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Rodent systematics in an age of discovery: recent advances and prospects

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With almost 2,600 species, Rodentia is the most diverse order of mammals. Here, we provide an overview of changes in our understanding of the systematics of living rodents, including species recognition and delimitation, phylogenetics, and classification, with emphasis on the last three decades. Roughly, this corresponds to the DNA sequencing era of rodent systematics, but the field is undergoing a transition into the genomic era. At least 248 species were newly described in the period 2000–2017, including novelties such as the first living member of Diatomyidae and a murid species without molars (*Paucidentomys vermidax*), thus highlighting the fact that our understanding of rodent diversity is going through an age of discovery. Mito-nuclear discordance (including that resulting from mitochondrial introgression) has been detected in some of the few taxonomic studies that have assessed variation of two or more unlinked loci. As studies incorporate more loci, incomplete lineage sorting and introgression are likely to gain recognition as widespread phenomena in the near future. Molecular phylogenetics has had a major impact in rodent phylogeny and allowed the identification of three major rodent clades, here recognized as suborders: 1) the Hystricomorpha (sometimes referred as the Ctenohystrica) and including two infraorders, Hystricognathi and Ctenodactylomorphi; 2) the Sciuromorpha; and 3) the Supramyomorpha, a new suborder that comprises the infraorders Castorimorphi, Anomalurimorphi, and Myomorphi. In spite of the greater understanding and ensuing stability of rodent phylogeny gained during the last three decades, several major areas of the rodent tree remain unresolved or poorly supported. We expect that the analysis of genomic-scale data will help resolve those areas of the radiation of Rodentia that still remain poorly understood.

Con casi 2.600 especies vivientes, los roedores componen el orden más diverso de mamíferos. En este trabajo, revisamos los cambios principales ocurridos durante las últimas 3 décadas, en aspectos de delimitación de especies, filogenia y clasificación del orden Rodentia. A grandes rasgos, este período corresponde a la era en que la secuenciación del ADN se incorporo a la sistemática de roedores, campo que actualmente está experimentando una transición hacia la era genómica. Al menos 248 nuevas especies fueron descritas en el período 2000–2017; entre estas se incluyen el primer miembro viviente de la familia Diatomyidae y una especie sin molares (*Paucidentomys vermidax*). El alto número de nuevas especies sugeridas indica que el campo de la diversidad de roedores está atravesando actualmente una era de descubrimiento. En algunos de los pocos estudios taxonómicos que han evaluado la variación de 2 o más loci no ligados, se ha detectado discordancia mito-nuclear (incluida la resultante de introgresión mitocondrial). Se sugiere que a medida que los estudios incorporen más loci, los casos reportados de reparto desigual de linajes e introgresión se incrementaran y serán considerados como procesos relativamente comunes en la diferenciación y demografía de roedores. El uso de caracteres moleculares ha tenido un gran impacto en la sistemática de Rodentia, permitiendo la identificación de tres principales clados de roedores, aquí reconocidos como subórdenes: 1) Hystricomorpha (referido como Ctenohystrica en algunos estudios) que incluye 2 infraorders, Hystricognathi y Ctenodactylomorphi; 2) Sciuromorpha, y 3) Supramyomorpha, nuevo suborden, que comprende los infraorders Castorimorphi, Anomalurimorphi y Myomorphi. A pesar de la mayor comprensión y la consiguiente estabilidad de la filogenia de roedores obtenida durante las últimas 3 décadas, partes importantes del árbol de roedores permanecen sin resolver o tienen un apoyo deficiente. Se espera que la incorporación de una perspectiva genómica ayude a resolver parte de las zonas aún no bien caracterizadas de la radiación de Rodentia.

Key words: classification, diversity, phylogeny, Rodentia, species recognition

Rodentia is the most diverse order of mammals, with almost 2,600 species, representing 40% of the living mammal species (Mammal Diversity Database 2018). In addition, this percentage tends to rise because most mammal species newly described or elevated from synonymy are rodents. Living rodents range in size from some species of mice weighing 5 g to capybaras (*Hydrochoerus hydrochaeris*), which can weigh over 70 kg. This range dramatically increases if extinct forms are considered; estimations of the weight of *Josephoartigasia monesi*, an extinct dinomyid, give values of nearly 1,000 kg, positing it as the largest known rodent (Millien 2008; Rinderknecht and Blanco 2008). However, most rodent species weigh less than 1 kg. Native rodents are found on all landmasses except Antarctica, New Zealand, and some oceanic islands, where they display a variety of forms and life histories. The rodent radiation includes subterranean species, gliding squirrels, and a large array of semiaquatic lineages, as well as the more common arboreal, scansorial, or cursorial forms.

