanese Bonin Islands. There are no terrestrial mammal species native to Antarctica. Open-water and coastal marine species, including the few Antarctic breeding species (e.g., leopard seals, *Hydrurga*), were grouped separately. Freshwater species (e.g., river dolphins, river otters) were sorted by their resident landmass.

Based on our newly curated list, we calculated the number of new species described each decade since the origin of binomial nomenclature (Linnaeus 1758) to determine the major eras of species discovery and taxonomic description. The year 1758 includes all the species described by Linnaeus that are still currently recognized. For each biogeographic realm, we calculated the total number of mammalian species recognized and the number of new species recognized since 2004. Note that the recognition of new species in a particular region can reflect greater research efforts per region or taxon and thus cannot be extrapolated to the expected number of undiscovered species in that region. We scaled the number of species by regional land area (km<sup>2</sup>—World Atlas 2017) to determine the most species-dense region.

## RESULTS

The MDD currently lists 6,495 valid species of mammals (6,399 extant, 96 recently extinct), which is 1,079 more species than were recognized in MSW3 (1,058 extant and 21 extinct) and a 19.9% increase in species during about 13 years (Table 1). The MDD recognizes 1,251 new species described since MSW3 in categories of splits (720 species; 58%) and de novo species descriptions (531 species; 42%), indicating that at least 172 species were lumped together since the release of MSW3. The MDD documents a total of 1,314 genera (increasing by 88 from MSW3), 167 families (increasing by 14), and 27 orders (decreasing by 2). The MDD also includes 17 domesticated species in the listing to facilitate the association of

**Table 1.**—Comparison of Mammal Diversity Database (MDD) taxonomic totals and those of *Mammal Species of the World* (MSW) editions 1–3 and the International Union of Conservation of Nature (IUCN) RedList, version 2017-1.

Taxa	MSW1 1982	MSW2 1993	MSW3 2005	IUCN 2017	MDD This study
Species					
<i>Total</i>	4,170	4,631 <sup>a</sup>	5,416	5,560	6,495
<i>Extinct</i>	NA	NA	75	85 <sup>b</sup>	96
<i>Living</i>	NA	NA	5,341	5,475	6,399
<i>Living wild</i>	NA	NA	5,338	5,475	6,382
Genera	1,033	1,135	1,230	1,267	1,314
Families	135	132	153	159	167
Orders	20	26	29	27	27

<sup>a</sup>Corrected total per Solari and Baker (2007).

<sup>b</sup>Extinct IUCN mammals include both “EX” (extinct) and “EW” (extinct in the wild).

these derivatives of wild populations with their often abundant trait data (e.g., DNA sequences, reproductive data). Details of the full MDD version 1 taxonomy, including associated citations and geographic region assignments, are provided in [Supplementary Data S1](#).

The largest mammalian families are in the order Rodentia—Muridae (834 species versus 730 in MSW3) and Cricetidae (792 species versus 681 in MSW3)—followed by the chiropteran family Vespertilionidae (493 species versus 407 in MSW3) and the eulipotyphlan family Soricidae (440 species versus 376 in MSW3). Unsurprisingly, the 2 most speciose orders (Rodentia and Chiroptera) witnessed the most species additions: 371 and 304 species, respectively. The most speciose rodent family besides Muridae and Cricetidae is Sciuridae (298 species) and 6 rodent families are monotypic: Aplodontiidae, Diatomyidae, Dinomyidae, Heterocephalidae, Petromuridae, and Zenkerellidae. The most speciose chiropteran families along with Vespertilionidae are Phyllostomidae (214 species) and Pteropodidae (197 species), whereas there is only 1 monotypic bat family: Craseonycteridae.

The increased number of recognized genera to 1,314 (from 1,230 in MSW3) results from the demonstrated parphyly of several speciose and widely distributed former genera. This includes *Spermophilus*, which was split into 8 distinct genera (*Spermophilus*, *Urocitellus*, *Callospermophilus*, *Otospermophilus*, *Xerospermophilus*, *Ictidomys*, *Poliocitellus*, and *Notocitellus*—[Helgen et al. 2009](#)) and *Oryzomys*, which was split into 11 genera (*Oryzomys*, *Aegialomys*, *Cerradomys*, *Eremoryzomys*, *Euryoryzomys*, *Hylaeamys*, *Mindomys*, *Nephelomys*, *Oreoryzomys*, *Sooretamys*, and *Transandinomys*—[Weksler et al. 2006](#)). Many smaller generic splits broke 1 genus into 2 or more genera and often involved the naming of a new genus, such as with *Castoria* (formerly *Akodon*—[Pardiñas et al. 2016](#)), *Paynomys* (formerly *Chelemys*—[Teta et al. 2016](#)), and *Petrosaltator* (formerly *Elephantulus*—[Dumbacher 2016](#)). Other genera were described on the basis of newly discovered taxa, such as *Laonastes* ([Jenkins et al. 2005](#)), *Xeronycteris* ([Gregorin and Ditchfield 2005](#)), *Rungwecebus* ([Davenport et al. 2006](#)), *Drymoreomys* ([Percequillo et al. 2011](#)), and *Paucidentomys* ([Esselstyn et al. 2012](#)). The most speciose currently recognized genera are *Crocodyra* (197 species), *Myotis* (126 species), and *Rhinolophus* (102 species). These also are the only genera of mammals that currently exceed 100 recognized and living species, with *Rhinolophus* reaching this level only recently.

