Introduction

Connor J. Burgin, Jane Widness and Nathan S. Upham

History of Mammalian Record Keeping

"Thomas, you will do the mammals." Poor Thomas murmured something about echinoderms, but the autocrat thundered: "You will do the mammals." Visions of countless sheep and cattle rushed into the lad's mind and, as Thomas put it, he hated those animals from a systematic point of view for ever more.

– Hinton's (1929) obituary of Oldfield Thomas, who went on to describe nearly 3000 genera, species, and subspecies of mammals from 1879–1929 after being assigned the task by Dr. Albert Günter, Keeper of Zoology at the British Museum of Natural History.

While the famed mammalogist Oldfield Thomas did not plan to study mammals, his diligent efforts are still tangible in the updated *Checklist of the Mammals of the World* now before you. Not only do many of Thomas's original descriptions remain valid (927 species and 174 genera), but his legacy continues to be engraved in taxonomic names themselves. Extending in time from *Thomasomys* Coues, 1884 to *Cyclopes thomasi* Miranda, Casali, Perini, Machado & Santos, 2018, the work of Thomas is herein recognized in the epithets of 21 species and one genus. That remarkable contribution to mammalogy has helped bring us to today (and from an aspiring echinodermologist!). Nevertheless, rather than a story about one exceptional scientist, which Thomas surely was, the key lesson from his prodigious output is that human knowledge of mammalian biodiversity has taken a winding path to reach where it is today.

Thomas began working on mammals barely a century after the publication of Linnaeus's 10th edition of *Systema Naturae* in 1758. Much was yet to be discovered from the view of western science. Thomas established a global network of field collectors and had a formidable team of volunteer zoologists on his staff, a "willing band of helpers" that he inspired with his vision for a great National Collection of Mammals (Hill 1990: 31). Development of new systematic measuring tools also aided this effort and might indeed be one reason why so many of Thomas's mammal taxa are still recognized as valid today. For example, he helped standardize basic skull measurements and tooth nomenclature (Thomas 1905) and created a simple device for measuring the angle of incisor protrusion in rodents, the "incisive index" (Thomas 1919). Thus, besides contributing voluminously to the description of species, Thomas's quantitative approach to assessing species limits helped spark methods of integrative taxonomy that are still used today.

The turn of the 20th century also saw the dawn of mammalian taxonomic compendia thanks to Édouard-Louis Trouessart of the National Museum of Natural History of Paris (Denys *et al.* 2012). Trouessart's *Catalogus mammalium tam viventium quam fossilium*, which he published in volumes and revisions from 1897–1905, was the first species-level inventory of global Mammalia. This remarkable undertaking included a list of all then-known species, including 980 pages of references to original descriptions that set a rigorous tone for later mammal compendia. Even at that time, evidence of the rapidly changing knowledge of species diversity was visible. For example, Trouessart noted that while 255 species of Primates were recognized in 1897, it increased by 35 species to 290 by 1904. That total included living and extinct forms, but the c.14% increase in less than a decade would foreshadow later flux in recognized species richness. Indeed, nearly a century later, volumes of *Mammal Species of the World* (Wilson & Reeder 1993, 2005) would increase the recognized species-level contents of Primates from 233 species to 376 — a dramatic 61% increase driven by changing technology and application of more granular taxonomic concepts (520 species are recognized herein).

Far from being isolated to Primates, changes to the species-level taxonomy of the rest of mammals have occurred in parallel. From the first volume of the *Mammal Species of the World* (Honacki *et al.* 1982) to this volume, *Illustrated Checklist of the Mammals of the World* (2020), there has been a 54% increase in the number of recognized species of living wild mammals (Table 1). Other compendia that have complemented this taxonomic flux include *A World List of Mammalian Species*, editions 1–3 (Corbet & Hill 1980, 1986, 1991) and *Walker's Mammals of the World* (starting with Walker 1964 and updated most recently by Nowak 1999). These modern compendia of mammals grew out of efforts during the late 1960s to establish numerical identifiers for taxonomic concepts, called the International Species Inventory System or ISIS (Seal & Makey, 1974). That forward-thinking idea, initially established in the context of zoological parks, unfortunately floundered after being acquired on a proprietary basis. If such a standardized numerical system been in place for the growth of digital biodiversity informatics in the 1990s and 2000s—not just for mammals but all taxa, it certainly would have made tracking taxonomic revisions more straightforward today.

The tradition of mammalogical scholarship shown by Thomas and Trouessart, and paralleled in the Americas by Gerrit Smith Miller, Jr, C. Hart Merriam, Annie Alexander, and Joseph Grinnell, is continued by modern efforts to answer the question "How many species of mammals are there?" That question was addressed most recently by an effort of the American Society of Mammalogists to build an online-only,

Table 1. Total number of mammals in major taxonomic compendia through time, comparing *Mammal Species of the World* (MSW) editions 1–3, *International Union of Conservation of Nature* (IUCN) *Red List* version 2020-2, and *Mammal Diversity Database* (MDD) v1.0 relative to the *Illustrated Checklist of the Mammals of the World* (CMW).

Taxa	MSW1 1982	MSW2 1993	MSW3 2005	IUCN 2008	MDD 2018	IUCN 2020	CMW 2020
Species							
Total	4170	4631[a]	5416	5513	6495	5899	6554
Extinct	NA	NA	75	79[b]	96	86[b]	103
Living	NA	NA	5341	5436	6399	5813	6451
Domesticated	0	0	0	0	16	0	19
Living wild	NA	NA	5338	5436	6382	5813	6432
Genera	1033	1135	1230	1226	1314	1291	1343
Families	135	132	153	149	167	162	167
Orders	20	26	29	24	27	27	27

[a] Corrected total per Solari & Baker (2007)
[b] Extinct IUCN mammals include both "EX" (extinct) and "EW" (extinct in the wild)

readily updatable taxonomic listing for mammal species called the *Mammal Diversity Database* or MDD (http://mammaldiversity.org; Burgin *et al.* 2018). By searching published literature directly, the MDD effort revealed a seismic jump of 1251 new species recognitions and 172 unions since 2005 (Table 1). That trajectory of rapid change has continued since that taxonomy's August 2017 cut-off and can be expected to continue well into the future, spurred on by advances in the integration of traditional morphometrics with improved genomic, ecological, and behavioral data.

Overall, reliance on formal taxonomic compendia in mammalian record keeping has often led to delays in the incorporation of systematic revisions. This is exemplified by the continual reference to *Mammal Species of the World*, Volume 3 (Wilson & Reeder 2005) as the starting point for all taxonomic arrangements in these volume, despite having been published 15 years ago. All vertebrate classes currently have online databases with updatable species lists (e.g., AmphibiaWeb, Reptile Database, AviBase, and FishBase), yet mammals were the exception until the creation of the MDD in 2018. The welcome fact that global Mammalia now has an updatable online database ensures that species-level mammalian taxonomy is more quickly adopted to inform diverse types of research from biodiversity conservation to zoonotic diseases.

Taxonomies are living documents, meant to change with our deepening knowledge of the natural world. You now hold in your hands the latest version of that knowledge, *Illustrated Checklist of the Mammals of the World*, summarizing and updating all nine volumes of Lynx's *Handbook of the Mammals of the World* (HMW) series (2009–2019). Before you open the covers, the two volumes will already be out of date. But fear not, because the quickening pace of increase in our biodiversity knowledge is exactly what is needed. These volumes provide nuanced information on mammalian taxonomy and distribution that are a highly useful piece in the biodiversity puzzle we aim to reconstruct. The beautiful and ecologically pivotal mammals that are this book's topic are dynamic entities that will continue to evolve along with our knowledge of them. So, as we venture forward, we should pause to thank generations of mammalogists that have collectively compiled this knowledge. Most importantly, let's thank Oldfield Thomas for choosing silky anteaters over spiny urchins!

The rest of this introduction focuses on various topics not discussed in the main text of the *Checklist* (e.g., macro-level systematics) and elaborates on processes behind speciation, species concepts, taxonomic advancement and controversies, nomenclature, and effects of taxonomy on species conservation.

Mammalian Phylogeny and Macrosystematics

The higher level taxonomy of mammals below the ordinal and above the familial levels is covered extensively in the HMW, but supraordinal systematics (macrosystematics) are not. Thus, this section focuses solely on relationships above the ordinal level, using as a reference the recent molecular phylogeny published by Upham and colleagues (2019; Figure 1).

The macrosystematic classification of mammals is historically riddled with polyphyletic and paraphyletic taxa (Figure 2). These taxa were often placed together on the basis of ecologically convergent morphologies and ecologies, with the former Insectivora being a prime example (now divided into five orders; Stanhope 1998). Fortunately, an assortment of molecular and paleontological studies over the last 20 years has substantially increased our knowledge of the evolutionary history of extant mammalian radiation. Since the *Checklist* focuses solely on extant and recently extinct mammals, this short synopsis will focus on the crown group Mammalia, which is defined as all currently extant mammal species, the common ancestor of these species, and all extinct ancestors descending from that common ancestor (whether or not they have any close extant relatives). As with the content of the *Checklist*, this treatment also excludes discussion of fossil lineages, instead focusing solely on the relationship between living radiations of mammals and their taxonomy. As a result, there is no discussion on the controversial relationships of Mesozoic mammals and mammaliaforms or the cladistic names associated with these clades. A succinct summary of advances in mammalian phylogenetics has been given by Zachos (2020) and Asher (2018), and for a review of Mesozoic mammal and synapsid relationships, see Angielczyk & Kammerer (2018) and Martin (2018).

The primary goal in producing a higher level taxonomy is to procure monophyletic taxa that meaningfully demonstrate the evolutionary relatedness for sequentially smaller, less encompassing taxa (e.g. molecularly and morphologically defined orders, families, genera, and species). Revisions most often occur when higher taxa

are proven to be either paraphyletic or polyphyletic (Figure 2). Mammalian macrosystematics has only recently become stable as a result of the advances in molecular and paleontological studies. The turn of the millennium ushered in a wave of mammalian molecular phylogenetic publications that raised unexpected questions regarding large portions of traditional ordinal and supraordinal mammalian arrangements (e.g. Springer *et al.* 1997, Stanhope *et al.* 1998, Madsen *et al.* 2001, Murphy *et al.* 2001a, Murphy *et al.* 2001b, Scally *et al.* 2001). These early molecular studies focused primarily on placental mammals, leading to the formation of Afrotheria and the concurrent breakdown of the highly polyphyletic Insectivora. During this time, cetaceans were confirmed to be derived from, and were best included in, Artiodactyla (here treated under Cetartiodactyla). Likewise, they established monotremes as the earliest diverging lineage of living mammals, the sister relationship between marsupial and placental mammals, and that there are four major supraordinal taxa encompassing placental radiation: Afrotheria, Xenarthra, Euarchontoglires, and Laurasiatheria (Springer *et al.* 2004, Foley *et al.* 2016). This arrangement has been fundamentally followed in virtually all taxonomic arrangements since then, as supported by all major phylogenetic studies. Nevertheless, ambiguity still remains regarding relationships among these clades.

Within the crown mammal radiation, the earliest divergence is between the two subclasses, Prototheria and Theria. Cladistic studies of stem mammals and early monotremes do not typically use the name Prototheria anymore because of the historical ambiguity regarding its content (Zachos 2020). In terms of extant taxa, only Monotremata is included under Prototheria, and the name is somewhat redundant other than the fact that it is a placeholder for a subclass sister to the subclass Theria in Linnaean classifications. For the purposes of this volume, it is worth noting that Prototheria is often used synonymously with Monotremata. The same can be said for Metatheria and Eutheria with Marsupialia and Placentalia, respectively, although the former two also include the stem fossil taxa of those crown groups.

Divergence-time estimates can be calculated using molecular clocks calibrated with fossils, giving an estimation of times when all taxa within a given clade shared a common ancestor. The most recent species-level molecular phylogeny of mammals (31 genes by 4098 species; Upham *et al.* 2019) estimated divergence times of crown mammals at c.167–211 million years ago (mya), the Metatheria-Eutheria split at c.156–166 mya, crown Marsupialia at c.68–93 mya, and crown Placentalia at c.77–105 mya (Figure 1). Those results are similar to a number of other recent molecular studies, albeit with some variation depending on the strictness of fossil age constraints (e.g. Meredith *et al.* 2011, Reis *et al.* 2012, Foley *et al.* 2016, Tarver *et al.* 2016). Nevertheless, all these studies reported higher age uncertainty deeper in the mammalian phylogeny.

Many phylogenetic studies have focused on placental interordinal relationships, given that placentals make up the majority of living mammal species. Marsupials are represented by c.385 species that are primarily restricted to the Neotropics and Australasia. The disparity in living diversity of placentals and marsupials has often been attributed to distinctions in reproductive mode between the two clades, suggesting that marsupials are subjected to different selective pressures due to their extensive post-uterine development. As discussed by Sánchez-Villagra (2013), however, the lack of modern marsupial diversity might have resulted from physiological and geographical factors in the Gondwanan origin (southern paleocontinent) of marsupial radiation in particular. Across mammals as a whole, clades with a Laurasian origin (northern paleocontinent) are generally more speciose in modern habitats. For example, the taxonomically and ecomorphologically diverse Laurasiatheria and Euarchontoglires appear to have originated in Laurasia, whereas the less diverse Afrotheria and Xenarthra originated in Gondwana (Beard 2002). The reason for this is not well understood, but one hypothesis is that the larger northern land area of Asia made the continent more likely to have a variety of habitats and thus more likely to have supported a diversity of mammalian radiations.

Marsupials have typically been arranged into two clades based on which continent they originated: Ameridelphia in the Americas and Australidelphia in Australasia. While this makes sense biogeographically, morphological and molecular data have shown the enigmatic Monito del Monte (*Dromiciops gliroides*, Microbiotheriidae) of South America to be sister to or embedded within Australidelphia, which is otherwise monophyletic. The other caveat to Ameridelphia/Australidelphia is that all three American marsupial orders are most commonly recovered as sequentially diverging prior to the origination of Australidelphia (Figure 1). The American marsupial orders are either recovered with Paucituberculata sister to Didelphimorphia + Australidelphia or with Didelphimorphia sister to Paucituberculata + Australidelphia. Earlier

molecular studies found more support for Didelphimorphia being sister to all other marsupial orders (e.g. Asher *et al.* 2004, Nilsson *et al.* 2004, Meredith *et al.* 2008), but more recent studies have reported Paucituberculata as the earliest diverging order (Meredith *et al.* 2011, Mitchell *et al.* 2014, May-Collado *et al.* 2015, Upham *et al.* 2019). In the most recent review of living and fossil taxa, Eldridge and colleagues (2019) favored the former arrangement while acknowledging that a third hypothesis, Paucituberculata and Didelphimorphia (true Ameridelphia) as sister taxa, has not been fully refuted.

Placement of the South American Microbiotheria (represented only by *Dromiciops gliroides*) is similarly unresolved, although to a greater extent than Paucituberculata or Didelphimorphia. Several molecular analyses (Meredith *et al.* 2008, 2011; Mitchell *et al.* 2014; Duchêne *et al.* 2018; Upham *et al.* 2019) have recovered Microbiotheria sister to all Australian marsupials (Figure 1); however, there is some evidence suggesting that Microbiotheria is embedded within the Australian marsupial radiation sister to Diprotodontia (May-Collado *et al.* 2015). The phylogenetic arrangement between the four Australian marsupial orders and Microbiotheriidae is comparatively well resolved unlike the relationship of the two basal American orders, although the relationship among Notoryctemorphia, Peramelemorphia, and Dasyuromorphia is still unresolved in some phylogenies. Notoryctemorphia is typically recovered sister to Dasyuromorphia + Peramelemorphia (as in Figure 1), although some studies have reported it as sister to Dasyuromorphia (Meredith *et al.* 2008) or Peramelemorphia (Duchêne *et al.* 2018). Earlier morphological findings support a sister relationship with Peramelemorphia. Regardless of the relationship among Notoryctemorphia, Peramelemorphia, and Dasyuromorphia, this clade is consistently recovered and has thus been named Agreodontia (Beck *et al.* 2014).

Many of the traditionally recognized placental mammalian orders based on morphology are still recognized following molecular studies. Past ambiguity has come from the recognition of Insectivora that was often regarded as a "wastebasket" taxon for species with insectivorous lifestyles, a trait that has proven to be convergently evolved among mammals (Zou & Zhang 2016, Harmon 2017). The history of the definition of insectivorans is complex and riddled with name changes, but in a broad sense, insectivorans were often placed in two ordinal groups consisting of Menotyphla (modern orders of Scandentia, Macroscelidea, and Dermoptera) and Lipotyphla (Eulipotyphla and Afrosoricida), or retained as Insectivora when including Macroscelidea, as was done by Simpson 1945 (see also Gregory 1910). As a result, the modern name Eulipotyphla is debated because Lipotyphla is the oldest name for the clade but represents a different definition of the clade. By adding the "Eu-", meaning true, at the beginning, the new concept for Eulipotyphla was established (this can also be seen in Euarchontoglires, based on Euarchonta [Primates, Dermoptera, and possibly Scandentia], previously referred to as Archonta in a broader sense). Nevertheless, molecular data demonstrated that these clades are not reciprocally monophyletic, with Scandentia and Dermoptera under Euarchontoglires, Macroscelidea and Afrosoricida close to Tubulidentata in Afrotheria, and Eulipotyphla as the earliest divergence within Laurasiatheria (Stanhope *et al.* 1998, Meredith *et al.* 2011). Thus, the archaic name Insectivora is now spread across three of the four placental superorders, all three of which have been defined primarily based on molecular data, with Xenarthra as the only superorder traditionally defined based on morphology and confirmed by molecular data.