All rodents have highly specialized gnawing dentition, which lacks canines and is composed of a single pair of upper and a single pair of lower continuously growing incisors. Posterior to the incisors is a diastema, followed by one or more pairs of molars and premolars, although the recently discovered *Paucidentomys* has no molariform teeth (Esselstyn et al. 2012). Rodent incisors are rootless, grow continuously, and have enamel only on their anterior and lateral surfaces. Although a dentition specialized for gnawing is not unique to rodents (for instance, extinct multituberculates and extant groups, such as wombats, hyraxes, aye-ayes, and lagomorphs, have a similar pattern), the group has specialized in gnawing to an extreme. Important muscles for chewing are the masseters, which show distinct patterns of bone insertions and associated usage in rodents (Druzinsky 2015). These patterns have historically been the basis to classify rodents (see below).

The recognition, characterization, classification, and understanding of rodent diversity and evolution have been, and continue to represent, major challenges in mammalian systematics. The publication of the influential Luckett and Hartenberger's (1985) edited book on rodent evolutionary relationships is a convenient summary of the challenges presented to rodent systematics, in particular rodent phylogenetics, three decades ago. There were, for example, unresolved questions about the identity and composition of major rodent groups and the phylogenetic significance of traditional myological, cranio-mandibular, and dental traits. The monophyly of major groups, such as caviomorphs, was in question on both morphological and immunological grounds. Uncertainties about the major routes of intercontinental dispersal of rodent lineages were rooted in such phylogenetic difficulties and associated controversies.

DNA amplification and sequencing allowed for an examination of these and other issues in rodent systematics with new impetus, providing access to a wealth of heritable variation to tackle systematic issues at all levels. Early applications of the polymerase chain reaction (PCR) were greatly facilitated by the reporting of "universal" primers to target the amplification and sequencing of fragments of the mitochondrial genome (Kocher et al. 1989). For instance, at the species level, PCR amplification and sequencing fueled the then emerging field of phylogeography (Avise 2009), which resulted in much increased power to uncover variation within and between species. Importantly, as recognized early on, phylogeography also represented a natural, tree-based link between population genetics and phylogenetics (Avise et al. 1987), which easily ties with some of the most widely used species concepts.

Currently, rodent systematics is undergoing a major transition into the "genomic era" (e.g., Lessa et al. 2014), whose impact we can only anticipate in general terms. Here, we describe major changes in rodent systematics as a component of major advances in mammalian systematics over the last decades, resulting primarily from the combination of DNA sequencing and phylogenetics.

The goals of this paper are: 1) to provide an overview of progress in rodent systematics, with emphasis on the last three decades, broadly corresponding to the "DNA sequencing era" of systematics; 2) to identify major remaining challenges in rodent systematics; and 3) to point to prospects for future advances in particularly promising areas. Although we allude to paleontological contributions in the field, our overview is strongly biased toward extant rodents.

Species Limits, Hybridization, and Introgression

Systematics at the species level entails the identification and taxonomic recognition of species, which requires an understanding of what constitutes variation within species, as well as what characterizes different, especially closely related, species. A review of the evolution of concepts and methods in this area is outside the scope of this article. Rather, we identify some of the major trends and refer to selected study cases in rodents that provide good examples and applications. We also examine in detail the consequences of changing concepts and practices of systematics for the current understanding of rodent taxonomy, most notably for the recognition of a much larger number of species than in earlier decades.

In particular, we examine how DNA data have been used in the recognition and characterization of rodent species, what we have learned about introgression and incomplete lineage sorting as complementary paths for the evolution of incongruences between gene trees and species trees, and what studies of contact zones and hybridization tell us about the nature of species divergence and isolation. This is an area in which genomic-scale studies are anticipated to have a great impact in the practice of systematics at the species level.