Higher-level taxonomy also was significantly altered since 2004, with the recognition of 14 additional families and 2 fewer orders than MSW3. In the MDD, we included 3 families (†Megaladapidae, †Palaeopropithecidae, †Archaeolemuridae) that were not in MSW3 but that may have gone extinct in the last 500 years ([McKenna and Bell 1997](#); [Montagnon et al. 2001](#); [Gaudin 2004](#); [Muldoon 2010](#)). The net addition of 11 other families in the MDD are the result of taxonomic splits and new taxon discoveries, as well as families lumped since MSW3. For example, Dipodidae was split into 3 families (Dipodidae, Zapodidae, Sminthidae—[Lebedev et al. 2013](#)), Hipposideridae

into 2 (Hipposideridae, Rhinonycteridae—[Foley et al. 2015](#)), and Bathyergidae into 2 (Bathyergidae, Heterocephalidae—[Patterson and Upham 2014](#)). One family, Diatomyidae, was added based on a species discovery (*Laonastes aenigmamus*—[Jenkins et al. 2005](#)), although it was already known as a prehistorically extinct family ([Dawson et al. 2006](#)). Additional newly recognized families are Chlamyphoridae, Cistugidae, Kogiidae, Lipotidae, Miniopteridae, Pontoporiidae, Potamogalidae, Prionodontidae, and Zenkerellidae. Three families recognized in MSW3 have since been subsumed: Myocastoridae and Heptaxodontidae inside Echimyidae ([Emmons et al. 2015](#)), and Aotidae inside Cebidae ([Schneider and Sampaio 2015](#); [Dumas and Mazzoleni 2017](#)). Note that Capromyidae is still recognized at the family level ([Fabre et al. 2017](#)). The order Cetacea also experienced major revisions, and is now included within the order Artiodactyla based on genetic and morphological data ([Gatesy et al. 1999](#); [Adams 2001](#); [Asher and Helgen 2010](#)). Soricomorpha and Erinaceomorpha also are grouped together in the order Eulipotyphla, given their shared evolutionary history demonstrated by genetic analyses ([Douady et al. 2002](#); [Meredith et al. 2011](#)).

On average, since 1758, 24.95 species have been described per decade, including 3 major spikes in species recognition in the 1820–1840s, 1890–1920s, and 2000–2010s ([Fig. 1](#)). These bursts of systematic and taxonomic development were followed by 2 major troughs from about 1850–1880 and 1930–1990 ([Fig. 1](#)). Currently, we detect an accelerating rate of species description per decade, increasing from the 1990s (207 species), 2000s (341 species), and 2010s so far (298 species). A linear regression on these data suggests that if trends in mammalian species discovery continue, 120.46 species are yet to be discovered this decade, potentially resulting in a total of 418 new species to be recognized between 2010 and 2020 ( $R^2 = 0.97$ ,  $P < 0.000$ ; [Fig. 1](#)).

Across biogeographic regions, the Neotropics harbors the greatest number of currently recognized mammalian species (1,617 species), followed by the Afrotropics (1,572 species), and the Palearctic (1,162 species), whereas Australasia-Oceania has the least (527 species) ([Fig. 2](#)). The Neotropics also has the most newly recognized species (362 species—169 de novo and 193 split), again followed by the Afrotropics (357 species—158 de novo and 199 split), and with the fewest new species described from Australasia-Oceania (48 species—18 de novo and 30 split). Other categories included the marine (124 total species—4 de novo and 5 split), domesticated (17 total species—0 de novo and 2 split), and extinct (96 total species—7 de novo and 4 split; [Fig. 2](#); [Table 2](#)) categories. When weighting the biogeographic realms by land area, we find the Neotropics and Afrotropics are also the most species-dense biogeographic regions (85.1 and 71.1 species per km<sup>2</sup>, respectively), followed closely by Australasia-Oceania (61.4 species per km<sup>2</sup>; [Table 2](#)). In all realms except the Indomalayan, more species were recognized via taxonomic splits than by de novo descriptions.