There are three competing hypotheses regarding the relationship among Afrotheria, Xenarthra, and Boreoeutheria that have distinct cladistic names associated with them: Epitheria (Afrotheria + Boreoeutheria sister to Xenarthra), Exafroplacentalia (Xenarthra + Boreoeutheria sister to Afrotheria), and Atlantogenata (Xenarthra + Afrotheria sister to Boreoeutheria). Although there is limited genetic support for Epitheria (O'Leary *et al.* 2013) and Exafroplacentalia (Romiguier *et al.* 2013), most molecular studies support the recognition of Atlantogenata as sister to Boreoeutheria (Reis *et al.* 2012, Morgan *et al.* 2013, Tarver *et al.* 2016, Esselstyn *et al.* 2017, Upham *et al.* 2019). Note, however, that considerable statistical uncertainty underlies this branching relationship (Figure 1). A key aspect of this debate appears to hinge on which molecular markers are used, their rates of evolution, and how their nucleotide content might be biased by life-history traits (Romiguier *et al.* 2013, Tarver *et al.* 2016, Esselstyn *et al.* 2017). Cladistic (Halliday *et al.* 2017) and biogeographic (Wildman *et al.* 2007) evidence supports the Atlantogenata relationship, suggesting that Afrotheria and Xenarthra might have diverged around the time of the opening of the South Atlantic c.100 mya, or soon after by dispersal over the narrow South Atlantic (Asher 2018). Molecular studies have variously reported divergence between Afrotheria and Xenarthra at 83–103 mya, further supporting the hypothesis

that overwater dispersal occurred across the South Atlantic, similarly to rodents and primates during the Eocene (Murphy *et al.* 2007, Reis *et al.* 2012, Tarver *et al.* 2016, Wu *et al.* 2017, Upham *et al.* 2019). Atlantogenata and Boreoeutheria are recognized as magnorders herein, but these superordinal interrelationships remain an open question in mammalian evolution.

There is a general consensus for two major clades within Afrotheria: Paenungulata (Sirenia, Hyracoidea, and Proboscidea) and Afroinsectiphilia (Tubulidentata, Afrosoricida, and Macroscelidea). Nevertheless, there is still some ambiguity regarding placement of Tubulidentata and interrelationships within Paenungulata. Although most studies found Tubulidentata sister to Afrosoricida + Macroscelidea, other studies suggested a sister relationship between Tubulidentata and Paenungulata (O'Leary *et al.* 2013). Within Paenungulata, Proboscidea and Sirenia are often considered to be sister based on morphological data, but many molecular studies found support for a sister relationship between Hyracoidea and Proboscidea to the exclusion of Sirenia, again except for O'Leary and colleagues (2013).

Within Euarchontoglires, there are two clades that are well supported in molecular studies: Glires (Lagomorpha and Rodentia) and Euarchonta (Dermoptera and Primates). Placement of Scandentia in this superorder is highly problematic, alternatively included as sister to Glires (Meredith *et al.* 2011), sister to Glires + Euarchonta (Tarver *et al.* 2016), sister to Dermoptera + Primates (Esselstyn *et al.* 2017), or sister to Dermoptera excluding Primates (Murphy *et al.* 2007, O'Leary *et al.* 2013, Upham *et al.* 2019). There appears to be more support for placement of Scandentia in Euarchonta, but the possibility that the order is sister to Glires cannot be ruled out.

Relationships among many internal branches of Laurasiatheria are unresolved and among the most contentious of all placental higher taxa (Zachos 2020). The position of Eulipotyphla as the earliest diverging order in Laurasiatheria (sister to a group called Scrotifera) and the sister relationship between Pholidota and Carnivora (together known as Ferae) are strongly supported. The position of Chiroptera, however, is unresolved within Scrotifera and has been variously placed as sister to the rest of Scrotifera (Tarver *et al.* 2016, Esselstyn *et al.* 2017, Upham *et al.* 2019, Jebb *et al.* 2020), sister to Perissodactyla + Artiodactyla (Meredith *et al.* 2011, O'Leary *et al.* 2013), sister to Perissodactyla + Ferae (Nishihara *et al.* 2006), or sister to Perissodactyla and then to Ferae (Zhang *et al.* 2013). The sister relationship between Perissodactyla and Cetartiodactyla is often assumed and has been supported by most recent molecular studies (Meredith *et al.* 2011, O'Leary *et al.* 2013, Tarver *et al.* 2016, Esselstyn *et al.* 2017, Upham *et al.* 2019), but other molecular studies have found Perissodactyla sister to either Ferae (Nishihara *et al.* 2006) or Chiroptera (Zhang *et al.*, 2013).

Phylogenetic relationships below the ordinal level have been covered throughout the HMW series and are not discussed here; however, it is important to note that relationships have been highly contentious within Rodentia and Chiroptera until relatively recently (e.g. Hystricomorpha rodents and Yangochiroptera and Yinpterochiroptera bats). Additional molecular studies using more inclusive phylogenies with larger sets of genetic, fossil, and morphological data will certainly be needed to fully understand the evolutionary history and taxonomy of mammals at the macrosystematic level.

Speciation, Species Concepts, and Controversies in Mammalian Taxonomy

Molecular Age Advancements and Genetics in Taxonomy

After more than a century of morphology's dominance in species delimitation, the rise of molecular methods dramatically changed the course of taxonomic research. In the days before DNA sequencing, techniques included analyses of chromosomal karyotypes, immunological distances, and protein electrophoretic gels. Karyotypic studies evaluate the macro-level structure and number of chromosomes rather than their nucleotide sequences. Individuals of the same species generally have the same karyotype, while individuals of different species usually do not. Karyotype analysis has proven particularly useful in speciose clades with low morphological divergence, such as *Ctenomys* and *Akodon* (Patton *et al.* 2015); however, it can be overly conservative when different species have the same karyotype and difficult to interpret when multiple karyotypes exist in a single species, such as in species of *Sorex* (Searle 1986), *Gazella* (Kingswood *et al.* 1994), *Vulpes* (Switonski *et al.* 2003), and *Aotus* (Defler & Bueno 2007).

Immunological distances work on the principle that closely related species have similar antigens, and more distantly related species have less similar antigens. A selected host species, for example domestic rabbit, will be primed to create antibodies against the antigens of a particular species, and then those antibodies will be tested against antigens of another species. A strong reaction means the rabbit antibodies

Table 2. Suprafamilial taxonomy of the world's mammals.

Subclass Prototheria
    Order Monotremata
        Family Tachyglossidae
        Family Ornithorhynchidae
Subclass Theria
  Infraclass Metatheria
    Order Didelphimorphia
        Family Didelphidae
    Order Paucituberculata
        Family Caenolestidae
    Order Microbiotheria
        Family Microbiotheriidae
    Order Notoryctemorphia
        Family Notoryctidae
    Order Dasyuromorphia
        Family Thylacinidae
        Family Myrmecobiidae
        Family Dasyuridae
    Order Peramelemorphia
        Family Thylacomyidae
        Family Chaeropodidae
        Family Peramelidae
    Order Diprotodontia
      Suborder Vombatiformes
        Family Phascolarctidae
        Family Vombatidae
      Suborder Phalangeriformes
        Family Burramyidae
        Family Phalangeridae
      Suborder Macropodiformes
        Superfamily Petauroidea
        Family Pseudocheiridae
        Family Petauridae
        Family Tarsipedidae
        Family Acrobatidae
        Superfamily Macropodoidea
        Family Hypsiprymnodontidae
        Family Potoroidae
        Family Macropodidae
  Infraclass Eutheria
  Magnorder Atlantogenata
  Superorder Afrotheria
    Order Afrosoricida
      Suborder Tenrecomorpha
        Family Tenrecidae
        Family Potamogalidae

      Suborder Chrysochloridea
        Family Chrysochloridae
    Order Macroscelidea
        Family Macroscelididae
    Order Tubulidentata
        Family Orycteropodidae
    Order Hyracoidea
        Family Procaviidae
    Order Proboscidea
        Family Elephantidae
    Order Sirenia
        Family Dugongidae
        Family Trichechidae
  Superorder Xenarthra
    Order Cingulata
        Family Dasypodidae
        Family Chlamyphoridae
    Order Pilosa
      Suborder Vermilingua
        Family Myrmecophagidae
        Family Cyclopedidae
      Suborder Folivora
        Family Megalonychidae
        Family Bradypodidae
  Magnorder Boreoeutheria
  Superorder Euarchontoglires
    Order Scandentia
        Family Ptilocercidae
        Family Tupaiidae
    Order Dermoptera
        Family Cynocephalidae
    Order Primates
      Suborder Strepsirrhini
      Infraorder Lemuriformes
        Superfamily Cheirogaleoidea
        Family Cheirogaleidae
        Superfamily Lemuroidea
        Family Lepilemuridae
        Family Megaladapidae
        Family Lemuridae
        Family Archaeolemuridae
        Family Palaeopropithecidae
        Family Indriidae
      Infraorder Chiromyiformes
        Family Daubentoniidae

      Infraorder Lorisiformes
        Family Galagidae
        Family Lorisidae
      Suborder Haplorhini
      Infraorder Tarsiiformes
        Family Tarsiidae
      Infraorder Simiiformes
      Parvorder Platyrrhini
        Family Callitrichidae
        Family Aotidae
        Family Cebidae
        Family Pitheciidae
        Family Atelidae
      Parvorder Catarrhini
        Superfamily Cercopithecoidea
        Family Cercopithecidae
        Superfamily Hominoidea
        Family Hylobatidae
        Family Hominidae
    Order Lagomorpha
        Family Ochotonidae
        Family Prolagidae
        Family Leporidae
    Order Rodentia
      Suborder Supramyomorpha
      Infraorder Castorimorphi
        Family Castoridae
        Family Heteromyidae
        Family Geomyidae
      Infraorder Anomaluromorphi
        Family Zenkerellidae
        Family Anomaluridae
        Family Pedetidae
      Infraorder Myomorphi
        Superfamily Dipodoidea
        Family Sminthidae
        Family Zapodidae
        Family Dipodidae
        Superfamily Muroidea
        Family Platacanthomyidae
        Family Spalacidae
        Family Calomyscidae
        Family Nesomyidae
        Family Cricetidae
        Family Muridae

Suborder Hystricomorpha
Infraorder Ctenodactylomorphi
Family Ctenodactylidae
Family Diatomyidae
Infraorder Hystricognathi
Incertae sedis
Family Hystricidae
Family Thryonomyidae
Family Petromuridae
Family Heterocephalidae
Family Bathyergidae
Superfamily Erethizontoidea
Family Erethizontidae
Superfamily Cavioidea
Family Cuniculidae
Family Caviidae
Family Dasyproctidae
Superfamily Chinchilloidea
Family Chinchillidae
Family Dinomyidae
Superfamily Octodontoidea
Family Abrocomidae
Family Ctenomyidae
Family Octodontidae
Family Echimyidae
Suborder Sciuromorpha
Family Aplodontiidae
Family Sciuridae
Family Gliridae
Superorder Laurasiatheria
Order Eulipotyphla
Family Erinaceidae
Family Soricidae
Family Talpidae
Family Nesophontidae
Family Solenodontidae
Order Chiroptera
Suborder Pteropodiformes
Superfamily Pteropodoidea
Family Pteropodidae
Superfamily Rhinolophoidea
Family Rhinopomatidae
Family Craseonycteridae
Family Megadermatidae
Family Rhinonycteridae
Family Hipposideridae
Family Rhinolophidae

Suborder Vespertilioniformes
Superfamily Emballonuroidea
Family Emballonuridae
Family Nycteridae
Family Myzopodidae
Superfamily Noctilionoidea
Family Mystacinidae
Family Noctilionidae
Family Furipteridae
Family Thyropteridae
Family Mormoopidae
Family Phyllostomidae
Superfamily Vespertilionoidea
Family Natalidae
Family Molossidae
Family Miniopteridae
Family Cistugidae
Family Vespertilionidae
Order Cetartiodactyla
Suborder Whippomorpha
Infraorder Cetacea
Parvorder Mysticeti
Family Balaenidae
Family Neobalaenidae
Family Balaenopteridae
Parvorder Odontoceti
Superfamily Physteroidea
Family Physeteridae
Family Kogiidae
Superfamily Ziphioidea
Family Ziphiidae
Superfamily Platanistoidea
Family Platanistidae
Superfamily Lipotoidea
Family Lipotidae
Superfamily Inioidea
Family Iniidae
Family Pontoporiidae
Superfamily Delphinoidea
Family Monodontidae
Family Delphinidae
Family Phocoenidae
Infraorder Ancodonta
Family Hippopotamidae
Suborder Ruminantia
Infraorder Tragulina
Family Tragulidae

Infraorder Pecora
Family Antilocapridae
Family Giraffidae
Family Cervidae
Family Moschidae
Family Bovidae
Suborder Suina
Family Suidae
Family Tayassuidae
Suborder Tylopoda
Family Camelidae
Order Perissodactyla
Suborder Hippomorpha
Family Equidae
Suborder Ceratomorpha
Family Tapiridae
Family Rhinocerotidae
Order Pholidota
Family Manidae
Order Carnivora
Suborder Feliformia
Infraorder Nandinioidea
Family Nandiniidae
Infraorder Feloidea
Family Prionodontidae
Family Felidae
Infraorder Viverroidea
Family Viverridae
Family Herpestidae
Family Eupleridae
Family Hyaenidae
Suborder Caniformia
Infraorder Canoidea
Family Canidae
Infraorder Arctoidea
Parvorder Ursida
Family Ursidae
Parvorder Pinnipedia
Family Otariidae
Family Odobenidae
Family Phocidae
Parvorder Musteloidea
Family Ailuridae
Family Mephitidae
Family Mustelidae
Family Procyonidae

Branch support
posterior probability
- ● ≥ 0·95
- ● 0·94–0·75
- ● < 0·75
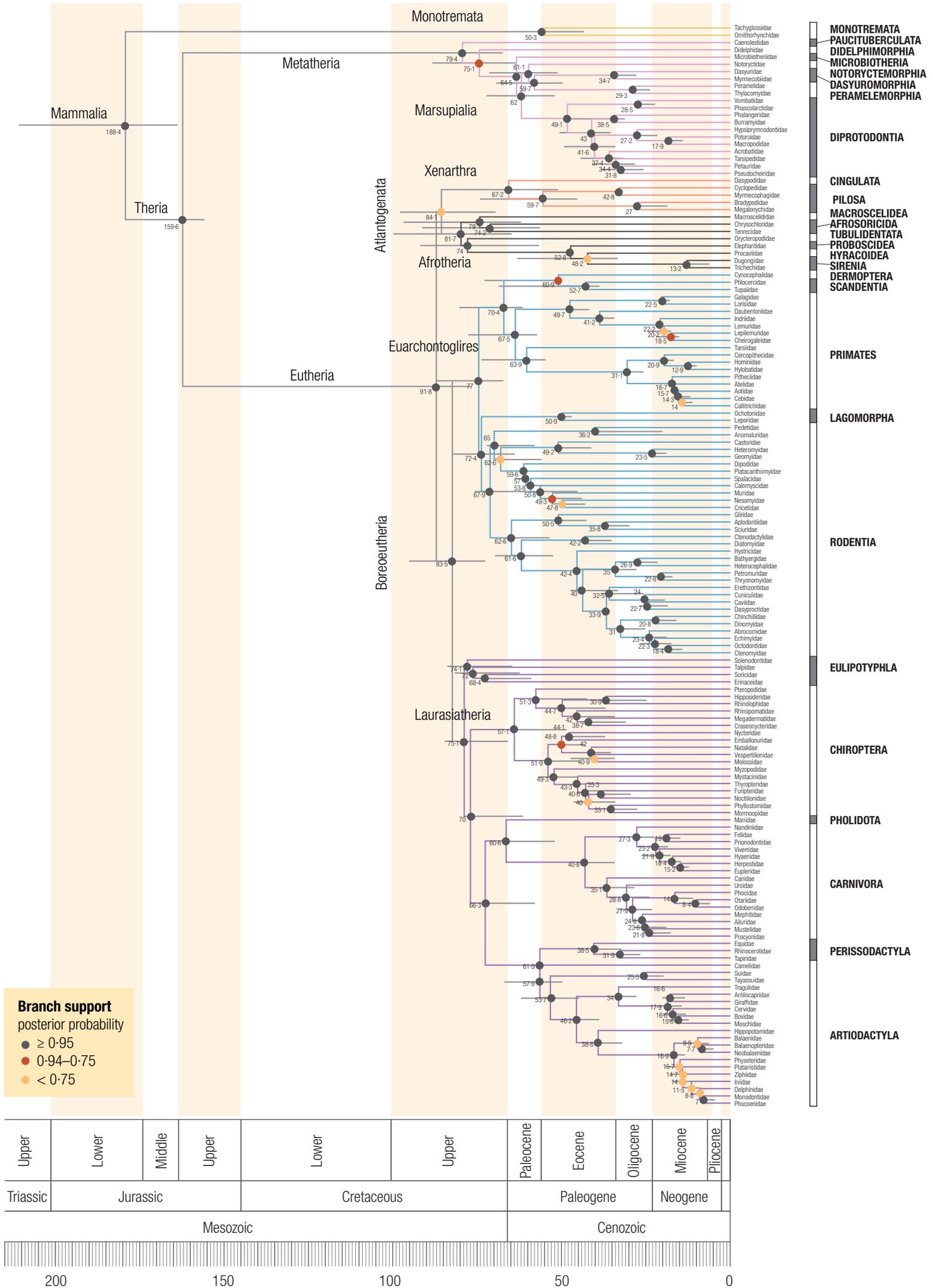
Figure 1. Family-level phylogenetic relationships of extant mammals as pruned from the VertLife mammal tree of 4098 species for which DNA sequences were available (Upham *et al.* 2019). One species was chosen to represent each extant family (149 total in that taxonomy) from the maximum clade-credibility (MCC) topology of the fossil node-dated phylogeny. The Mammalia wide phylogeny was estimated from a supermatrix of 31 genes using a two-step Bayesian approach in which the backbone-level divergence times (among higher taxa) were estimated separately from subtending species-level clades, and then the two were joined together into credible sets of 10,000 time-scaled trees. These trees are downloadable from http://vertlife.org/phylosubsets/ for subsets of mammal species. Shown here are the statistical support values for each of the family-level branching relationships, quantified as posterior probabilities ≥ 0·95 (black, strong support), between 0·94–0·75 (gray, moderate support), and < 0·75 (white, weak support). Superordinal groups are shown with branches colored according to their labels. Numbers at nodes are the mean divergence times (in millions of years) from the credible set of trees; note that branching times of the topology shown are that of the MCC tree, which might differ in some cases from overall mean divergence times printed at the nodes. The geological timescale follows Gradstein *et al.* (2012). The 27 extant orders of mammals are labeled in capital letters on the right side.