## DISCUSSION

Mammalogists have a collective responsibility to serve the most current taxonomic information about mammalian biodiversity

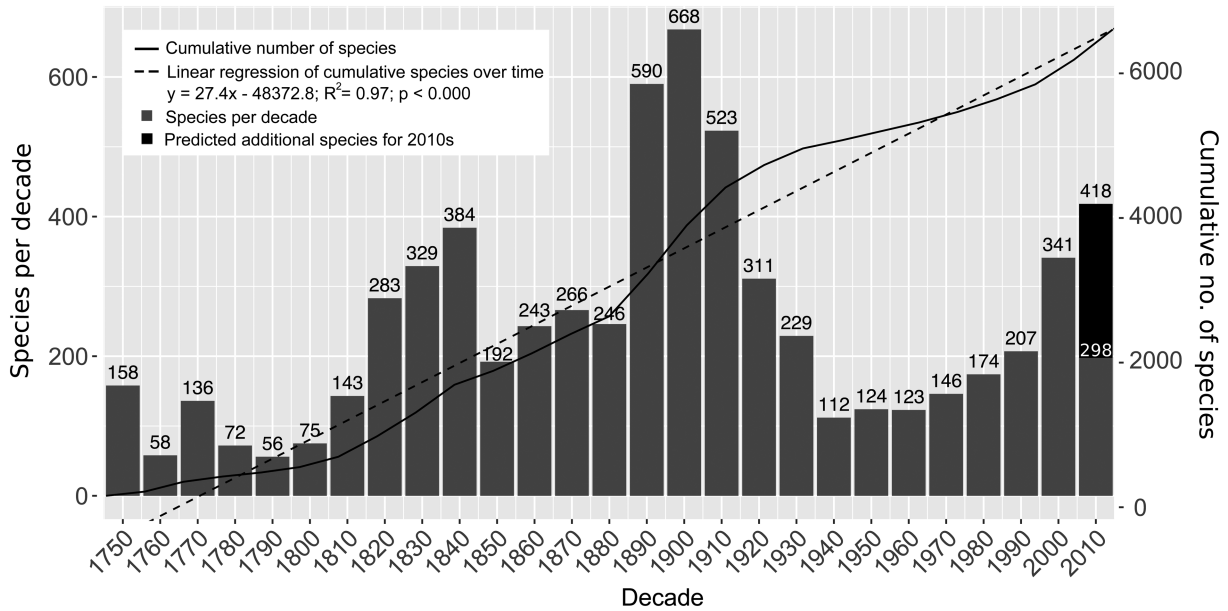


Fig. 1.—Cumulative and decadal descriptions of taxonomically valid extant mammal species from 1758 to 15 August 2017.

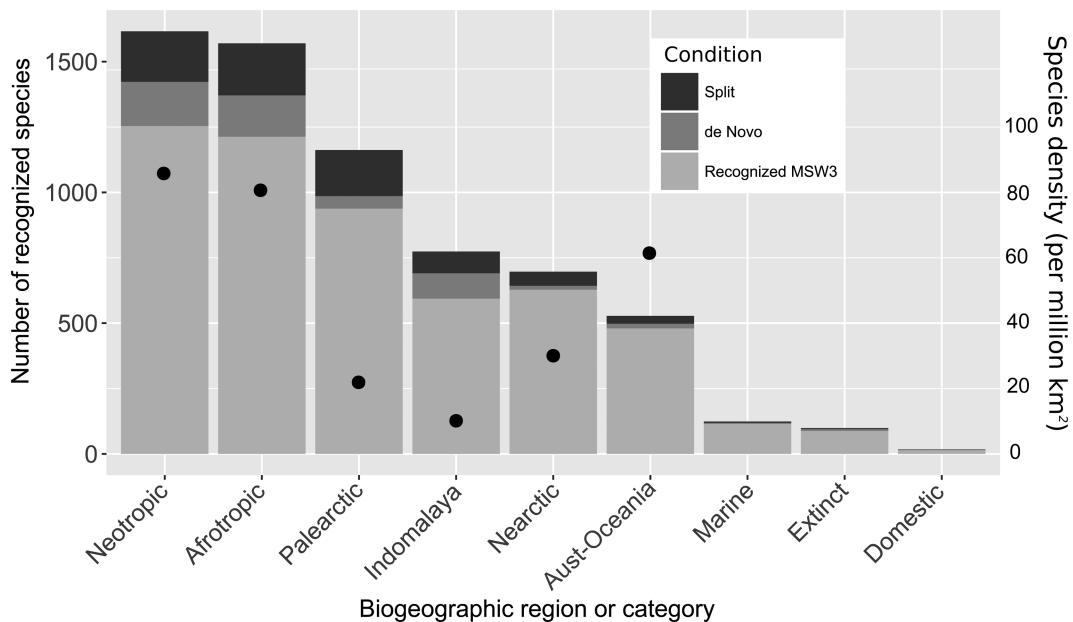


Fig. 2.—The number of mammalian species distributed in each biogeographical region: Palearctic, Afrotropic, Indomalayan, Nearctic, Neotropic, and Australasia-Oceania (i.e., Aust-Oceania), with marine, extinct, and domestic species in separate categories. Each group is divided into species recognized in both MSW3 and MDD, and new species in the MDD in categories of newly coined species epithet (de novo) versus existing species epithet (splits). The dot within each bar indicates the relative species density per km<sup>2</sup> land area, values are available in Table 2. MDD = Mammal Diversity Database; MSW3 = 3rd edition of *Mammal Species of the World*.

to the general public. The need for mammalian taxonomy to reflect our current understanding of species boundaries and evolutionary relationships is only expected to grow as efforts to synthesize “big data” increase in frequency, scope, and sophistication. Studies at this macroscale address major questions in evolution, ecology, and biodiversity conservation across the tree of life (e.g., Rabosky et al. 2012; Hedges et al. 2015; Hinchliff et al. 2015), yielding results relevant to global issues of sustainability that require our best data on biodiversity (Pascual et al. 2017). Mammalogists, in turn, benefit from easy

access to this biodiversity data for purposes of study design, classroom teaching, analyses, and writing. The release of the MDD therefore addresses a key need in the mammalogical and global biodiversity communities alike. Whether we study the behavioral ecology of desert rodents or the macroevolution of tetrapods, biologists collectively need accurate measurements of species diversity—the most commonly assessed (but not the only) dimension of biodiversity (Jarzyna and Jetz 2016).

The MDD represents the most comprehensive taxonomic compendium of currently recognized mammals, documenting

**Table 2.**—The total number of mammal species in the Mammal Diversity Database (MDD) as compared to *Mammal Species of the World*, volume 3 (MSW3) that live within each biogeographic realm and those belonging to domestic and extinct categories. Numbers correspond to Fig. 2. Note that some species are found within multiple regions, so column totals do not correspond to taxonomic totals.

Category	Total species	Shared with MSW3	De novo	Split	Area (million km <sup>2</sup> )	Density (species/km <sup>2</sup> )
Neotropic	1,617	1,255	169	193	19.0	85.1
Afrotropic	1,572	1,215	158	199	22.1	71.1
Palaearctic	1,162	938	48	176	54.1	21.5
Indomalaya	954	774	97	83	7.5	12.7
Nearctic	697	628	15	54	22.9	30.4
Aust-Oceania	527	479	18	30	8.6	61.4
Marine	124	115	4	5		
Domestic	17	15		2		
Extinct	96	85	7	4		

6,399 extant species (Tables 1 and 3) as well as 96 recently extinct species for a total of 6,495 species. This database is updateable and digitally searchable, tracking primary sources of species descriptions and phylogenetic studies of higher-level (genus or family) taxonomic changes and compiling them into a single listing. The MDD thus closes the gap between proposed taxonomic changes and integration into a broader understanding of mammalian diversity, and it then distributes this information to the scientific community and lay public as it is published in scientific literature. We aim for the MDD to build on this capacity as a record keeper to be a resource for hosting histories of taxonomic change. For example, the MDD records both the description of *Tapirus kabomani* (Cozzuol et al. 2013) and the later synonymy of this taxon under *T. terrestris* (Voss et al. 2014). Likewise, the revision of *Spermophilus* ground squirrels into 8 genera (Helgen et al. 2009) altered the binomial names of 28 species, a rearrangement that usefully established generic monophyly, but one that has not been readily summarized for workers without easy access to libraries. The MDD compiles data on genus transfers published since 2004 across all of Mammalia, helping to release researchers from undertaking piecemeal taxonomic updates for their projects.

Preliminary findings from the MDD compilation indicate that Primates has been a nexus of new species discovery, which is unexpected given their large body sizes. An incredible 148 primate species have been recognized since the publication of MSW3, including 67 de novo and 81 splits (Tables 1 and 3), a taxonomic outcome that is striking for our closest human relatives. Taxonomic revisions have centered around New World monkey families (Cebidae—Boubli et al. 2012; Pitheciidae—Marsh 2014) and many de novo species descriptions also occurred among Malagasy lemurs (Cheirogaleidae—Lei et al. 2014; Lepilemuridae—Louis et al. 2006). However, persistent taxonomic uncertainty within the family Cercopithecidae (Groves 2007a, 2007b; Mittermeier et al. 2013) suggests that the species-level diversity of Primates is not yet stable and will continue to fluctuate.