found the antigens of the second species to be similar to the first, and thus, they are probably closely related (Faith 1985). This technique was used in early studies of relationships among Primates, Diprotodontia, Artiodactyla, Perissodactyla, and Carnivora (Sarich & Wilson 1966, Wilson *et al.* 1974, Goodman 1989, Baverstock *et al.* 1989, Wayne *et al.* 1991)

Protein electrophoresis is the process of running samples of protein across a starch gel using an electric charge, allowing the proteins to separate on the gel depending on their size and intrinsic charge. Protein electrophoresis is a conservative technique because less than one-third of amino acid substitutions change the net charge on a protein (Micales & Bonde 1995). Thus, while different species might have fixed genetic differences, the proteins produced might appear the same in electrophoresis. This technique was used to study relationships across Mammalia, for example in Primates, Chiroptera, Diprotodontia, Rodentia, Carnivora, and Eulipotyphla (Johnson & Wicks 1959, Johnson 1968, Richardson *et al.* 1973).

Because immunological distance and protein electrophoresis are essentially proxies for understanding nucleotide sequences, both have fallen out of favor with the rise of cheaper and faster DNA sequencing technologies. Karyotype analysis is still used in taxonomic research, often in conjunction with DNA or RNA sequencing.

Most modern taxonomic work of mammals involves some amount of genetic sequencing, usually from the mitochondrion but often from the nuclear genome. In mitochondrial sequencing, part or all of the DNA inside the maternally (very rarely paternally; e.g. Gyllensten 1991) inherited mitochondria (mtDNA) is sequenced for comparison. There are a number of reasons researchers prefer working with mtDNA: it has a relatively high mutation rate, it has little to no recombination, it is present in the cell in large quantities, and it has an abundance of priming sites available (Sorenson *et al.* 1999). There are also disadvantages to sequencing only mtDNA, the most serious of which is that multiple mechanisms exist that can make mtDNA phylogenies incongruent with species phylogenies; for example, incomplete lineage sorting and introgressive hybridization (Figure 3). Certain life-history or behavioral characteristics can also be associated with higher levels of mito-nuclear discordance, like sex-biased dispersal or high intra-sex reproductive skew (Ting *et al.* 2008, Pilot *et al.* 2010, Toews & Brelsford 2012, Dávalos & Russell 2014).

As nuclear sequencing has become cheaper, faster, and easier, more researchers are recognizing the taxonomic value of using both mtDNA and nuclear DNA (nDNA)

in comparative studies. For example, using mtDNA and nDNA, Wang *et al.* (2018) argued that the phylogeny of the European Wisent (*Bos bonasus*) was best explained by incomplete lineage sorting. In Cercopithecini, a tribe known for intraspecific and intrageneric hybridization, comparisons of incongruent mtDNA and nDNA phylogenies gave new insights into the radiation of this lineage (Guschanski *et al.* 2013).

Overall, advances in molecular technologies and DNA sequencing technologies in particular have contributed greatly to our understanding of mammalian taxonomy at all levels of the tree. Continued improvements in technology, integrated with more traditional methods of taxonomic work, will undoubtedly reveal more about phylogenetic relationships of mammals in the years and decades to come.

The Rise of Big Data in Mammal Research

Although early mammal research was done mainly by a select few individuals depositing specimens in museums and publishing in journals with limited readership, new tools and technologies have increased the number of individuals participating in data collection and increased availability of biodiversity data. Through initiatives like VertNet (Guralnick & Constable 2010) and iDigBio (Beach *et al.* 2010), records of museum specimens have been digitized and published for scientists and the general public. Basic records include data like species name and date and location of collection. More complete records in some cases also have information like body mass and total length (i.e. trait data). The most thorough records have a digitization of the specimen, usually in the form of photographs but sometimes as three-dimensional scans or computed tomography.

In addition to specimen digitization, the rising use of smartphones has contributed to a dramatic increase in data collected by citizen scientists. These types of records are usually limited to just photographs, but they have other advantages, for example, of having precise GPS-enabled locations, immediate digitization, and thus wider geographical coverage in public databases.

The final location for most digital records is the Global Biodiversity Information Facility (GBIF), an international aggregator and repository with standardized data fields (Edwards 2004). The GBIF currently contains more than 17 million mammal records, including more than 30,000 type specimens. Museum voucher specimens constitute c.7 million records, while the remainder are observational. Since 2000, yearly additions of museum specimens have held relatively steady, while observational records have approximately tripled, and new observational records now outnumber new museum specimen records by more than 10 to 1.

Figure 2. As genetics become more important in species delineation, maintaining taxa as monophyletic has become a guiding force in mammalian systematics. A priority in modern taxonomic treatments is to maintain monophyly within all taxonomic levels, from subspecies to all higher taxa—monophyly being a named taxon that includes a common ancestor and all its descendants. Taxonomic revisions are often spurred when molecular analysis proves that a taxon is either paraphyletic (a named taxon not including all descendants from the common ancestor of the included members) or polyphyletic (a named taxon where the common ancestor of the included taxa is not included within it). Revisions occur at all taxonomic levels as a result of para- and polyphyly, but the generic level is often the most noticeable, in which large genera formerly used as "wastebasket" taxa are broken up into multiple genera. The genus *Spermophilus* is a prime example because it was shown to be paraphyletic with respect to *Marmota*, *Cynomys*, and *Ammospermophilus*, resulting in recognition of eight distinct genera previously considered under *Spermophilus: Notocitellus*, *Urocitellus*, *Spermophilus*, *Otospermophilus*, *Callospermophilus*, *Ictidomys*, *Poliocitellus*, and *Xerospermophilus* (Herron *et al.* 2004, Helgen *et al.* 2009). Many revisions result in the splitting up of genera, either by resurrecting previously synonymized names (e.g. *Spermophilus* as above) or by describing a new name for the genus, as has been done for species of *Parahypsugo*, which were previously included in *Hypsugo* (Hutterer *et al.* 2019). On some occasions, however, these revisions lead taxa to be subsumed, as was the case with the former families Capromyidae and Myocastoridae, which were shown to be molecularly embedded in Echimyidae, making the family paraphyletic unless both were included within it (Fabre *et al.* 2014, 2017; Upham & Patterson 2015; Courcelle *et al.* 2019).

Monophyletic group   Paraphyletic group   Polyphyletic group
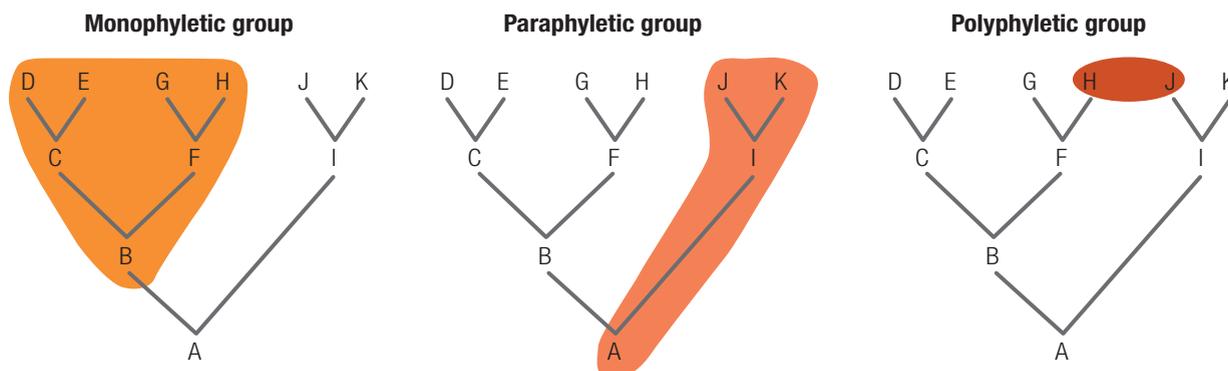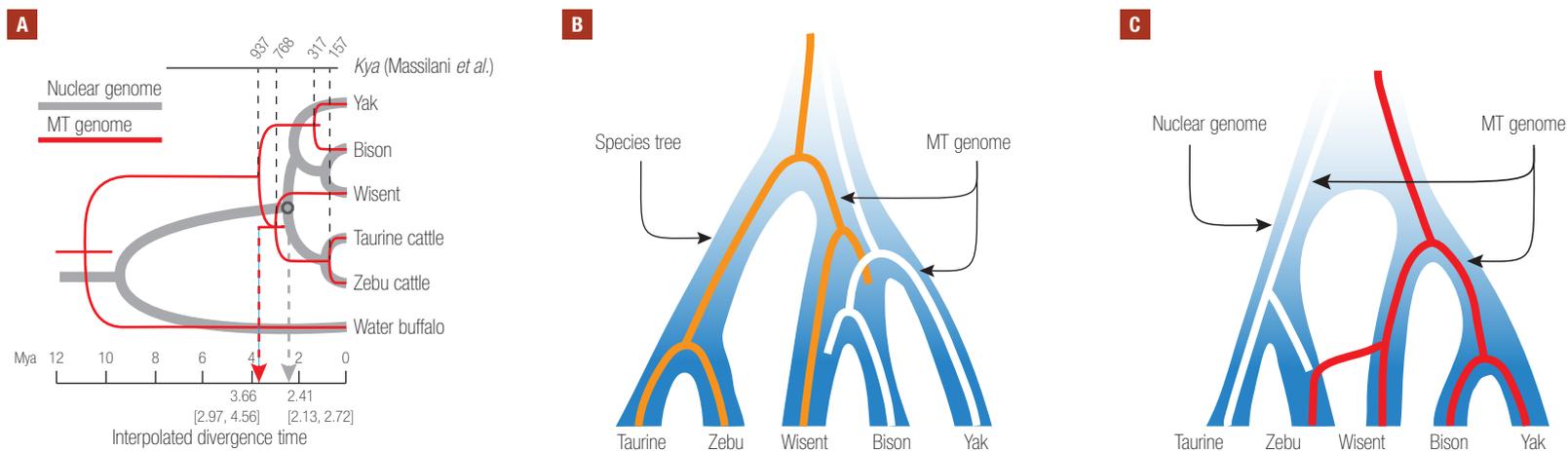
Figure 3. With the rise of nuclear DNA sequencing, it is now recognized that mitochondrial-nuclear discordance is a common phenomenon in mammalian taxonomy. (A) When trees constructed from nuclear and mitochondrial sequences are overlaid, mismatches in the tree structures indicate mito-nuclear discordance. (B) This discordance can arise via incomplete lineage sorting, where a mitochondrial lineage from an ancestral population is lost early along one branch of the tree and lost much later along a more distantly related branch, making them appear more closely related than they are. (C) Introgressive hybridization can also cause mito-nuclear discordance. In this scenario, the nuclear tree and the mitochondrial tree match until a hybridization event replaces a mitochondrial lineage with a more distantly related lineage. Figure source: Wang *et al*. 2018.

All these digitized records are freely available for research and have been used to address various topics including species responses to climate change (Guralnick 2007), areas of endemism (Escalante *et al.* 2013), and spread of invasive species (Padayachee *et al.* 2017). Most relevant for taxonomy, these large datasets can be used to model species distributions and understand distinct niches of closely related species (Kalkvik *et al.* 2012). As with all datasets, however, there are challenges to overcome prior to publication. Records are not always updated to reflect taxonomic changes, leading to different labels for the same species; for example, *Loxodonta africana* and *L. cyclotis* for elephants in Central Africa (Figure 4). There are also taxonomic and geographical biases in large-scale biodiversity (Beck *et al.* 2014, Troudet *et al.* 2017), which will only improve by dedicated efforts of researchers and funding agencies over time. For now, analyzing these data requires thoughtful and deliberate data processing techniques. Ongoing improvements to large-scale data collection, management, and processing will allow new avenues of research for the next generation of mammalogists.

Morphology, Biogeography, Behavior, and Coevolution in Species Delimitation

Species can be distinct from each other in many ways. Because taxonomic work has traditionally focused mainly on preserved specimens, morphology has been the primary metric used for species delimitation. Specimens can be measured for multiple linear characters, such as skull length, total length, and length of hindfoot, and if consistent differences of sufficient magnitude are found, they can be suggestive of species-level status. Other morphological characters commonly used in mammalian taxonomy include number of mammae, tooth number and shape, and form of the

baculum. Pelage differences have also historically been used to support species status, but they have proven to be unreliable and highly variable within species and thus should not be used as the sole diagnostic criterion (Musser 1968, Jarrín-Valladares & Kunz 2008, Schiaffini *et al.* 2013, Kitchener *et al.* 2017, Pine & Gutiérrez 2018).

With specimens of known origin, biogeography can also be considered in species delimitation. This discipline seeks to explain current and past biological diversity and distribution in the context of geological and environmental factors, such as volcanic eruptions, glacial cycles, and river formation (Sanmartín 2012). Islands in particular are likely to cause speciation when populations of a formerly continuously distributed species become permanently separated. Insular speciation is a proposed mechanism for the high diversity of *Pteropus* bats found on Indo-Pacific islands and also of fossorial *Ctenomys* rodents of South America, whose "islands" are separate burrow systems (Upham *et al.* 2020). Biogeographical evidence has also been invoked to explain species distribution patterns in *Pan* (Takemoto *et al.* 2015), *Cephalophus* and *Philantomba* (Ntie *et al.* 2017), *Marmosa* (Gutiérrez *et al.* 2010), *Dremomys* (Hawkins *et al.* 2016), and *Sorex* (Demboski & Cook 2001), among others.

Behavioral divergence is another line of evidence used to support taxonomic decisions in mammals. Closely related species can differ in temporal patterns of activity such as the nocturnal *Cephalophus dorsalis* and diurnal *C. callipygus*, in timing of reproduction such as *S. putorius* and *Spilogale gracilis* (Mead 1968), or in social organization such as *Equus quagga* and *E. grevyi* (Klingel 1975). Vocalizations are the most commonly analyzed behavioral variation in delimitation of mammal species. Nocturnal mammals in particular are likely to use sound rather than vision for individual and species recognition, thus reproductive isolation often occurs quickly

Figure 4. GBIF occurrence records of (1) *Loxodonta cyclotis* and (2) *Loxodonta africana*. Because submitters can choose which species concept they use, some records of what would be *L. cyclotis* in the Congo Basin and West Africa have been submitted under a single *L. africana* concept. Map sources: OpenStreetMap contributors, OpenMapTiles, ESRI.
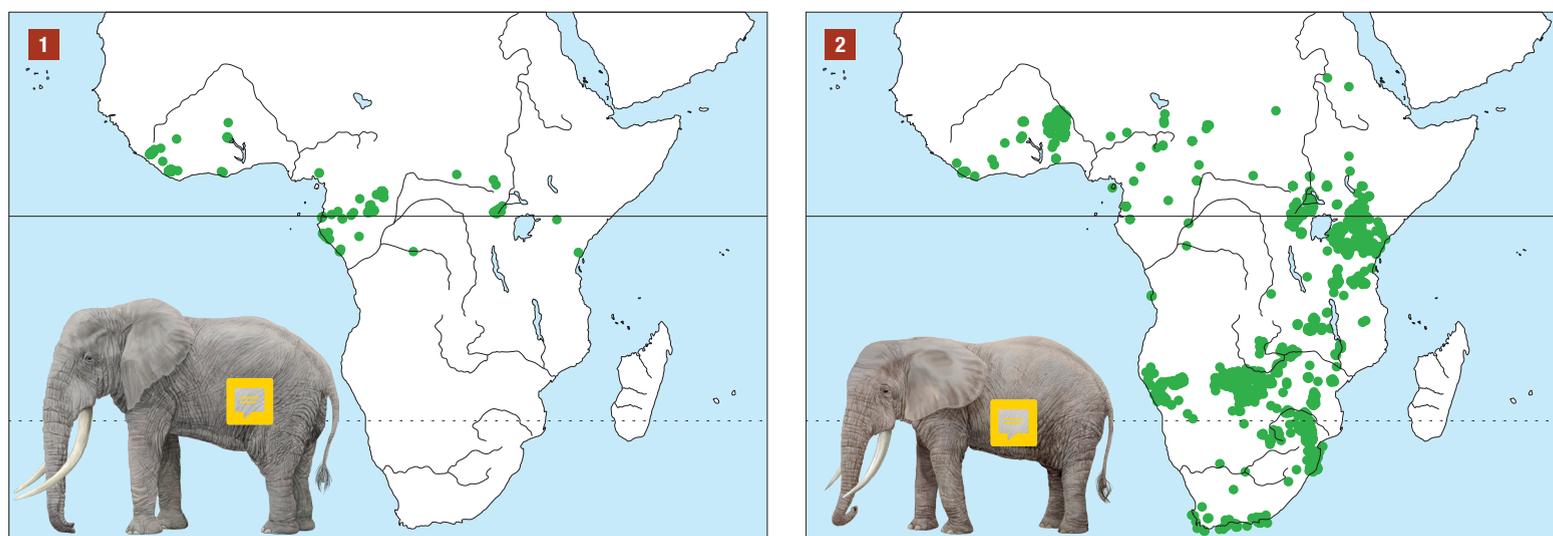
with divergence in acoustic parameters. Among nocturnal primates, acoustic divergence has been documented in *Tarsius* (Merker *et al.* 2010), *Microcebus* (Braune *et al.* 2008), *Galagoides* (Svensson *et al.* 2017), and *Sciurocheirus* (Ambrose 2003). Bat species are also commonly identified by species-specific vocalizations. For example, *Hipposideros kunzi* is easily distinguished from its congener *H. bicolor* by the frequency of its echolocation call, and a number of cryptic species within *Pteronotus parnellii* have been supported through acoustic analysis (Clare *et al.* 2013).