Among other taxonomic changes, the MDD documents the addition of 371 species of Rodentia, 304 species of Chiroptera, 86 species of Eulipotyphla, and 227 species of Artiodactyla, including many species from historically well-studied geographic regions (Table 2; Rausch et al. 2007; Castiglia et al. 2017). While the addition of > 300 species each of rodents and

bats is unsurprising given their existing diversity, these clades may reasonably contain disproportionately high levels of cryptic diversity (e.g., Ruedi and Mayer 2001; Belfiore et al. 2008), and thus the application of genetic sequence data may continue to yield greater insights. Within Eulipotyphla (most particularly in shrews), we expect that the discovery of new species will continue given their rate of recent discoveries and frequency of morphological cryptic (Esselstyn et al. 2013). The species richness in *Sorex* (86 species) and *Crocidura* (197 species) suggests that genus-level revisions are needed and, when conducted, are likely to yield further taxonomic rearrangements (Castiglia et al. 2017; Matson and Ordóñez-Garza 2017).

The MDD includes a total of 465 species of non-cetacean Artiodactyla and Perissodactyla recognized by Groves and Grubb (2011) with select modifications based on taxonomic refinements published after the release of the latter (e.g., 4 species of *Giraffa* [Bercovitch et al. 2017] versus 8 [Groves and Grubb 2011]). This total compares to 240 species in these orders recognized in MSW3 (> 93% increase). Although some researchers have argued that the changes proposed by Groves and Grubb (2011) exemplify an extreme form of taxonomic inflation (Lorenzen et al. 2012; Zachos et al. 2013; Harley et al. 2016), the increase in species richness is comparable to concurrent rates of increase in the richness of Rodentia, Chiroptera, Eulipotyphla, and Primates. For now, inclusion of the taxonomy of Groves and Grubb (2011) in the MDD ensures that these taxa are vetted by the greater mammalogical community using multiple tiers of evidence (de Queiroz et al. 2007; Voss et al. 2014).

Following the publication of Linnaeus's 10th edition of *Systema Naturae* in 1758, the number of described species of mammals has increased at various rates, punctuated by factors including the efforts of prolific systematists and world events (Fig. 1). For example, Oldfield Thomas (1858–1929) of the British Museum (now the Natural History Museum, London), considered one of the “greatest taxonomists [...] who ever lived” (Flannery 2012), was responsible for nearly 3,000 new names for genera, species, and subspecies (Hill 1990). In turn, reduced rates of species descriptions in the mid-20th century may be linked to periods of political instability and limited scientific activity during World War I (1914–1918) and II (1939–1945). Methodological innovations such as polymerase chain reaction (PCR—Mullis et al. 1989) may have driven

**Table 3.**—Totals of the genera and species per families and orders currently listed in the Mammal Diversity Database (MDD) online compilation, along with new species described since *Mammal Species of the World* volume 3 (MSW3) in categories of split or de novo, based on whether the specific epithet already existed or was newly coined, respectively.

	Genera	Species	New species since MSW3	
			Splits	De novo
<b>Class Mammalia</b>	1,314	6,495	720	531
<i>Subclass Prototheria</i>	3	5		
<b>Order Monotremata</b>	3	5		
Family Ornithorhynchidae	1	1		
Family Tachyglossidae	2	4		
<i>Subclass Theria</i>	1,311	6,490	720	531
<i>Infraclass Marsupialia</i>	91	379	32	29
<b>Order Didelphimorphia</b>	18	111	15	18
Family Didelphidae	18	111	15	18
<b>Order Paucituberculata</b>	3	7		1
Family Caenolestidae	3	7		1
<b>Order Microbiotheria</b>	1	3		2
Family Microbiotheriidae	1	3		2
<b>Order Notoryctemorphia</b>	1	2		
Family Notoryctidae	1	2		
<b>Order Dasyuromorpha</b>	19	78	5	5
Family Dasyuridae	17	76	5	5
Family Myrmecobiidae	1	1		
Family †Thylacinidae	1	1		
<b>Order Peramelemorphia</b>	8	23	1	1
Family †Chaeropodidae	1	1		
Family Peramelidae	6	20	1	1
Family Thylacomyidae	1	2		
<b>Order Diprotodontia</b>	41	155	11	2
Family Acrobatidae	2	3	1	
Family Burramyidae	2	5		
Family Hypsiprymnodontidae	1	1		
Family Macropodidae	13	67	3	
Family Petauridae	3	12		1
Family Phalangeridae	6	30	3	1
Family Phascolarctidae	1	1		
Family Potoroidae	4	12	1	
Family Pseudocheiridae	6	20	3	
Family Tarsipedidae	1	1		
Family Vombatidae	2	3		
<i>Infraclass Placentalia</i>	1,220	6,111	684	502
<i>Superorder Afrotheria</i>	34	89	8	6
<b>Order Tubulidentata</b>	1	1		
Family Orycteropodidae	1	1		
<b>Order Afrosoricida</b>	20	55	1	3
Family Chrysochloridae	10	21		
Family Potamogalidae <sup>a</sup>	2	3		
Family Tenrecidae	8	31	1	3
<b>Order Macroscelidea</b>	5	20	2	3
Family Macroscelididae	5	20	2	3
<b>Order Hyracoidea</b>	3	5	1	
Family Procaviidae	3	5	1	
<b>Order Proboscidea</b>	2	3		
Family Elephantidae	2	3		
<b>Order Sirenia</b>	3	5		
Family Dugongidae	2	2		
Family Trichechidae	1	3		
<i>Superorder Xenarthra</i>	14	30		
<b>Order Cingulata</b>	9	20		
Family Chlamyphoridae <sup>b</sup>	8	13		
Family Dasypodidae	1	7		
<b>Order Pilosa</b>	5	10		
Family Bradypodidae	1	4		
Family Cyclopedidae	1	1		
Family Megalonychidae	1	2		
Family Myrmecophagidae	2	3		