Host-parasite coevolution is an interesting but relatively rarely discussed topic in species delimitation. In theory, parasites that have very particular needs evolve along with their hosts, such that host species that are closely related to each other also have closely related parasites. While these congruent phylogenies can break down through extinction events, failure to speciate, and host switching, there is often remarkable correspondence between co-diversifying phylogenies of hosts and parasites (Light *et al.* 2010). Within mammals, host-parasite coevolution has been explored in Vespertilionidae and Rhinolophidae (Bruyndonckx *et al.* 2009), Primates (Switzer *et al.* 2005), Sciuridae (Musser *et al.* 2010), and Geomyidae (Hafner *et al.* 1994).

A thorough investigation of species delimitation involves analyzing multiple lines of evidence. With morphological, biogeographical, and behavioral evidence in agreement, there is a much stronger argument for species status than with just one or two signals. Even so, care must be taken to include adequate sample sizes, consider within-species variation, and account for potential differences between age-sex classes of specimens. Modern taxonomists do just this when they take an integrative approach to species delimitation.

Speciation, Species Concepts, and Conservation Implications of Taxonomy

How a species should be defined is seriously debated among systematists. This is understandable, considering that the process of speciation makes nearly any species concept partially ambiguous and subjective because of its continuous and chaotic nature. Thus, to understand species concepts requires considering processes of speciation.

Speciation is a continuous process in that species are continually evolving (not necessarily at a constant rate) through four primary processes: selection, mutation, genetic drift, and gene flow (Coyne & Orr 2004). When some form of isolation occurs, whether it is geographical, behavioral, or physiological, the former three evolutionary processes accumulate genotypic and phenotypic distinctions between isolated populations, slowly leading them toward speciation in the absence of gene flow. There are four primary forms of speciation that result from distinct forms of isolation: allopatric, peripatric, sympatric, and parapatric, all of which also describe associated distributional situations (Figure 5). These terms might be used to describe distributional relations among species throughout the main text.

Allopatric speciation is the most commonly observed mode of speciation in mammals (Baker & Bradley 2006), resulting from geographically separated populations becoming genetically isolated long enough to develop reproductive barriers. Peripatric speciation is similar in that it involves geographical distance, although it occurs when peripheral populations of a species become isolated leading to speciation. Allopatrically evolving species might come into contact again (secondary contact; e.g. due to elimination of a geographical barrier), causing the species to develop a hybrid zone if reproductive isolation is incomplete. The evolutionary history of *Martes americana* and *M. caurina* is a prime example of allopatrically diverging species coming in secondary contact when geographical barriers were eliminated (glaciers in a warming climate), creating fertile hybrids and giving the appearance of parapatrically evolving species (Dawson *et al.* 2017).

Sympatric speciation is considerably rarer and arguably might not exist (Coyne & Orr 2004). To exist, sister species must arise from the same population, usually as hypothesized via ecological niche partitioning. Although sympatric speciation is rare in nature, there are various examples of species that have evolved through allopatry or parapatry before later becoming sympatric (secondary sympatry). In some cases, recently diverged species with sympatric distributions might be able to produce fertile offspring but occupy distinct niches that prevent them from reproducing. Thus, a key problem with identifying sympatric speciation is distinguishing it from allopatric or peripatric speciation with secondary sympatry. Sympatric speciation might have occurred between *Acrobates pygmaeus* and *A. frontalis*, which have a broadly sympatric distribution along the eastern Australian coast and appear to share very similar ecological niches; however, molecular studies are needed to determine the speciation history of these taxa (see Figure 5; Aplin 2013).

Species can also evolve through parapatry when two subpopulations diverge while continuing to exchange genes. Parapatric speciation appears to be more common than previously thought in mammals, as exemplified by *Piliocolobus*, which includes a number of parapatrically evolving species with numerous hybrid swarms where species populations meet (Cardini & Elton 2011). Parapatry was also observed among species of *Petrogale* along the eastern coast of Australia, producing a chain of recently diverged and small-ranging species with extensive karyotypic variation (see Figure 5; Potter *et al.* 2017).

A "species concept" is the philosophy of how a species should be defined. Because the practice of delimiting species requires considering the process of speciation, naming species requires quantifying levels of gene flow and hybridization or introgression. Under the Biological Species Concept (BSC), species considered distinct based upon morphological, ecological, and genetic criteria might not be considered distinct because the BSC states that speciation requires (mostly) complete reproductive isolation between populations. This creates a problem for many of the species traditionally thought to be recognizable but that can hybridize freely with other related species, as is the case between most species of the genus *Canis*, among which extensive introgression has been documented (Gopalakrishnan *et al.* 2018). The other commonly discussed concept is the Phylogenetic Species Concept (PSC), which has gained significant traction among mammalogists since the dawn of the genetic era. The PSC states that a species is the least inclusive monophyletic clade in which the species is diagnosable according to any dimension of evidence from genetics to behavior (Gutiérrez & Garbino 2018). The PSC thus relates to the recognition of species based on their evolutionary significance (Evolutionary Species Concept), with the term Evolutionarily Significant Unit (ESU) used in roughly the same context as a subspecies or putative species, but without applying a Linnaean name.

Although there is philosophical debate over preferred species concepts, the more generalized debate within mammalian systematics is that of "lumpers" and "splitters," or the propensity to either retain a broader definition of a species by grouping species together (lumping) or to retain a more specific definition of species by splitting a taxon into multiple species (splitting). The goal of both situations is to maintain the monophyly of species, but the difference is the point at which the species-level cutoff is drawn. There has been a string of publications criticizing (e.g. Zachos & Lovari 2013; Zachos *et al.* 2013; Zachos 2015, 2016, 2018) and supporting the PSC and splitting (e.g. Gippoliti *et al.* 2013, 2018; Gippoliti 2019; Groves 2013, 2014; Groves *et al.* 2017; Gutiérrez & Garbino 2018) that decently demonstrate the polarization of these two ideologies, including consequences for biodiversity conservation that each hold. The perpetual debate between lumpers and splitters is beyond the scope of this publication, and although a stance on the issue is not strictly taken here, the taxonomy presented roughly follows the PSC, which is inclined to recognize split species. Recently, a review by Gutiérrez & Garbino (2018) analyzed the primary criticisms of the PSC, showing that the claims against it lack supporting evidence and are anecdotal. Lumping species is not frowned on, and species are subsumed given the proper evidence throughout the text, but there is less of a trend toward lumping mammalian species in the cited literature. Taxonomic changes in *Checklist* were based primarily on the most recent treatment of the species in publications, if and when those publications used valid empirical datasets and provided evidence in support of splitting rather than lumping species together.

The ever-changing nature of mammalian taxonomy has been argued to present a problem for conservation organizations and governments that intend to make policy decisions based on species-level entities (Garnett & Christidis 2017). When new mammal species are described yearly and many currently recognized species are being split into multiple species or lumped together, such changes can negatively impact efforts to protect natural habitats. An alternative perspective is that our biodiversity infrastructures, which are now mostly digital and in online databases, need to be more flexible in their integration of different taxonomic perspectives for the same organisms (Sterner *et al.* 2020). Indeed, taxonomy is a science based on hypotheses for the evolutionary relationships among species, and the need for a robust science of taxonomy is not the issue in dispute (Raposo *et al.* 2017, Garnett & Christidis 2017). As it stands, global biodiversity databases are unable to keep up with taxonomic flux, at least in mammals. For example, the *IUCN Red List* currently recognizes 5899 mammalian species versus the 6554 species recognized here, mainly because of political pragmatism and lack of coordinated infrastructure to keep track of all those taxonomic changes. Because conservation organizations are focused heavily on the species level, less emphasis has been given to specific populations and subspecies within those species. Subspecies are occasionally as-
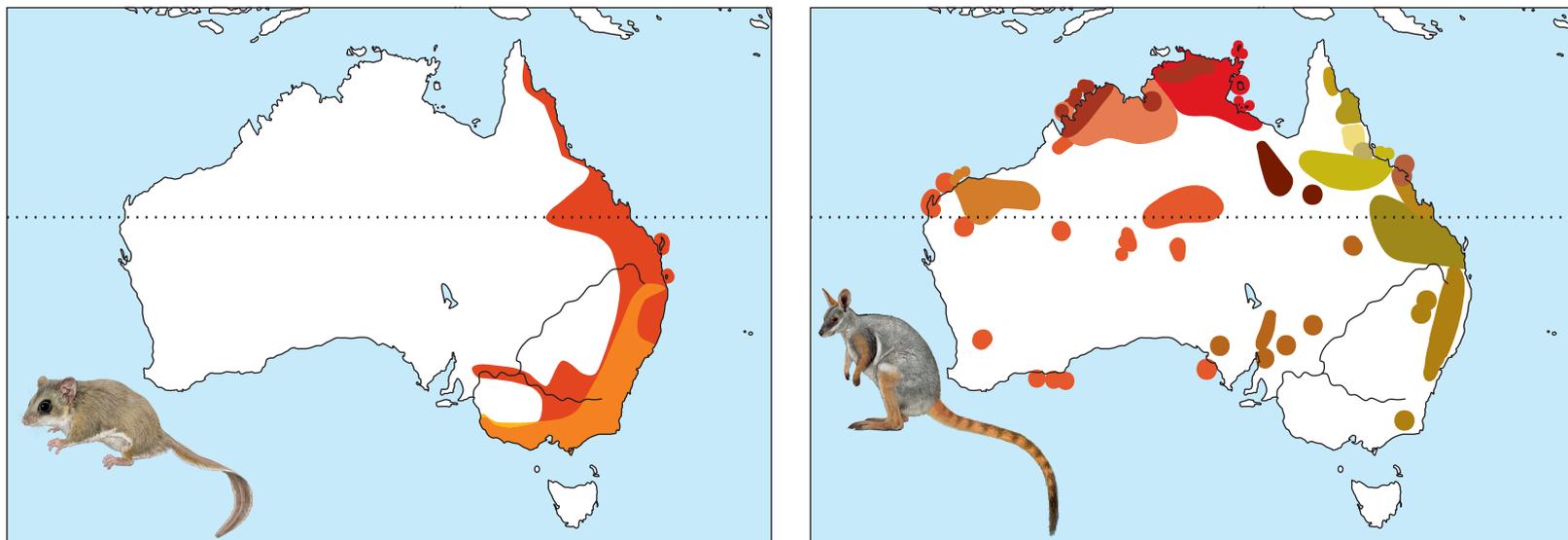
Figure 5. Allopatric, parapatric, and sympatric distributions exemplified by species distributions of *Acrobates* (sympatric) and *Petrogale* (allopatric and parapatric), as included in this volume. *Acrobates* includes two species (formerly one species) that have been recognized based on molecular and morphological distinctions (Aplin 2013, Jackson & Groves 2015). Nevertheless, their morphology is cryptic, and they share nearly the same ecological niche with extensive distributional overlap, suggesting that they might have evolved through sympatric speciation. Within *Petrogale*, there appears to be multiple forms of speciation occurring, with allopatrically evolving populations of *P. xanthopus* and *P. lateralis* (currently recognized as subspecies) in western and central Australia and a parapatrically evolving radiation across the north and west coastal regions of Australia. The allopatric subspecies and species are broadly separated, whereas parapatric species have distributions immediately adjacent to one another, with some degree of contact to their neighboring species.

sessed separately on the IUCN (e.g. various primates and *Giraffa camelopardalis*) but are generally not emphasized in most mammals. This also has to do with the ambiguity surrounding the definition of a subspecies, which is poorly defined within the taxonomic realm. Overall, keeping track of subspecific entities (e.g. ESUs) and their associated taxonomic treatments could assist with the goal to build more flexible taxonomic databases.

Most subspecies were traditionally recognized as morphologically identifiable populations within a species, although the definition in recent years has shifted toward populations of incipient species (moving toward speciation, perhaps forming a monophyletic group but not distinct enough to be called species). As mentioned before, this vague definition is problematic, especially within groups like rodents where numerous subspecies were named historically based on older taxonomic practices (e.g. describing taxa based on pelage color; see *Thomomys bottae*, which has 128 subspecies recognized herein). Because of this vagueness, subspecies are generally not treated as being important in the realm of conservation. There are conflicting views regarding this dilemma (see the Zachos, Groves, and Gippoliti papers referenced earlier), but the general consensus in *Checklist* is to retain historically defined subspecies as distinct until proven otherwise with strong evidence.

That being said, the particular taxonomic arrangement presented by Groves & Grubb (2011) in *Ungulate Taxonomy* has only been partially followed in this *Checklist*. They split many of the traditionally recognized species of ungulates (Perissodactyla and Artiodactyla) into poorly defined species-level units based primarily on morphometric and morphological characteristics and generally small sample sizes. For most families, this taxonomy has been ignored, in part because subsequent studies have ignored it, either because most evidence points toward the traditional arrangement or because the species were too vaguely defined in Groves & Grubb (2011) to treat them separately. Nevertheless, for Bovidae, their arrangement is followed within this revision from HMW Volume 2, which appears to have gained some traction within the mammalogical community. It is emphasized, however, that although this taxonomic arrangement is included in full, there is certainly a need for it to be fully vetted by future molecular, morphological, and behavioral studies to elucidate what taxa are and are not species. A similar situation occurred with Primates with the publication of *Primate Taxonomy* (Groves 2001); however, that volume was partially spurred by inertia in primate systematics at that time, and ultimately resulted in an explosive increase in the number of integrative taxonomic works that supported recognizing additional Primate species. The hope is that ungulates will now travel a similar journey. Ungulates have generally received little taxonomic attention in the modern era, leading to several groups in need of integrative systematic revision.

One example of a recent ungulate revision is in *Giraffa*, which currently includes three species (Figure 7). Traditionally, only a single species was recognized (*G. ca-*

melopardalis), but eight distinct species were recognized by Groves & Grubb (2011). Subsequent molecular studies investigating the species status of different giraffe populations suggested two different species models: a four-species model (*G. giraffa, G. camelopardalis, G. tippelskirchi*, and *G. reticulata*; Fennessy *et al.* 2016) and a three-species model (*G. giraffa, G. camelopardalis*, and *G. tippelskirchi*; Petzold & Hassanin 2020). The more recent, three-species arrangement is followed here based on the most complete dataset, but there is sure to be additional debate. The *IUCN Red List* continues to recognize only a single *Giraffa* species with nine subspecies, each assessed separately. Although this retains all subspecies as units for conservation, the taxonomic ambiguity of the genus has caused the *IUCN Red List* to avoid making judgements at this time. This might have conservation implications (e.g. in captive breeding programs and potential reintroduction or translocation efforts) because determining what populations represent what species is essential to those efforts.

Mammalian taxonomy is highly dynamic, with 40–60 new names described yearly and additional species being resurrected from synonymy due to ongoing revisionary work (Burgin *et al.* 2018). The increasing accessibility and power of molecular analyses have facilitated revisionary work throughout most major mammalian groups. As an example of this, the genus *Cyclopes* typically included one species until a recent systematic revision using molecular and morphometric analyses split the species into seven distinct species (Miranda *et al.* 2017). Such integrative taxonomic work is essential to future progress, ideally incorporating information on nuclear and mitochondrial genomes, morphology, cytogenetics, distributions, and ecological and behavioral niche partitioning. The *Checklist* aims to only include those new species for which integrative taxonomic revisions have been conducted; however, some species have certainly been better studied than others. Future work to database the categories of evidence supporting (or refuting) given taxonomic hypotheses will be welcomed.

Nomenclature

The distinction between nomenclature and taxonomy is not always apparent, but it is an important distinction nonetheless. **Taxonomy** is the science of attempting to put all relevant taxa into a meaningful order or scheme, and **nomenclature** is the process of creating names for each taxon. The complexities of scientific nomenclature in zoology are governed by the International Code of Zoological Nomenclature, often abbreviated as "**the ICZN Code**," published by the International Commission of Zoological Nomenclature (**ICZN**). For any doubts in the connection with this subject, readers are referred to the ICZN Code, which is available online (https://www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/). For readers who are unfamiliar with the terminology and potentially more obscure parts of the text, this section gives a quick summation of the key terms used in the *Checklist* and their

meaning. Nevertheless, it should be stressed that the intricacies of the ICZN Code are often less straight forward than they seem, and the summaries here should be taken as general indications of what each term refers to.

A **taxon** (plural taxa) is any taxonomic unit with the assumption that all of its included members are interrelated, being monophyletic rather than para- or polyphyletic. This is comparable to the phylogenetic term clade, which does not always have a name associated with it but is rather a monophyletic grouping based on a specific node in a phylogeny. Taxon is typically used for species or genera in the *Checklist*, but it can be equally applied to higher level names. Each species level taxon is given an associated **type specimen** (or specimens), an individual museum specimen against which the identity of any closely related taxa can be compared. Except in early publications, a specimen is individually indicated by its museum specimen number in the formal scientific description of the name and is marked in the museum by a species label (usually red). If the type is a single specimen, it is referred to as the **holotype**, but if it is a series of specimens, they are **syntypes**. If the type has been lost, a **neotype** can be designated under strict rules and preconditions. If a group of syntypes proves to refer to a mix of more than one taxon, one of the syntypes can be designated as the **lectotype**, and it gains the same status as the holotype. This system is similar in higher ranking taxa: each genus has a type species, and each family its type genus for which its name is based. For a family group name to be valid, the genus name for which it is based must be available but not necessarily in use. Each species is also assigned a **type locality**, which is theoretically the place of collection of the type specimen, the general idea being to have a geographical site and populations that helps define the taxon, so the individuals observed at the same locality are likely to belong to the same taxon (whether it be species or subspecies). In older publications, type localities were often broadly listed as regions, in which case later publications can **restrict the type locality** based on evidence supporting its restriction, occasionally coupled with the designations of a neotype or lectotype.

Regarding the names themselves, a name that has been correctly described in the scientific literature is said to be **available** regardless of whether the name is currently in use as a species or subspecies, or is a synonym of a recognized name. As long as the name complies with the requirements of the ICZN Code, the name can be used for a valid taxon. The oldest name available (dating no earlier than 1758) is normally the name to be applied to a taxon through the system of **priority**. A **nomen nudum** is a name that for one or several possible reasons does not comply with the conditions of the ICZN Code and is thus unavailable for use. A **nomen dubium** is a name of doubtful application, which generally means that the name cannot reliably be applied to a particular taxon. A **nomen oblitum** is typically a name that has not been used for more than a century and is most often used when an old, unused name is found in the literature and refers to a taxon that is now normally known by another more recent name, in which case the unused name would lose its right of priority and be considered a **senior synonym** of the newer and typically used name. Normally when two names are identified as applying to the same taxon, the younger name would be considered a **junior synonym** of the older one. In some cases, two identical names might have been used to denote different animal taxa, which are known as **homonyms**. They are spelled identically (or at some taxonomic levels, they can have different suffixes) but were proposed separately, usually but not necessarily by different authors in different publications at different times. For example, the name *Platypus* Shaw, 1799 was the original generic name applied to the Platypus (*Ornithorhynchus anatinus*), but the name was applied earlier to a genus of beetle, *Platypus* Herbst, 1793. No two fully identical complete names for taxa can be simultaneously valid in zoology, so the generic name of the Platypus was changed to the next available name, *Ornithorhynchus* Blumenbach, 1800. Within any one genus, no two taxa can have the same species level name (including subspecies and synonyms). Species group names can be brought into **secondary homonymy** by the transfer of a taxon from one genus to another. If both are recognized as distinct taxa, the younger of the names is deemed **preoccupied** by the older name, and the name must be changed to the next available name chronologically.

The **original spelling** of a name, as published in the original scientific description, is largely sacrosanct and can only be modified in certain ways or in certain circumstances. The change that is often the least controversial but often most difficult to track is the modification of species group names involved in mandatory gender agreement with the respective genus name when applicable. Any other intentional change made to the original spelling is considered an **emendation** and can be either justified or unjustified depending on what the ICZN Code specifies. Although the ICZN Code provides precise rules for these issues, there are many situations where there is considerable scope for personal interpretation of these rules, and thus different spellings can sometimes be found in different taxonomic treatments. A justified emendation can only be based directly on the rules themselves and the original publication. Thus, if a name is based on the misspelling of a proper name, the scientific name cannot be amended unless there is internal evidence within the original publication that clearly shows the misspelling to have been unintentional. Another issue revolving spelling is the number of 'i's at the end of names that are based on the names of people. Earlier editions of the ICZN Code emended all names with two 'i's to be amended to one 'i' unless the name was in common usage (used by more than 100 publications with that spelling), but later retracted this concept in the newer version of the ICZN Code. Now, the number of 'i's depends on how the name was presented in the original publication, although newer descriptions cannot use two 'i's. Other specific emendations are discussed in the volume as necessary.

There are specific situations where the ICZN steps in to determine the best solution to a confusing or controversial systematic decision through the use of published **Opinions**. A special case designating the names of domesticated species and their wild counterparts was enacted by the ICZN Code for a number of mammal species, known as Opinion 2027 (ICZN 2003). For domesticated species, there was considerable confusion regarding the use of domesticated and wild form names, especially when domesticated and wild forms were considered to represent the same species. Because the wild forms were typically used in publications relating to conservation and ecology of that species, they were designated as having priority over the domesticated forms (which are typically the older name) when considered a single species. Nevertheless, recent publications have suggested listing domesticated taxa as distinct species rather than as being included as subspecies under their wild forms. This arrangement is followed here, and all domesticated taxa are treated as distinct from their wild forms and any feral forms originating from domesticated stock (e.g. European Mouflon under *Ovis aries* and Dingoes under *Canis familiaris*; Gentry *et al.* 2004, Jackson *et al.* 2019).

Using the Checklist

Higher Level Taxa
Because the main body of this *Checklist* deals exclusively with taxonomy of mammals below the familial level, it does not mention suprafamilial taxa other than the Order. The taxa mentioned above the generic level in the main text include Order, Family, Subfamily, and Tribe. This was decided to include the maximum number of species and text associated with each plate. The higher level taxonomy of mammals below the ordinal and above the familial levels is covered extensively in the HMW series, but the supraordinal systematics are not. Thus, a Mammalian Phylogeny and Macrosystematics discussion occurs earlier in the Introduction, along with an associated table of suprafamilial taxa (Table 2) and an updated phylogeny of the world's mammal families (Figure 1). Within the text of these volumes, there are some cases where familial, subfamilial, or tribal taxa have small comments associated with them regarding recent taxonomic changes or issues, which include citations if necessary in the same fashion as other parts of the text. Taxon authority is also not listed for any suprageneric taxa, but the common name of each family is included in parentheses next to the family name within a red box.

Genera
As with species, genera are highly dynamic and regularly changing taxonomic units and are thus an important part of these volumes. The baseline generic taxonomy of the *Checklist* started with the taxonomy presented by the authors of the HMW series, which was then compared with subsequent studies and updated accordingly. In the main text, genera are listed in red text before the first included species, and all subsequent species are included under that genus until the next genus is listed. The authority and date are listed in smaller print immediately to the right of the generic name, and taxonomic notes are present for genera with recent taxonomic changes.

Species Accounts
The main text of the *Checklist* focuses heavily on taxa at the species level, including the species account for each taxon. This account has a banner of color that includes the common name next to a number identifying placement of the species in each family, the full specific epithet of the species, its conservation status, and where the species can be found in the HMW series. The banners are also color-coded based on whether or not the species is extant and wild (beige), extinct (gray), or domesticated

Figure 6. Maps of *Giraffa* species distributions under various species concepts. (A) The single species concept of *Mammal Species of the World*, Volume 3 (Wilson & Reeder 2005). (B) The three species concept of Petzold & Hassanin (2020). The species recognized are *G. giraffa* (blue), *G. camelopardalis* (green), and *G. tippelskirchi* (red). (C) The four species concept of Fennessy *et al.* (2016). The species recognized are *G. giraffa* (blue), *G. camelopardalis* (green), *G. tippelskirchi* (red), and *G. reticulata* (yellow). (D) The eight species concept of Groves & Grubb (2011). The species recognized are *G. giraffa* (blue), *G. camelopardalis* (green), *G. tippelskirchi* (red), *G. reticulata* (yellow), *G. angolensis* (purple), *G. thornicrofti* (orange), *G. antiquorum* (pink), and *G. peralta* (gray). Map sources: IUCN, OpenStreetMap contributors, OpenMapTiles, ESRI.
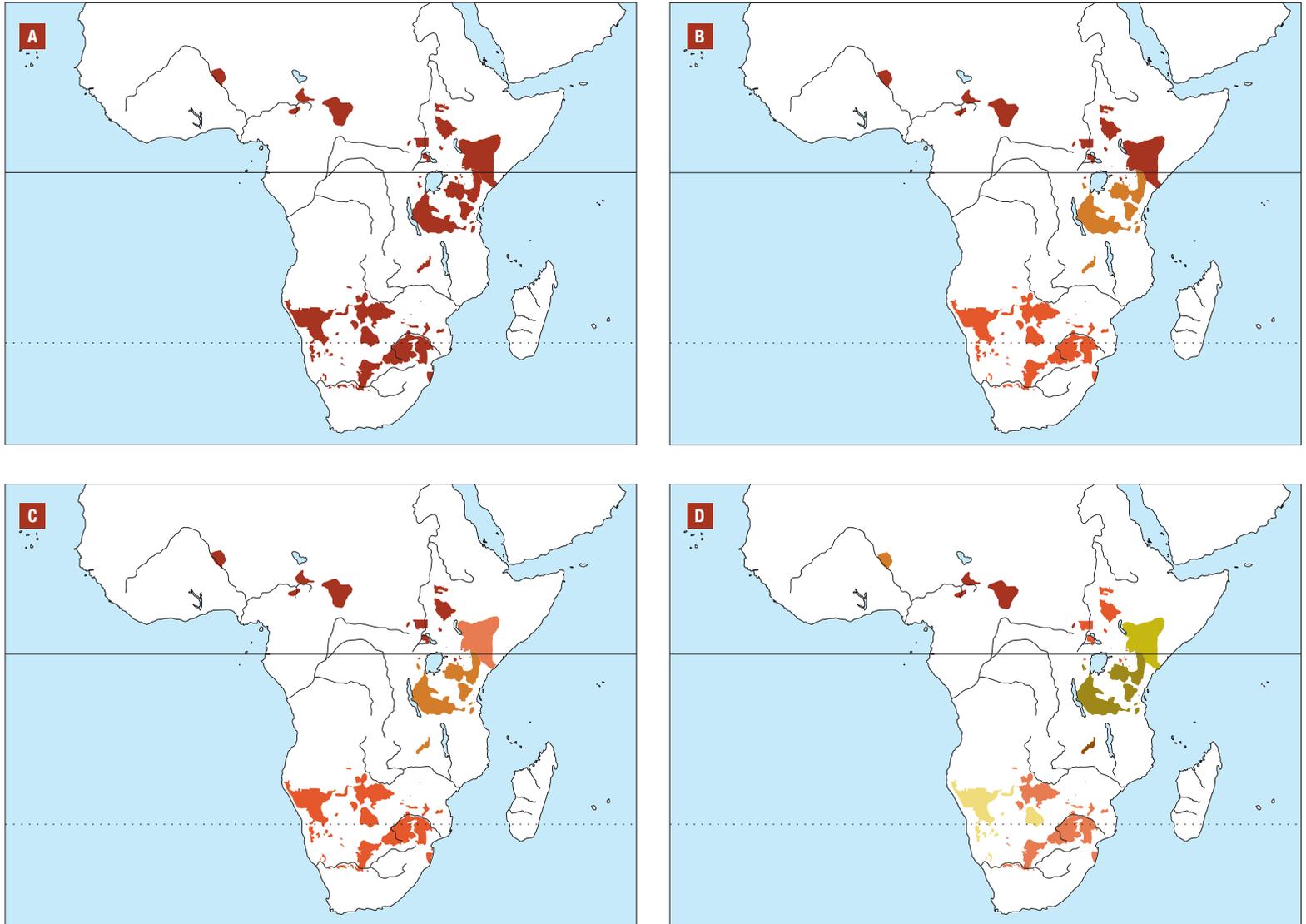
G. reticulata

G. peralta
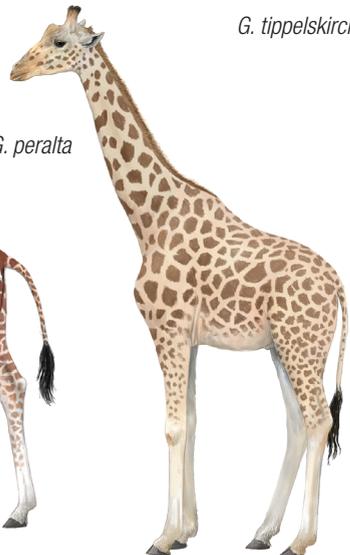
G. tippelskirchi

G. angolensis

G. giraffa
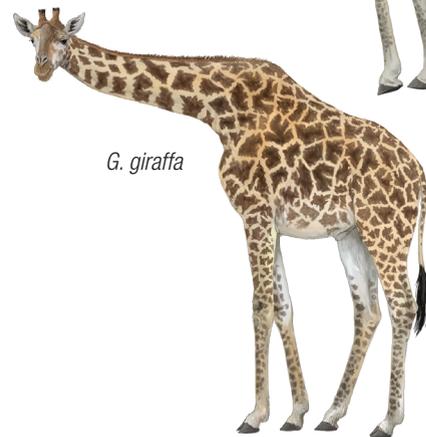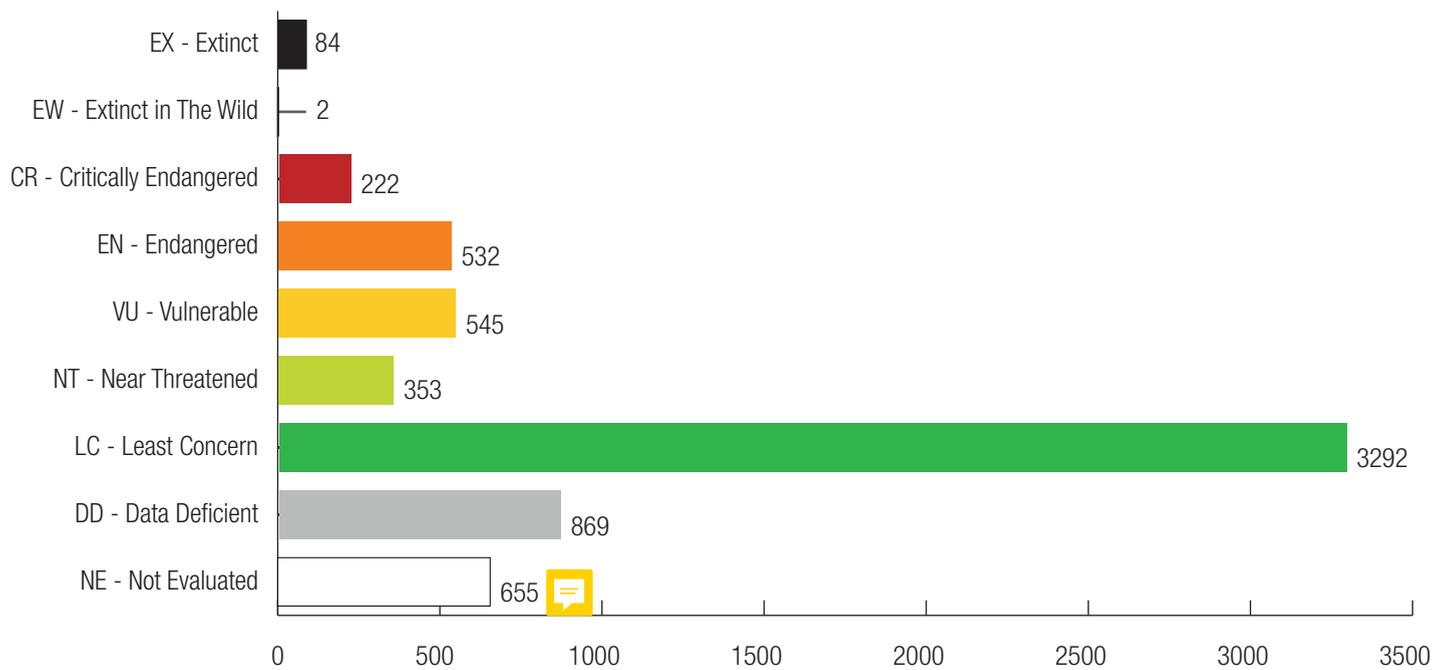
Figure 7. Distribution of IUCN conservation statuses among recognized species within the *Checklist*. As of 2020, the IUCN Red List has not assessed 655 species that are currently recognized in these volumes. This demonstrates that despite significant progress in mammalogical research, the IUCN is only able to catch up through slow updates, adding a few species yearly. Groups like Primates appear to be updated more regularly than Rodentia and Chiroptera, which is generally understandable because the conservation status of most Primates is much less secure. This delay in publication comes from the fact that there is no centralized species listing that the IUCN bases its taxonomy on and the ambiguity surrounding the taxonomic status of many of the recently recognized species (see Figure 6 for Giraffe example).