Table 3.—Continued

	Genera	Species	New species since MSW3	
			Splits	De novo
<i>Superorder Euarchontoglires</i>	616	3,194	285	249
<b>Order Scandentia</b>	4	24	4	
Family Ptilocercidae	1	1		
Family Tupaiidae	3	23	4	
<b>Order Dermoptera</b>	2	2		
Family Cynocephalidae	2	2		
<b>Order Primates</b>	84	518	81	67
Family †Archaeolemuridae <sup>c</sup>	1	2		
Family Atelidae	4	25	3	
Family Cebidae <sup>d</sup>	11	89	27	2
Family Cercopithecidae	23	160	24	5
Family Cheirogaleidae	5	40	1	20
Family Daubentoniiidae	1	1		
Family Galagidae	6	20	2	2
Family Hominidae	4	7		
Family Hylobatidae	4	20	3	2
Family Indriidae <sup>e</sup>	3	19	2	6
Family Lemuridae	5	21	2	
Family Lepilemuridae	1	26		16
Family Lorisidae	4	15	6	1
Family †Megaladapidae <sup>c</sup>	1	1		
Family †Palaeopropithecidae <sup>c</sup>	1	1		
Family Pitheciidae	7	58	9	9
Family Tarsiidae	3	13	2	4
<b>Order Lagomorpha</b>	13	98	10	1
Family Leporidae	11	67	5	1
Family Ochotonidae	1	30	5	
Family †Prolagidae	1	1		
<b>Order Rodentia</b>	513	2,552	190	181
Family Abrocomidae	2	10		
Family Anomaluridae	2	6		
Family Aplodontiidae	1	1		
Family Bathyergidae	5	21	3	4
Family Calomyscidae	1	8		
Family Capromyidae	7	17		
Family Castoridae	1	2		
Family Caviidae	6	21	3	
Family Chinchillidae	3	7		1
Family Cricetidae	145	792	75	61
Family Ctenodactylidae	4	5		
Family Ctenomyidae	1	69	5	6
Family Cuniculidae	1	2		
Family Dasyproctidae	2	15	2	1
Family Diatomyidae <sup>f</sup>	1	1		1
Family Dinomyidae	1	1		
Family Dipodidae	13	37	3	
Family Echimyidae <sup>g</sup>	25	93	6	3
Family Erethizontidae	3	17	1	2
Family Geomyidae	7	41	8	1
Family Gliridae	9	29		1
Family Heterocephalidae <sup>h</sup>	1	1		
Family Heteromyidae	5	66	6	2
Family Hystricidae	3	11		
Family Muridae	157	834	41	84
Family Nesomyidae	21	68	1	6
Family Octodontidae	7	14		1
Family Pedetidae	1	2		
Family Petromuridae	1	1		
Family Platacanthomyidae	2	5	2	1
Family Sciuridae	62	298	18	5
Family Sminthidae <sup>i</sup>	1	14	2	