(salmon). Under each banner, text is separated into a Taxonomy section and a Distribution/Subspecies and Distribution section.

English names

Common names of mammals are widely variable and are considerably less regulated than common names of birds. With this in mind, the names presented in the *Checklist* reflect the most widely used and uncontroversial common names associated with each species. The goal is to avoid ambiguity of common names for each species. An example of this would be the use of the common name Elk, which refers to *Alces alces* in Europe but to *Cervus canadensis* in North America. To avoid ambiguity, Elk is not used for the common name of either species, and the names Moose (*Alces alces*) and Wapiti (*Cervus canadensis*) are used instead. In most cases, names within names are also avoided. This is often an issue when a species is split into multiple species, as was the Lutrine Opossum (*Lutreolina crassicaudata*). When a second species was described in the genus, *L. massoia*, the common name for that species was designated as Massoia's Lutrine Opossum, and instead of leaving *L. crassicaudata* as the Lutrine Opossum, the name was changed to the Big Lutrine Opossum to more clearly define the separation between these two species. There is also an effort made throughout the text to maintain consistent common names within genera or families (e.g. use of Deermouse for all *Peromyscus* and White-toothed Shrew for all *Crocidura*). In terms of structure, all separate words within the common name are capitalized, with the exception of the second part of hyphenated words, including directional words (e.g. White-footed Deermouse and South-western Myotis). For newly recognized species, a common name is typically sought out by investigating preexisting sources such as subspecies names in guides, but if no name is available, a new name is invented based on the species diagnostic features, distribution, or scientific name's etymology. In most cases, the species is preferably named after a defining feature or its distribution, but if no other name fits, the species might be named after the species the specific epithet was named by or after (if applicable).

IUCN Red List 2020.2 categories

There are seven categories based on the IUCN Red List of Endangered Species: Extinct = EX; Extinct in the Wild = EW; Critically Endangered = CR, also with the tags CR(PE) for Critically Endangered (Possibly Extinct); Endangered = EN; Vulnerable = VU; Near Threatened = NT; Least Concern = LC; and Data Deficient = DD. Definitions of these categories can be found in the guidelines of the IUCN Red List. Because the taxonomy presented here does not match the IUCN, species not assessed under the IUCN Red List are marked as Not Evaluated = NE (data up to 27th July 2020).

Linkage to HMW

Because the *Checklist* cannot include all information that was included in the HMW series, there certainly will be times when readers wish to compare taxonomic treatments or look up the text associated with that species. Here, the volume in which each species is treated and the page number are referenced under the conservation status for each species that was treated in the HMW series. If only the volume and page number is included, the scientific name of the species has not changed. If any part of the scientific name has been altered from the HMW series to the *Checklist*, the name that the taxon was included under is listed next to it, either as a subspecies or as the species it was considered a synonym of. If a species was described between the publication of the HMW volume it would have been included in and the *Checklist*, it will read "described too recently for inclusion" and neither a volume nor page number will be referenced.

French, German and Spanish names

For the most part, these follow those given in the HMW series, but the same sources used by HMW have been consulted for updated corrections to spellings, new group-names necessitated by new phylogenetic positions, and name changes required by the splitting or lumping of species.

Other common names

This entry is discretionary and depends on whether or not alternative names for a species exist. For the most part, alternative English common names are included with relatively loose criteria and written in the same style as the "official" common name used in the text (all words capitalized except for subsequent parts of hyphenated words). The names were sourced variously from field guides, recent journal publications, and local names for species. Major sources have been *Mammal Species of the World*, *IUCN Red List*, *Mammals of Africa*, *Mammals of South America*, *South Asian Mammals*, *Mammals of Australia*, *Bats of the World* and ASM websites. In some cases, other common names are associated with subspecies or geographical areas, in which the subspecies or region in which the name is associated is mentioned in parentheses following the name. Names that only differ slightly from each other (e.g. North-western Myotis vs. Northwestern Myotis) are not typically included.

Taxonomic notes

The first line of the taxonomic notes includes the original scientific name of the species in italics, followed by the name authority, the year the name was described, and the type locality associated with it. When more than three authors are included in the

authority of a species, the author line is abbreviated with "*et al.*" following the first author. Rather than quoting the exact type locality within the text, the type locality is paraphrased to reflect the current names of geographical localities (e.g. Burma = Myanmar) and restrictions to the original type locality. When the type locality was not given or was originally given from a drastically wrong locality, specification is added regarding the new or correct type locality. The text following the initial line includes comments regarding recent changes or developments in the taxonomy, phylogenetic relationship, biogeographic structure, or nomenclature of the species. These data were originally sourced from the HMW series, and thus much of the information has been summarized and updated from the HMW taxonomic text. References to species groups or subgenera generally start this section off when applicable, although the text is very flexibly written on a case-by-case basis. With limited space in the *Checklist*, taxonomic notes are primarily limited to recent changes in the systematics of the species, and older systematic issues have been left out unless they are still pertinent to the species current systematic situation. Any nomenclatural issues or name spelling changes are also indicated in this section. The last sentence of the taxonomic section references how many subspecies the species has, and if no subspecies are recognized, the text reads "Monotypic."

Distribution/Subspecies and Distribution

When subspecies are present, they are listed below this section in alphabetical order, except for the nominate subspecies, which is listed first. In the case of extinct subspecies, there is a cross (†) just before the trinomial name. Generic and species names are abbreviated, and only the subspecific name is given fully, followed by the authority and year the name was described. In deviation from common usage, the authorities are not included in brackets when the genus is different from the name used in the original description of the subspecies. The text outlines the distribution of each of the subspecies following a standard geographical sequence (north–south, west–east), but flexibly depending on logic and best fit, seeking a level of detail beyond simply country and cardinal points, with extensive use of provincial and regional divisions in certain countries. Cardinal directions are abbreviated as N, S, E, and W and central is abbreviated as C; mountain and mountains are abbreviated as Mt and Mts, respectively; and island and islands are abbreviated as I and Is, respectively. If the species has been introduced outside of its native distribution or if the subspecies from a specific region in which the species occurs is unknown, a separate line of text describing these cases is included under the last subspecies. For species with no subspecies, the distribution of the species is presented fully following the "Distribution" label.

Recently Extinct and Domesticated Species

Unlike in the HMW series, recently extinct and domesticated species are treated in *Checklist* in the same way that extant wild species are, including common names, *IUCN Red List* categories (except in domesticated species because they are not included on *The IUCN Red List*), taxonomic notes, and distributions. The decision to include extinct and domesticated species was based on the importance of having a complete checklist that effectively discusses the taxonomy of all currently recognized mammals, including those that have been affected by humans, either by being domesticated by people in ancient times or by going extinct as a result of human activities. Domesticated species are also all treated as distinct from their wild counterparts (see the section above on the nomenclature of domesticated species). Unlike traditional species accounts, extinct and domesticated species are not illustrated and do not have distribution maps or a number associated with their text in the HMW series. Extinct species also have a cross (†) next to the common name replacing the number. For domesticated species, a short description on the domestication process and timing is given for each species, and for extinct species, a short summary of the causes of extinction and final records is included.

Bibliographical references in the text

All cited sources of information used in *Checklist* are listed alphabetically in the bibliography at the end of the second volume. Nevertheless, not all references used in the relevant sections of the HMW have been listed here, and only the most recent studies and revisions that have led to taxonomic changes or improved current knowledge have been included in the *Checklist*.

Plates and Distribution Maps

A major deviation from other taxonomic compendia is the way in which species are organized. The ordering of all taxa within the volumes of *Checklist* is based on phylogenetic relatedness rather than the typical alphabetical style of most taxonomic compendia, ensuring that species are more easily comparable to other related species. With this in mind, the organization of the book is also limited by the size of the volumes, and some plates might split up the species in genera to ensure that the maximum number of species are included within each plate based on the size of the text that can fit on the left page or number of illustrations that can fit on the right.

Illustrations are included for every species of currently recognized living mammal species with wild representatives, illustrating at least the typical male form of the nominate subspecies when applicable and females when sexually dimorphic, phenotypic variation within the species, and distinct subspecies when included. Species are marked with the number associated with the text on the page to the left and the full specific epithet of that species. Illustrations within a plate are to scale with one another, and each plate includes a scale in inches and centimeters (cm). In some cases, species within the plate are represented at different scales, in which case they are separated by yellow lines. When multiple families are included on a plate, red lines are used to separate them. Most illustrations were originally published in the HMW series, but new illustrations have been created for 164 newly recognized taxa and another 641 for Primates.

Along with illustrations, each species includes a distribution map updated from the maps included in the HMW series, with new maps created for newly recognized species. The maps show important rivers in regions across the world rather than political boundaries, and distributions of terrestrial species are shown in green, whereas those of aquatic species are shown in blue. Arrows on the map are also included to highlight outlying records or hard to see parts of a species distribution. Unlike in the HMW series, maps are included on the plates next to the illustrations rather than within the text. To facilitate identification of which species each map belongs to, a small arrow points to the species involved. When there are multiple subspecies or variants, there might be more than one arrow pointing to the different illustrations.

Index and Bibliography

All bibliographical sources used in the *Checklist* are listed alphabetically in the bibliography at the end of the second volume. Published references are presented in the same style as in HMW. These are numbered to match the citation number given in superscripts in the main text. Names of Korean, Chinese, and Indochinese authors typically consist of the surname followed by the given name, but in some publications, these are reversed to conform with standard Western style, leading to great potential confusion. In the bibliography of *Checklist*, for clarity, the given names of such authors are retained in full, with the surname always placed first.

The index is organized to allow searches for extant and extinct taxa by scientific name of family, genus, species, and subspecies and by English name of family and species (with both parts of a compound name). All extant taxa (and also those only possibly extinct) are in black print, and all extinct and domesticated taxa are in blue.

Acknowledgements

when necessary, newly created by Gustav Peters and Rainer Hutterer (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany). The Spanish names were reviewed and new names prepared by Luis Javier Palomo from the Sociedad Española para la Conservación y el Estudio de los Mamíferos (SECEM).

A key constituency to thank here is all the authors of texts in HMW 1–9 (see pages 17–19), since a large part of this *Checklist* takes the texts of these authors as the starting point, to which changes and additions have been made as deemed appropriate. And, of course, we thank the talented artists who have brought all of these mammals to life (see pages 17–19).

We are extremely grateful to Razan Al Mubarak for writing the Foreword to this work. We also thank Jane Widness and Nathan Upham, who have greatly contributed to the writing of the Introduction with Connor Burgin.

On behalf of the individual authors and team members of the *Illustrated Checklist of the Mammals of the World*, we thank the ASM Mammal Diversity Database for its key input on taxonomic situation and we offer our sincere appreciation for his great kindness and assistance in various ways to Rudolf Haslauer.

We would like to end by expressing our gratitude to our families, friends, and colleagues for their tireless support.

References

Ambrose, L. (2003). Three acoustic forms of Allen's galagos (Primates; Galagonidae) in the Central African region. *Primates* **44**: 25–39.

Angielczyk, K.D. & Kammerer, C.F. (2018). Non-mammalian synapsids: the deep roots of the mammalian family tree. Pp. 117–198 in: Zachos, F.E. & Asher, R.J. eds. (2018). *Handbook of Zoology: Mammalia: Mammalian Evolution, Diversity and Systematics*. De Gruyter, Berlin.

Aplin, K.P. (2013). Broad-toed feathertail glider, *Acrobates frontalis*. Page 86 in: Van Dyck, S.M., Gynther, I. & Baker, A. (2013). *Field Companion to the Mammals of Australia*. New Holland Publishers, Chatswood, New South Wales.

Asher, R.J. (2018). Diversity and relationships within crown Mammalia. Pp. 301–352 in: Zachos, F.E. & Asher, R.J. eds. (2018). *Handbook of Zoology: Mammalia: Mammalian Evolution, Diversity and Systematics*. De Gruyter, Berlin.

Asher, R.J., Horovitz, I. & Sánchez-Villagra, M.R. (2004). First combined cladistic analysis of marsupial mammal interrelationships. *Mol. Phylogenet. Evol.* **33**: 240–250.

ASM (American Society of Mammalogists). (2020). *ASM Mammal Diversity Database*. URL: https://www.mammaldiversity.org/ (download 23 July 2020).

Baker, R.J. & Bradley, R.D. (2006). Speciation in mammals and the genetic species concept. *J. Mammal.* **87**: 643–662.

Baverstock, P.R., Richardson, B.J., Birrell, J. & Krieg, M. (1989). Albumin immunologic relationships of the Macropodidae (Marsupialia). *Syst. Zool.* **38**: 38–50.

Beach, J., Blum, S., Donoghue, M., Ford, L., Guralnick, R., Mares, M., Thiers, B., Westneat, M., Wheeler, Q., Wiegmann, B. & the Network Integrated Biocollection Alliance. (2010) *A Strategic Plan for Establishing a Network Integrated Biocollections Alliance*. URL: http://digbiocol.wordpress.com/brochure (download 23 July 2020).

Beard, C. (2002). East of Eden at the Paleocene/Eocene boundary. *Science* **295**: 2028–2029.

Beck, J., Böller, M., Erhardt, A. & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecol. Informatics* **19**: 10–15.

Beck, R.M.D., Travouillon, K.J., Aplin, K.P., Godthelp, H. & Archer, M. (2014). The osteology and systematics of the enigmatic Australian oligo-Miocene metatherian *Yalkaparidon* (Yalkaparidontidae; Yalkaparidontia; ?Australidelphia; Marsupialia). *J. Mammal. Evol.* **21**: 127–172.

Blumenbach, J.F. (1800). Sur un nouveau genre de quadrupède edénté, nommé *Ornithorhynchus paradoxus. Bull. Sci., Soc. Philom. Paris* **2(39)**: 113.

Braune, P., Schmidt, S. & Zimmermann, E. (2008). Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* ssp.). *BMC Biol.* **6**: 19. 10 pp.

Bruyndonckx, N., Dubey, S., Ruedi, M. & Christe, P. (2009). Molecular cophylogenetic relationships between European bats and their ectoparasitic mites (Acari, Spinturnicidae). *Mol. Phylogenet. Evol.* **51**: 227–237.

Burgin, C.J., Colella, J.P., Kahn, P.L. & Upham, N.S. (2018). How many species of mammals are there? *J. Mammal.* **99**: 1–14.

Cardini, A. & Elton, S. (2011). GeMBiD, a geometric morphometric approach to the study of biological diversity: an example study of the red colobus (*Procolobus* [*Piliocolobus*]) species complex. *Int. J. Primatol.* **32**: 377–389.

Clare, E.L., Adams, A.M., Maya-Simões, A.Z., Eger, J.L., Hebert, P.D.N. & Fenton, M.B. (2013). Diversification and reproductive isolation: cryptic species in the only New World high-duty cycle bat, *Pteronotus parnellii. BMC Evol. Biol.* **13**: 26. 18 pp.

Corbet, G.B. & Hill, J.E. (1980). *A World List of Mammalian Species.* British Museum (Natural History), London.

Corbet, G.B. & Hill, J.E. (1986). *A World List of Mammalian Species.* 2nd edition. British Museum (Natural History), London.

Corbet, G.B. & Hill, J.E. (1991). *A World List of Mammalian Species.* 3rd edition. Oxford University Press, Oxford.

Coues, E. (1884). *Thomasomys*, a new subgeneric type of *Hesperomys. Am. Nat.* **18**: 1275.

Courcelle, M., Tilak, M.K., Leite, Y.L.R., Douzery, E.J.P. & Fabre, P.H. (2019). Digging for the spiny rat and hutia phylogeny using a gene capture approach, with the description of a new mammal subfamily. *Mol. Phylogenet. Evol.* **136**: 241–253.

Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinauer, Sunderland, Massachusetts.

Dávalos, L.M. & Russell, A.L. (2014). Sex-biased dispersal produces high error rates in mitochondrial distance-based and tree-based species delimitation. *J. Mammal.* **95**: 781–791.

Dawson, N.G., Colella, J.P., Small, M.P., Stone, K.D., Talbot, S.L. & Cook, J.A. (2017). Historical biogeography sets the foundation for contemporary conservation of martens (genus *Martes*) in northwestern North America. *J. Mammal.* **98**: 715–730.

Defler, T.R. & Bueno, M.L. (2007). *Aotus* diversity and the species problem. *Primate Conserv.* **22**: 55–70.

Demboski, J.R. & Cook, J.A. (2001). Phylogeography of the dusky shrew, *Sorex monticolus* (Insectivora, Soricidae): insight into deep and shallow history in northwestern North America. *Mol. Ecol.* **10**: 1227–1240.

Denys, C., Callou, C. & Mellier, B. (2012). The contribution of Edouard-Louis Trouessart to mammalogy. *Mammalia* **76**: 355–364.

Duchêne, D.A., Bragg, J.G., Duchêne, S., Neaves, L.E., Potter, S., Moritz, C., Johnson, R.N., Ho, S.Y.W. & Eldridge, M.D.B. (2018). Analysis of phylogenomic tree space resolves relationships among marsupial families. *Syst. Biol.* **67**: 400–412.

Edwards, J.L. (2004). Research and societal benefits of the Global Biodiversity Information Facility. *BioScience* **54**: 485–486.

Eldridge, M.D.B., Beck, R.M.D., Croft, D.A., Travouillon, K.J. & Fox, B.J. (2019). An emerging consensus in the evolution, phylogeny, and systematics of marsupials and their fossil relatives (Metatheria). *J. Mammal.* **100**: 802–837.

Escalante, T., Morrone, J.J. & Rodríguez-Tapia, G. (2013). Biogeographic regions of North American mammals based on endemism. *Biol. J. Linn. Soc.* **110**: 485–499.

Esselstyn, J.A., Oliveros, C.H., Swanson, M.T. & Faircloth, B.C. (2017). Investigating difficult nodes in the placental mammal tree with expanded taxon sampling and thousands of ultraconserved elements. *Genome Biol. Evol.* **9**: 2308–2321.

Fabre, P.H., Upham, N.S., Emmons, L.H., Justy, F., Leite, Y.L.R., Loss, A.C., Orlando, L., Tilak, M.K., Patterson, B.D. & Douzery, E.J.P. (2017). Mitogenomic phylogeny, diversification, and biogeography of South American spiny rats. *Mol. Biol. Evol.* **34**: 613–633.

Fabre, P.H., Vilstrup, J.T., Raghavan, M., Sarkissian, C.D., Willerslev, E., Douzery, E.J.P. & Orlando, L. (2014). Rodents of the Caribbean: origin and diversification of hutias unravelled by next generation museomics. *Biol. Lett.* **10**: 20140266. 5 pp.

Faith, D.P. (1985). A model of immunological distances in systematics. *J. Theor. Biol.* **114**: 511–526.

Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M.A., Vamberger, M., Fritz, U. & Janke, A. (2016). Multi-locus analyses reveal four giraffe species instead of one. *Curr. Biol.* **26**: 2543–2549.

Foley, N.M., Springer, M.S. & Teeling, E.C. (2016). Mammal madness: is the mammal tree of life not yet resolved? *Philos. Trans. Roy. Soc. London B, Biol. Sci.* **371**: 20150140. 11 pp.

Gardner, A.L. ed. (2008). *Mammals of South America*. Vol. 1. Marsupials, Xenarthrans, Shrews, and Bats. The University of Chicago Press, Chicago, Illinois.

Garnett, S.T. & Christidis, L. (2017). Taxonomy anarchy hampers conservation. *Nature* **546**: 25–27.

Garnett, S.T., Christidis, L., Conix, S., Costello, M.J., Zachos, F.E., Bánki, O.S., Bao Yiming, Barik, S.K., Buckeridge, J.S., Hobern, D., Lien, A., Montgomery, N., Nikolaeva, S. Pyle, R.L., Thomson, S.A., van Dijk, P.P., Whalen, A., Zhang Zhiqiang & Thiele, K.R. (2020). Principles for creating a single authoritative list of the world's species. *PLoS Biol.* **18**: e3000736. 10 pp.

GBIF (Global Biodiversity Information Facility). (2020a). Occurrence Search. URL: https://www.gbif.org/occurrence/search?taxon_key=359 (download 21 July 2020).

GBIF (Global Biodiversity Information Facility). (2020b). GBIF Occurrence Download. URL: https://doi.org/10.15468/dl.drqfpu (23 July 2020).

GBIF (Global Biodiversity Information Facility). (2020c). GBIF Occurrence Download. URL: https://doi.org/10.15468/dl.zxuyn7 (23 July 2020).

Gentry, A., Clutton-Brock, J. & Groves, C.P. (2004). The naming of wild animal species and their domestic derivatives. *J. Archaeol. Sci.* **31**: 645–651.

Gippoliti, S. (2019). Species delimitation in mammals: A comment on Zachos (2018). *Mammal. Biol.* **94**: 127–131.

Gippoliti, S., Cotterill, F.P.D. & Groves, C.P. (2013). Mammal taxonomy without taxonomists: a reply to Zachos and Lovari. *Hystrix* **24**: 145–147.

Gippoliti, S., Cotterill, F.P.D., Zinner, D. & Groves, C.P. (2018). Impacts of taxonomic inertia for the conservation of African ungulate diversity: an overview. *Biol. Rev.* **93**: 115–130.

Goodman, M. (1989). Evolution of the immunologic species specificity of human serum proteins. *Hum. Biol.* **61**: 879–924.

Gopalakrishnan, S., Sinding, M.H.S., Ramos-Madrigal, J., Niemann, J., Samaniego, J.A., Vieira, F.G., Carøe, C., Montero, M.M., Kuderna, L., Serres, A., González-Basallote, V.M., Liu Yanhu, Wang Guodong, Marques-Bonet, T., Mirarab, S., Fernandes, C., Gaubert, P., Koepfli, K.P., Budd, J., Rueness, E.K., Sillero, C., Heide-Jørgensen, M.P., Petersen, B., Sicheritz-Ponten, T., Bachmann, L., Wiig, Ø., Hansen, A.J. & Gilbert, M.T. (2018). Interspecific gene flow shaped the evolution of the genus *Canis. Curr. Biol.* **28**: 3441–3449.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (2012). *The Geologic Time Scale 2012*. Elsevier, Amsterdam, The Netherlands.

Gregory, W.K. (1910). The orders of mammals. *Bull. Am. Mus. Nat. Hist.* **27**: 1–524.

Groves, C.P. (2001). *Primate Taxonomy*. Smithsonian Institution Press, Washington, D.C.

Groves, C.P. (2013). The nature of species: A rejoinder to Zachos *et al. Mammal. Biol.* **78**: 7–9.

Groves, C.P. (2014). Primate taxonomy: inflation or real? *Ann. Rev. Anthropol.* **43**: 27–36.

Groves, C.P. & Grubb, P. (2011). *Ungulate Taxonomy*. The Johns Hopkins University Press, Baltimore, Maryland.

Groves, C.P., Cotterill, F.P.D., Gippoliti, S., Robovský, J., Roos, C., Taylor, P.J. & Zinner, D. (2017). Species definitions and conservation: a review and case studies from African mammals. *Conserv. Genet.* **18**: 1247–1256.

Guralnick, R. (2007). Differential effects of past climate warming on mountain and flatland species distributions: a multispecies North American mammal assessment. *Global Ecol. Biogeogr.* **16**: 14–23.

Guralnick, R. & Constable, H. (2010). VertNet: Creating a data-sharing community. *BioScience* **60**: 258–259.

Guschanski, K., Krause, J., Sawyer, S., Valente, L.M., Bailey, S., Finstermeier, K., Sabin, R., Gilissen, E., Sonet, G., Nagy, Z.T., Lenglet, G., Mayer, F. & Savolainen, V. (2013). Next-generation museomics disentangles one of the largest primate radiations. *Syst. Biol.* **62**: 539–554.

Gutiérrez, E.E. & Garbino, G.S.T. (2018). Species delimitation based on diagnosis and monophyly, and its importance for advancing mammalian taxonomy. *Zool. Res.* **39**: 301–308.

Gutiérrez, E.E., Jansa, S.A. & Voss, R.S. (2010). Molecular systematics of mouse opossums (Didelphidae: *Marmosa*): Assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography. *Am. Mus. Novit.* **3692**: 1–22.

Gyllensten, U., Wharton, D., Josefsson, A. & Wilson, A.C. (1991). Paternal inheritance of mitochondrial DNA in mice. *Nature* **352**: 255–257.

Hafner, M.S., Sudman, P.D., Villablanca, F.X., Spradling, T.A., Demastes, J.W. & Nadler, S.A. (1994). Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* **265**: 1087–1090.

Halliday, T.J.D., Upchurch, P. & Goswami, A. (2017). Resolving the relationships of Paleocene placental mammals. *Biol. Rev.* **92**: 521–550.

Harmon, L.J. (2017). Evolution: Contingent predictability in mammalian evolution. *Curr. Biol.* **27**: R425–R428.

Hawkins, M.T.R., Helgen, K.M., Maldonado, J.E., Rockwood, L.L., Tsuchiya, M.T. & Leonard, J.A. (2016). Phylogeny, biogeography and systematic revision of plain long-nosed squirrels (genus *Dremomys*, Nannosciurinae). *Mol. Phylogenet. Evol.* **94B**: 752–764.

Helgen, K.M., Cole, F.R., Helgen, L.E. & Wilson, D.E. (2009). Generic revision in the Holarctic ground squirrel genus *Spermophilus. J. Mammal.* **90**: 270–305.

Herbst, J.F.W. (1793). *Natursystem aller bekannten in- und ausländischen Insekten, als eine Fortsetzung der von Büffonschen Naturgeschichte*. Der Käfer. Vol. 5. J. Pauli, Berlin.

Herron, M.D., Castoe, T.A. & Parkinson, C.L. (2004). Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (*Spermophilus*). *Mol. Phylogenet. Evol.* **31**: 1015–1030.

Hill, J.E. (1990). A memoir and bibliography of Michael Rogers Oldfield Thomas, F.R.S. *Bull. Brit. Mus. (Nat. Hist.), Hist. Ser.* **18**: 25–113.

Hinton, M.A.C. (1929). Mr. M. R. Oldfield Thomas, F.R.S. *Nature* **124**: 101–102.

Honacki, J.H., Kinman, K.E. & Koeppl, J.W. (1982). *Mammal Species of the World: A Taxonomic and Geographic Reference*. Allen Press, Lawrence, Kansas.

Hutterer, R., Decher, J., Monadjem, A. & Astrin, J. (2019). A new genus and species of vesper bat from West Africa, with notes on *Hypsugo*, *Neoromicia*, and *Pipistrellus* (Chiroptera: Vespertilionidae). *Acta Chiropterol.* **21**: 1–22.

ICZN (International Commission on Zoological Nomenclature). (2003). Opinion 2027 (Case 3010). Usage of 17 specific names based on wild species which are pre-dated by or contemporary with those based on domestic animals (Lepidoptera, Osteichthyes, Mammalia): conserved. *Bull. Zool. Nomencl.* **60**: 81–84.

IUCN (International Union for Conservation of Nature). (2020). *The IUCN Red List of Threatened Species*. Version 2020.2. URL: http://www.iucnredlist.org (download 23 July 2020).

Jackson, S.M. & Groves, C.P. (2015). *Taxonomy of Australian Mammals*. CSIRO Publishing, Clayton South, Victoria.

Jackson, S.M., Fleming, P.J.S., Eldridge, M.D.B., Ingleby, S., Flannery, T.F., Johnson, R.N., Cooper, S.J.B., Mitchell, K.J., Souilmi, Y., Cooper, A., Wilson, D.E. & Helgen, K.M. (2019). The Dogma of Dingoes—Taxonomic status of the dingo: A reply to Smith *et al. Zootaxa* **4564**: 198–212.

Jarrín-Valladares, P. & Kunz, T.H. (2008). Taxonomic history of the genus *Anoura* (Chiroptera: Phyllostomidae) with insights into the challenges of morphological species delimitation. *Acta Chiropterol.* **10**: 257–269.

Jebb, D., Huang Zixia, Pippel, M., Hughes, G.M., Lavrichenko, K., Devanna, P., Winkler, S., Jermiin, L.S., Skirmuntt, E.C., Katzourakis, A., Burkitt-Gray, L., Ray, D.A., Sullivan, K.A.M., Roscito, J.G., Kirilenko, B.M., Dávalos, L.M., Corthals, A.P., Power, M.L., Jones, G., Ransome, R.D., Dechmann, D.K.N., Locatelli, A.G., Puechmaille, S.J., Fedrigo, O., Jarvis, E.D., Hiller, M., Vernes, S.C., Myers, E.W. & Teeling, E.C. (2020). Six reference-quality genomes reveal evolution of bat adaptations. *Nature* **583**: 578–584.

Johnson, M.L. (1968). Application of blood protein electrophoretic studies to problems in mammalian taxonomy. *Syst. Biol.* **17**: 23–30.

Johnson, M.L. & Wicks, M.J. (1959). Serum protein electrophoresis in mammals—Taxonomic implications. *Syst. Zool.* **8**: 88–95.

Kalkvik, H.M., Stout, I.J., Doonan, T.J. & Parkinson, C.L. (2012). Investigating niche and lineage diversification in widely distributed taxa: phylogeography and ecological niche modeling of the *Peromyscus maniculatus* species group. *Ecography* **35**: 54–64.

Kingdon, J., Happold, D.C.D., Butynski, T.M., Hoffmann, M., Happold, M. & Kalina, J. eds. (2013). *Mammals of Africa*. Vols. 1–6. Bloomsbury Publishing, London.

Kingswood, S.C., Kumamoto, A.T., Sudman, P.D., Fletcher, K.C. & Greenbaum, I.F. (1994). Meiosis in chromosomally heteromorphic goitered gazelle, *Gazella subgutturosa* (Artiodactyla, Bovidae). *Chrom. Res.* **2**: 37–46.

Kitchener, A.C., Breitenmoser-Würsten, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A., Yamaguchi, N., Abramov, A.V., Christiansen, P., Driscoll, C., Duckworth, J.W., Johnson, W., Luo Shujin, Meijaard, E., O'Donoghue, P., Sanderson, J., Seymour, K., Bruford, M., Groves, C.P., Hoffmann, M., Nowell, K., Timmons, Z. & Tobe, S. (2017). A revised taxonomy of the Felidae: The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. *Cat News* **80** (Special Issue): 1–79.

Klingel, H. (1975). Social organization and reproduction in equids. *J. Reprod. Fertil.* **23** (Suppl.): 7–11.

Light, J.E., Smith, V.S., Allen, J.M., Durden, L.A. & Reed, D.L. (2010). Evolutionary history of mammalian sucking lice (Phthiraptera: Anoplura). *BMC Evol. Biol.* **10**: 292. 15 pp.

Linnaeus, C. (1758). *Systema Naturæ per Regna Tria Naturæ, secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis*. Vol. 1. 10th edition. Laurentius Salvius, Holmia [Stockholm].

Madsen, O., Scally, M., Douady, C.J., Kao, D.J., DeBry, R.W., Adkins, R., Amrine, H.M., Stanhope, M.J., de Jong, W.W. & Springer, M.S. (2001). Parallel adaptive radiations in two major clades of placental mammals. *Nature* **409**: 610–614.

Martin, T. (2018). Mesozoic mammals. Pp. 199–299 in: Zachos, F.E. & Asher, R.J. eds. (2018). *Handbook of Zoology: Mammalia: Mammalian Evolution, Diversity and Systematics*. De Gruyter, Berlin.

May-Collado, L.J., Kilpatrick, C.W. & Agnarsson, I. (2015). Mammals from 'down under': a multi-gene species-level phylogeny of marsupial mammals (Mammalia, Metatheria). *PeerJ* **3**: e805. 27 pp.

Mead, R.A. (1968). Reproduction in western forms of the spotted skunk (genus *Spilogale*). *J. Mammal.* **49**: 373–389.

Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., Goodbla, A., Eizirik, E., Simão, T.L.L., Stadler, T., Rabosky, D.L., Honeycutt, R.L., Flynn,

J.J., Ingram, C.M., Steiner, C., Williams, T.L., Robinson, T.J., Burk-Herrick, A., Westerman, M., Ayoub, N.A., Springer, M.S. & Murphy, W.J. (2011). Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* **334**: 521–524.

Meredith, R.W., Westerman, M., Case, J.A. & Springer, M.S. (2008). A phylogeny and timescale for marsupial evolution based on sequences for five nuclear genes. *J. Mammal. Evol.* **15**: 1–36.

Merker, S., Driller, C., Dahruddin, H., Wirdateti, Sinaga, W., Perwitasari-Farajallah, D. & Shekelle, M. (2010). *Tarsius wallacei*: a new tarsier species from Central Sulawesi occupies a discontinuous range. *Int. J. Primatol.* **31**: 1107–1122.

Micales, J.A. & Bonde, M.R. (1995). Isozymes: methods and applications. Pp. 115–130 in: Singh, R.P. & Singh, U.S. eds. (1995). *Molecular Methods in Plant Pathology.* CRC Press, Boca Raton, Florida.

Miranda, F.R., Casali, D.M., Perini, F.A., Machado, F.A. & Santos, F.R. (2018). Taxonomic review of the genus *Cyclopes* Gray, 1821 (Xenarthra: Pilosa), with the revalidation and description of new species. *Zool. J. Linn. Soc.* **183**: 687–721.

Mitchell, K.J., Pratt, R.C., Watson, L.N., Gibb, G.C., Llamas, B., Kasper, M., Edson, J., Hopwood, B., Male, D., Armstrong, K., Meyer, M., Hofreiter, M., Austin, J., Donnellan, S.C., Lee, M.S.Y., Phillips, M.J. & Cooper, A. (2014). Molecular phylogeny, biogeography, and habitat preference evolution of marsupials. *Mol. Biol. Evol.* **31**: 2322–2330.

Mittermeier, R.A. Rylands, A.B. & Wilson, D.E. eds. (2013). *Handbook of the Mammals of the World.* Vol. 3. Primates. Lynx Edicions, Barcelona.

Morgan, C.C., Foster, P.G., Webb, A.E., Pisani, D., McInerney, J.O. & O'Connell, M.J. (2013). Heterogeneous models place the root of the placental mammal phylogeny. *Mol. Biol. Evol.* **30**: 2145–2156.

Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang Yaping, Ryder, O.A. & O'Brien, S.J. (2001a). Molecular phylogenetics and the origins of placental mammals. *Nature* **409**: 614–618.

Murphy, W.J., Eizirik, E., O'Brien, S.J., Madsen, O., Scally, M., Douady, C.J., Teeling, E.C., Ryder, O.A., Stanhope, M.J., de Jong, W.W. & Springer, M.S. (2001b). Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* **294**: 2348–2351.

Murphy, W.J., Pringle, T.H., Crider, T.A., Springer, M.S. & Miller, W. (2007). Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Res.* **17**: 413–421.

Musser, G.G. (1968). *A Systematic Study of the Mexican and Guatemalan Gray Squirrel,* Sciurus aureogaster *F. Cuvier (Rodentia: Sciuridae).* Miscellaneous Publications **137**. Museum of Zoology, University of Michigan, Ann Arbor, Michigan. 112 pp.

Musser, G.G., Durden, L.A., Holden, M.E. & Light, J.E. (2010). Systematic review of endemic Sulawesi squirrels (Rodentia, Sciuridae), with descriptions of new species of associated sucking lice (Insecta, Anoplura), and phylogenetic and zoogeographic assessments of sciurid lice. *Bull. Am. Mus. Nat. Hist.* **339**: 1–260.

Nilsson, M.A., Arnason, U., Spencer, P.B.S. & Janke, A. (2004). Marsupial relationships and a timeline for marsupial radiation in South Gondwana. *Gene* **340**: 189–196.

Nishihara, H., Hasegawa, M. & Okada, N. (2006). Pegasoferae, an unexpected mammalian clade revealed by tracking ancient retroposon insertions. *Proc. Natl. Acad. Sci. USA* **103**: 9929–9934.

Nowak, R.M. (1999). *Walker's Mammals of the World*. Vols. 1 & 2. 6th edition. The Johns Hopkins University Press, Baltimore, Maryland.

Ntie, S., Davis, A.R., Hils, K., Mickala, P., Thomassen, H.A., Morgan, K., Vanthomme, H., Gonder, M.K. & Anthony, N.M. (2017). Evaluating the role of Pleistocene refugia, rivers and environmental variation in the diversification of central African duikers (genera *Cephalophus* and *Philantomba*). *BMC Evol. Biol.* **17**: 212. 17 pp.

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo Zhexi, Meng Jin, Ni Xijun, Novacek, M.J., Perini, F.A., Randall, Z.S., Rougier, G.W., Sargis, E.J., Silcox, M.T., Simmons, N.B., Spaulding, M., Velazco, P.M., Weksler, M., Wible, J.R. & Cirranello, A.L. (2013). The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science* **339**: 662–667.

Padayachee, A.L., Irlich, U.M., Faulkner, K.T., Gaertner, M., Procheş, Ş., Wilson, J.R.U. & Rouget, M. (2017). How do invasive species travel to and through urban environments? *Biol. Invasions* **19**: 3557–3570.

Patton, J.L., Pardiñas, U.F.J. & D'Elía, G. eds. (2015). *Mammals of South America.* Vol. 2. Rodents. The University of Chicago Press, Chicago, Illinois.

Petzold, A. & Hassanin, A. (2020). A comparative approach for species delimitation based on multiple methods of multi-locus DNA sequence analysis: A case study of the genus *Giraffa* (Mammalia, Cetartiodactyla). *PLoS ONE* **15**: e0217956. 28 pp.

Pilot, M., Dahlheim, M.E. & Hoelzel, A.R. (2010). Social cohesion among kin, gene flow without dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*). *J. Evol. Biol.* **23**: 20–31.

Pine, R.H. & Gutiérrez, E.E. (2018). What is an 'extant' type specimen? Problems arising from naming mammalian species-group taxa without preserved types. *Mammal Rev.* **48**: 12–23.

Potter, S., Bragg, J.G., Blom, M.P.K., Deakin, J.E., Kirkpatrick, M., Eldridge, M.D.B. & Moritz, C. (2017). Chromosomal speciation in the genomics era: Disentangling phylogenetic evolution of rock-wallabies. *Front. Genet.* **8**: 10. 18 pp.

Raposo, M.A., Stopiglia, R., Brito, G.R.R., Bockmann, F.A., Kirwan, G.M., Gayon, J. & Dubois, A. (2017). What really hampers taxonomy and conservation? A riposte to Garnett and Christidis (2017). *Zootaxa* **4317**: 179–184.

Reis, M., Inoue, J., Hasegawa, M., Asher, R.J., Donoghue, P.C. & Yang Ziheng. (2012). Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proc. Roy. Soc. London B, Biol. Sci.* **279**: 3491–3500.

Richardson, B.J., Johnston, P.G., Clark, P. & Sharman, G.B. (1973). An evaluation of electrophoresis as a taxonomic method using comparative data from the Macropodidae (Marsupialia). *Biochem. Syst. Ecol.* **1**: 203–209.

Romiguier, J., Ranwez, V., Delsuc, F., Galtier, N. & Douzery, E.J.P. (2013). Less is more in mammalian phylogenomics: AT-rich genes minimize tree conflicts and unravel the root of placental mammals. *Mol. Biol. Evol.* **30**: 2134–2144.

Sánchez-Villagra, M.R. (2013). Why are there fewer marsupials than placentals? On the relevance of geography and physiology to evolutionary patterns of mammalian diversity and disparity. *J. Mammal. Evol.* **20**: 279–290.

Sanmartín, I. (2012). Historical biogeography: Evolution in time and space. *Evol. Educ. Outreach* **5**: 555–568.

Sarich, V.M. & Wilson, A.C. (1966). Quantitative immunochemistry and the evolution of primate albumins: micro-complement fixation. *Science* **154**: 1563–1566.

Scally, M., Madsen, O., Douady, C.J., de Jong, W.W., Stanhope, M.J. & Springer, M.S. (2001). Molecular evidence for the major clades of placental mammals. *J. Mammal. Evol.* **8**: 239–277.

Schiaffini, M.I., Gabrielli, M., Prevosti, F.J., Cardoso, Y.P., Castillo, D., Bo, R., Casanave, E. & Lizarralde, M. (2013). Taxonomic status of southern South American *Conepatus* (Carnivora: Mephitidae). *Zool. J. Linn. Soc.* **167**: 327–344.

Seal, U.S., Makey, D.G. & International Species Inventory System. (1974). *Mammalian Taxonomic Directory*. Minnesota Zoological Garden, Saint Paul, Minnesota.

Searle, J.B. (1986). Factors responsible for a karyotypic polymorphism in the common shrew, *Sorex araneus. Proc. Roy. Soc. London B, Biol. Sci.* **229**: 277–298.

Shaw, G. (1799). The duck-billed platypus. *Nat. Misc.* **10**: unnumbr. pp., ppl. 385–386.

Simmons, N.B. & Cirranello, A.L. (2020). *Bats of the World: A Taxonomic and Geographic Database.* URL: http://batnames.org/ (download 23 July 2020).

Simpson, G.G. (1945). The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**: 1–350.

Solari, S. & Baker, R.J. (2007). *Mammal Species of the World: A Taxonomic and Geographic Reference* by D. E. Wilson; D. M. Reeder. *J. Mammal.* **88**: 824–830.

Sorenson, M.D., Ast, J.C., Dimcheff, D.E., Yuri, T. & Mindell, D.P. (1999). Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Mol. Phylogenet. Evol.* **12**: 105–114.

Springer, M.S., Cleven, G.C., Madsen, O., de Jong, W.W., Waddell, V.G., Amrine, H.M. & Stanhope, M.J. (1997). Endemic African mammals shake the phylogenetic tree. *Nature* **388**: 61–64.

Springer, M.S., Stanhope, M.J., Madsen, O. & de Jong, W.W. (2004). Molecules consolidate the placental mammal tree. *Trends Ecol. Evol.* **19**: 430–438.

Stanhope, M.J., Waddell, V.G., Madsen, O., de Jong, W.W., Hedges, S.B., Cleven, G.C., Kao, D. & Springer, M.S. (1998). Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *Proc. Natl. Acad. Sci. USA* **95**: 9967–9972.

Sterner, B., Witteveen, J. & Franz, N. (2020). Coordinating dissent as an alternative to consensus classification: insights from systematics for bio-ontologies. *Hist. Philos. Life Sci.* **42**: 8. 25 pp.

Svensson, M.S., Bersacola, E., Mills, M.S.L., Munds, R.A., Nijman, V., Perkin, A., Masters, J.C., Couette, S., Nekaris, K.A.I. & Bearder, S.K. (2017). A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola. *Am. J. Phys. Anthropol.* **163**: 30–43.

Switonski, M., Rogalska-Niznik, N., Szczerbal, I. & Baer, M. (2003). Chromosome polymorphism and karyotype evolution of four canids: the dog, red fox, arctic fox and raccoon dog. *Caryologia* **56**: 375–385.

Switzer, W.M., Salemi, M., Shanmugam, V., Gao Feng, Cong, M.E., Kuiken, C., Bhullar, V., Beer, B.E., Vallet, D., Gautier-Hion, A., Tooze, Z., Villinger, F., Holmes, E.C. & Heneine, W. (2005). Ancient co-speciation of simian foamy viruses and primates. *Nature* **434**: 376–380.

Takemoto, H., Kawamoto, Y. & Furuichi, T. (2015). How did bonobos come to range south of the Congo River? Reconsideration of the divergence of *Pan paniscus* from other *Pan* populations. *Evol. Anthropol.* **24**: 170–184.

Tarver, J.E., Reis, M., Mirarab, S., Moran, R.J., Parker, S., O'Reilly, J.E., King, B.L., O'Connell, M.J., Asher, R.J., Warnow, T., Peterson, K.J., Donoghue, P.C.J. & Pisani, D. (2016). The interrelationships of placental mammals and the limits of phylogenetic inference. *Genome Biol. Evol.* **8**: 330–344.

Thomas, O. (1905). Suggestions for the nomenclature of the cranial length measurements and of the cheek-teeth of mammals. *Proc. Biol. Soc. Washington* **18**: 191–196.

Thomas, O. (1919). The method of taking the incisive index in rodents. *Ann. Mag. Nat. Hist., 9th Ser.* **4**: 289–290.

Ting, N., Tosi, A.J., Li Ying, Zhang Yaping & Disotell, T.R. (2008). Phylogenetic incongruence between nuclear and mitochondrial markers in the Asian colobines and the evolution of the langurs and leaf monkeys. *Mol. Phylogenet. Evol.* **46**: 466–474.

Toews, D.P.L. & Brelsford, A. (2012). The biogeography of mitochondrial and nuclear discordance in animals. *Mol. Ecol.* **21**: 3907–3930.

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R. & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Sci. Rep.* **7**: 9132. 14 pp.

Trouessart, E.L. (1897–1905). *Catalogus Mammalium tam Viventium quam Fossilium*. R. Friedländer & Sohn, Berolini [Berlin].

Upham, N.S. & Patterson, B.D. (2015). Evolution of caviomorph rodents: A complete phylogeny and timetree for living genera. Pp. 63–120 in: Vassallo, A.I. & Antenucci, D. eds. (2015). *Biology of Caviomorph Rodents: Diversity and Evolution*. Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Buenos Aires.

Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**: e3000494. 44 pp.

Upham, N.S., Esselstyn, J.A. & Jetz, W. (2020). Ecological causes of uneven speciation and species richness in mammals. *BioRxiv*: 504803. 37 pp.

Van Dyck, S.M. & Strahan, R. eds. (2008). *The Mammals of Australia*. 3rd edition. Reed New Holland, Sydney, New South Wales.

Walker, E.P. (1964). *Mammals of the World*. The Johns Hopkins University Press, Baltimore, Maryland.

Wang Kun, Lenstra, J.A., Liu Liang, Hu Quanjun, Ma Tao, Qiu Qiang & Liu Jianquan. (2018). Incomplete lineage sorting rather than hybridization explains the inconsistent phylogeny of the wisent. *Commun. Biol.* **1**: 169. 9 pp.

Wayne, R.K., Van Valkenburgh, B. & O'Brien, S.J. (1991). Molecular distance and divergence time in carnivores and primates. *Mol. Biol. Evol.* **8**: 297–319.

Wildman, D.E., Uddin, M., Opazo, J.C., Liu Guozhen, Lefort, V., Guindon, S., Gascuel, O., Grossman, L.I., Romero, R. & Goodman, M. (2007). Genomics, biogeography, and the diversification of placental mammals. *Proc. Natl. Acad. Sci. USA* **104**: 14395–14400.

Wilson, A.C., Maxson, L.R. & Sarich, V.M. (1974). Two types of molecular evolution. Evidence from studies of interspecific hybridization. *Proc. Natl. Acad. Sci. USA* **71**: 2843–2847.

Wilson, D.E. & Mittermeier, R.A. eds. (2009). *Handbook of the Mammals of the World*. Vol. 1. Carnivores. Lynx Edicions, Barcelona.

Wilson, D.E. & Mittermeier, R.A. eds. (2011). *Handbook of the Mammals of the World*. Vol. 2. Hoofed Mammals. Lynx Edicions, Barcelona.

Wilson, D.E. & Mittermeier, R.A. eds. (2014). *Handbook of the Mammals of the World*. Vol. 4. Sea Mammals. Lynx Edicions, Barcelona.

Wilson, D.E. & Mittermeier, R.A. eds. (2015). *Handbook of the Mammals of the World*. Vol. 5. Monotremes and Marsupials. Lynx Edicions, Barcelona.

Wilson, D.E. & Mittermeier, R.A. eds. (2018). *Handbook of the Mammals of the World*. Vol. 8. Insectivores, Sloths, and Colugos. Lynx Edicions, Barcelona.

Wilson, D.E. & Mittermeier, R.A. eds. (2019). *Handbook of the Mammals of the World*. Vol. 9. Bats. Lynx Edicions, Barcelona.

Wilson, D.E. & Reeder, D.M. eds. (1993). *Mammal Species of the World: A Taxonomic and Geographic Reference*. 2nd edition. Smithsonian Institution Press, Washington, D.C.

Wilson, D.E. & Reeder, D.M. eds. (2005). *Mammal Species of the World: A Taxonomic and Geographic Reference*. 3rd edition. The Johns Hopkins University Press, Baltimore, Maryland.

Wilson, D.E., Lacher, T.E. & Mittermeier, R.A. eds. (2016). *Handbook of the Mammals of the World*. Vol. 6. Lagomorphs and Rodents I. Lynx Edicions, Barcelona.

Wilson, D.E., Lacher, T.E. & Mittermeier, R.A. eds. (2017). *Handbook of the Mammals of the World*. Vol. 7. Rodents II. Lynx Edicions, Barcelona.

Wu Jiaqi, Yonezawa, T. & Kishino, H. (2017). Rates of molecular evolution suggest natural history of life history traits and a post-K-Pg nocturnal bottleneck of placentals. *Curr. Biol.* **27**: 3025–3033.

Zachos, F.E. (2015). Taxonomic inflation, the Phylogenetic Species Concept and lineages in the tree of life – a cautionary comment on species splitting. *J. Zool. Syst. Evol. Res.* **53**: 180–184.

Zachos, F.E. (2016). *Species Concepts in Biology: Historical Development, Theoretical Foundations and Practical Relevance*. Springer International Publishing, Cham, Switzerland.

Zachos, F.E. (2018). Mammals and meaningful taxonomic units: the debate about species concepts and conservation. *Mammal Rev.* **48**: 153–159.

Zachos, F.E. (2020). Mammalian phylogenetics: A short overview of recent advances. Pp. 1–18 in: Hackländer, K. & Zachos, F.E. eds. (2020). *Handbook of the Mammals of Europe*. Springer International Publishing, Cham, Switzerland.

Zachos, F.E. & Lovari, S. (2013). Taxonomic inflation and the poverty of the Phylogenetic Species Concept – a reply to Gippoliti and Groves. *Hystrix* **24**: 142–144.

Zachos, F.E., Apollonio, M., Bärmann, E.V., Festa-Bianchet, M., Göhlich, U., Habel, J.C., Haring, E., Kruckenhauser, L., Lovari, S., McDevitt, A.D., Pertoldi, C., Rössner, G.E., Sánchez-Villagra, M.R., Scandura, M. & Suchentrunk, F. (2013). Species inflation and taxonomic artefacts—A critical comment on recent trends in mammalian classification. *Mammal. Biol.* **78**: 1–6.

Zhang Guojie, Cowled, C., Shi Zhengli, Huang Zhiyong, Bishop-Lilly, K.A., Fang Xiaodong, Wynne, J.W., Xiong Zhiqiang, Baker, M.L., Zhao Wei, Tachedjian, M., Zhu Yabing, Zhou Peng, Jiang Xuanting, Ng, J., Yang Lan, Wu Lijun, Xiao Jin, Feng Yue, Chen Yuanxin, Sun Xiaoqing, Zhang Yong, Marsh, G.A., Crameri, G., Broder, C.C., Frey, K.G., Wang Linfa & Wang Jun. (2013). Comparative analysis of bat genomes provides insight into the evolution of flight and immunity. *Science* **339**: 456–460.

Zou Zhengting & Zhang Jianzhi. (2016). Morphological and molecular convergences in mammalian phylogenetics. *Nature Commun.* **7**: 12758. 9 pp.

CLASS MAMMALIA