Table 3.—Continued

	Genera	Species	New species since MSW3	
			Splits	De novo
Family Spalacidae	7	28	8	
Family Thryonomyidae	1	2		
Family Zapodidae <sup>l</sup>	3	12	6	1
Family Zenkerellidae <sup>l</sup>	1	1		
<i>Superorder Laurasiatheria</i>	556	2,798	399	247
<b>Order Eulipotyphla<sup>h</sup></b>	56	527	23	63
Family Erinaceidae	10	24		
Family †Nesophontidae	1	6		
Family Solenodontidae	1	3		
Family Soricidae	26	440	16	55
Family Talpidae	18	54	7	8
<b>Order Chiroptera</b>	227	1,386	130	174
Family Cistugidae <sup>l</sup>	1	2		
Family Craseonycteridae	1	1		
Family Emballonuridae	14	54		3
Family Furipteridae	2	2		
Family Hipposideridae	7	88	6	8
Family Megadermatidae	5	6		1
Family Miniopteridae <sup>l</sup>	1	35	7	9
Family Molossidae	19	122	12	13
Family Mormoopidae	2	17	8	
Family Mystacinidae	1	2		
Family Myzopodidae	1	2		1
Family Natalidae	3	11	3	
Family Noctilionidae	1	2		
Family Nycteridae	1	16		
Family Phyllostomidae	62	214	22	37
Family Pteropodidae	45	197	5	12
Family Rhinolophidae	1	102	10	14
Family Rhinonycteridae <sup>m</sup>	4	9	1	3
Family Rhinopomatidae	1	6	1	1
Family Thyropteridae	1	5		2
Family Vespertilionidae	54	493	55	70
<b>Order Carnivora</b>	130	305	23	2
Family Ailuridae	1	2	1	
Family Canidae	13	39	3	
Family Eupleridae	7	8		
Family Felidae	14	42	5	
Family Herpestidae	16	36	2	
Family Hyaenidae	3	4		
Family Mephitidae	4	12	1	
Family Mustelidae	23	64	5	1
Family Nandiniidae	1	1		
Family Odobenidae	1	1		
Family Otariidae	7	16		
Family Phocidae	14	19		
Family Prionodontidae <sup>n</sup>	1	2		
Family Procyonidae	6	14	2	1
Family Ursidae	5	8		
Family Viverridae	14	37	4	
<b>Order Pholidota</b>	3	8		
Family Manidae	3	8		
<b>Order Perissodactyla</b>	8	21	4	
Family Equidae	1	12	4	
Family Rhinocerotidae	4	5		
Family Tapiridae	3	4		
<b>Order Artiodactyla<sup>o</sup></b>	132	551	219	8
Family Antilocapridae	1	1		
Family Balaenidae	2	4		
Family Balaenopteridae	2	8		1
Family Bovidae	54	297	152	2
Family Camelidae	2	7	1	

**Table 3.**—Continued

	Genera	Species	New species since MSW3	
			Splits	De novo
Family Cervidae	18	93	43	
Family Delphinidae	17	40	3	3
Family Eschrichtiidae	1	1		
Family Giraffidae	2	5	3	
Family Hippopotamidae	2	4		
Family Iniidae	1	3	1	1
Family Kogiidae <sup>a</sup>	1	2		
Family Lipotidae <sup>a</sup>	1	1		
Family Monodontidae	2	2		
Family Moschidae	1	7		
Family Neobalaenidae	1	1		
Family Phocoenidae	3	7	1	
Family Physeteridae	1	1		
Family Platanistidae	1	1		
Family Pontoporiidae <sup>a</sup>	1	1		
Family Suidae	6	28	11	
Family Tayassuidae	3	5	2	
Family Tragulidae	3	10	1	1
Family Ziphiidae	6	22	1	

<sup>a</sup>Split from Tenrecidae.

<sup>b</sup>Split from Dasypodidae.

<sup>c</sup>Recently extinct families not included in MSW3.

<sup>d</sup>Includes Aotidae and Callitrichidae.

<sup>e</sup>Was spelled as “Indridae” in MSW3.

<sup>f</sup>Recognized as extant based on *Laonastes aenigmamus*.

<sup>g</sup>Includes Heptaxodontidae and Myocastoridae.

<sup>h</sup>Split from Bathyergidae.

<sup>i</sup>Split from Dipodidae.

<sup>j</sup>Split from Anomaluridae.

<sup>k</sup>Includes Soricomorpha and Erinaceomorpha.

<sup>l</sup>Split from Vespertilionidae.

<sup>m</sup>Split from Hipposideridae.

<sup>n</sup>Split from Felidae.

<sup>o</sup>Includes Cetacea.

<sup>p</sup>Split from Physeteridae.

<sup>q</sup>Split from Iniidae.

<sup>r</sup>Extinct.

later bursts of species descriptions by allowing morphologically cryptic but genetically divergent evolutionary lineages to be recognized as species. For example, over one-half of the species described since 2004 appear to have stemmed from taxonomic splits (~58%), many based in part or whole on genetic data, to go with at least 172 species unions (lumps) during the same period. As we continue to progress within the genomic era, where data on millions of independent genetic loci can be readily generated for taxonomic studies, there is a growing understanding that hybridization and introgression commonly occur among mammalian species that may otherwise maintain genetic integrity (e.g., Larsen et al. 2010; Miller et al. 2012; vonHoldt et al. 2016). Characterizing species and their boundaries using multiple tiers of evidence will continue to be essential given the profound impact of species delimitation on legislative decisions (e.g., U.S. Endangered Species Act of 1973—Department of the Interior, U.S. Fish and Wildlife Service 1973).

At the current rate of taxonomic description of mammals (~25 species/year from 1750 to 2017), we predict that 7,342 mammalian species will be recognized by 2050 and 8,590 by 2100. Alternatively, if we consider the increased rate of taxonomic descriptions since the advent of PCR (~30 species/year from 1990 to 2017), our estimates increase to 7,509 species recognized by 2050 and 9,009 by 2100. These estimates surpass Reeder and Helgen’s (2007) prediction of > 7,000 total mammalian species, but echo their observation that mammals

contain considerably greater species diversity than is commonly recognized. Remarkably, the same estimate of ~25 species/year was derived somewhat independently from tracking 14 estimates of global diversity (1961–1999—Patterson 2001) and from species-level changes between MSW2 and MSW3 (Reeder and Helgen 2007), thereby affirming the robustness of that estimate across both data sources and eras.

Assumed in all taxonomic forecasts is the stability of global ecosystems, scientific institutions, and natural history collections. With mammals being disproportionately impacted by human-induced extinctions (Ceballos et al. 2017), especially in insular regions like the Caribbean (Cooke et al. in press), efforts to protect threatened habitats and their resident mammalian species are key to the continued persistence, existence, and discovery of mammals. The Neotropics is the most species-dense biogeographic region in the world, followed closely by the Afrotropics and Australasia-Oceania, the latter of which is one of the least explored terrestrial regions on Earth, with the second fewest de novo species descriptions (18 species; Table 2). Inventory efforts may thus be fruitfully prioritized in northern Australia, Melanesia, Sulawesi, and other oceanic islands east of Wallace’s Line. However, we note that obtaining collecting permissions is a barrier to species description in any region. The continued description and discovery of mammalian species diversity hinges on investment in both natural history collecting and in the physical collections that house the specimens essential for taxonomic research. Natural history collections are

repositories for the genetic and morphological vouchers used to describe every new species listed in the MDD, a fact that highlights the indispensable role of museums and universities in understanding species and the ecosystems in which they live (McLean et al. 2015). As our planet changes, the need to support geographically broad and site-intensive biological archives only grows in relevance. Collections represent time series of change in biodiversity and often harbor undiscovered species (e.g., Helgen et al. 2013), including those vulnerable or already extinct.

Acting under the supervision of the American Society of Mammalogists' Biodiversity Committee, the MDD has a 2018–2020 plan to further integrate synonym data, track Holocene-extinct taxa, and add links to outside data sources. While full synonymies are not feasible, inclusion of common synonyms will facilitate tracking taxonomic changes through time, especially within controversial groups (e.g., Artiodactyla and Perissodactyla—Groves and Grubb 2011). Controversial taxonomic assignments also will be “flagged” as tentative or pending further scientific investigation. The MDD aims to link taxon entries to a variety of relevant per-species and per-higher taxon data pages on other web platforms, including geographic range maps, trait database entries, museum records, genetic resources, and other ecological information. *Mammalian Species* accounts, published by the American Society of Mammalogists since 1969 and consisting of over 950 species-level treatments, will be linked to relevant MDD species pages, including synonym-based links. In this manner, the MDD's efforts parallel initiatives in other vertebrate taxa to digitize taxonomic resources (amphibians—AmphibiaWeb 2017; Amphibian Species of the World—Frost 2017; birds: Avibase—LePage et al. 2014; IOC World Bird List—Gill and Donsker 2017; the Handbook of the Birds of the World Alive—del Hoyo et al. 2017; non-avian reptiles, turtles, crocodiles, and tuatara—Uetz et al. 2016; and bony fish: FishBase—Froese and Pauly 2017; Catalog of Fishes—Eschmeyer et al. 2017). The new mammalian taxonomic database summarized herein aims to advance the study of mammals while bringing it to par with the digital resources available in other tetrapod clades, to the benefit of future mammalogists and non-mammalogists alike.

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#### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online. **Supplementary Data SD1.**—Details of the full Mammal Diversity Database (MDD) version 1 taxonomy, including associated citations and geographic regions.

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