Species concepts and species delimitation.—During the past century, there was a large debate on species concepts, known as the species problem, centered on how to define the species category (Hey 2001). About 30 species definitions have been proposed; however, in a series of papers, de Queiroz (1995, 2005, 2007) advanced a unifying species concept, in which species are envisioned as "separately evolving metapopulations, or more specifically [with] segments of such lineages," in the so-called General Lineage Concept of Species (GLC). The widespread adoption of this concept (but see Hausdorf 2011) allowed overcoming of the species problem—i.e., providing a species concept that can be applied throughout the tree of life. Under the GLC, other properties, such as reproductive isolation, monophyly, and morphological differentiation, which originally were suggested as necessary properties of species (e.g., Mayr 1963), are not considered indispensable. However, these properties are seen as secondary properties relevant to species delimitation because they constitute operational criteria to infer lineage separation (de Queiroz 2007). As noted, species may or may not acquire these properties during the course of their existence; in addition, the order in which these properties are eventually acquired varies among species. Therefore, after a speciation event, there is a gray zone in which a given secondary criterion may fail to delimit the two sister species (figure 1 in de Queiroz 2007). For instance, it is well known that even in absence of gene flow, for a gene neutral to speciation, two sister species would become reciprocally monophyletic only after a period of time that is mostly a function of population sizes (Pamilo and Nei 1988). Given these difficulties, delimitation of species is one of the most challenging tasks of organismal biology (Coyne and Orr 2004).

The rapid adoption of PCR in systematics fostered a flurry of applications in phylogeography (Avise 2009; Riddle and Jezkova 2019) and related studies of variation within species, many of which turned out to be highly structured and were suspected to be multispecies aggregates. Applications of protein electrophoresis and chromosomal assessments, which had earlier opened new ways for species discovery and delimitation in earlier decades, declined and were only partially replaced by microsatellite and other nuclear DNA assays.

The recent recognition of a cryptic species of flying squirrel in the North American Pacific northwest (*Glaucomys oregonensis*) illustrates the use of DNA data for species recognition and delimitation (Arbogast et al. 2017, and references therein). Phylogeographic studies of flying squirrels in North America had uncovered two, largely allopatric mitochondrial clades, that differed by > 12% sequence divergence, within *Glaucomys volans*. Such divergence is unusually high relative to reported intraspecific variation in mammals (Baker and Bradley 2006). Microsatellite data uncovered no evidence of hybridization in a few localities in which these two forms were found in sympatry; furthermore, one microsatellite locus showed mutually exclusive sets of alleles between these two clades (Arbogast et al. 2017). A review of the taxonomic literature indicated that the name *G. oregonensis* was to be applied to one of the two clades, whereas the other corresponded to a more restricted understanding of *G. volans*. It was shown that the latter was phylogenetically closer to *G. sabrinus* than either to *G. oregonensis*. Finally, as noted by the authors, morphological variation within and between these species needs to be reanalyzed in light of the patterns of molecular divergence. The traits used in the original description to diagnose *G. oregonensis* are not those used to recognize it as a distinct species.

Mito-nuclear discordance and introgression.—PCR-based studies of geographical variation have also uncovered cases of incongruence between loci, or between mitochondrial DNA (mtDNA) and other types of information (e.g., earlier species or subspecies designations, karyotypes, morphology). Perhaps the simplest (and most widely documented) case of mito-nuclear discordance is the result of mitochondrial capture. The starting point is an observation of congruence among nuclear variants that contrasts with an incongruent distribution of mitochondrial haplotypes. An early example was provided by a study of the relationships between species of pocket gophers of the genus *Thomomys*. Specifically, allozyme data and sequences of one nuclear locus were consistent with *T. bottae* being paraphyletic relative to a monophyletic *T. townsendii*, whereas the latter was polyphyletic in its mtDNA (Patton and Smith 1994). Mitochondrial introgression from *T. bottae* into *T. townsendii*, facilitated by mating asymmetry (Patton and Smith 1993), was documented to be in part responsible for this pattern.

Introgression implies horizontal gene transfers (in the example above, of mitochondrial genomes) between species that are more recent than the speciation event separating those species (Fig. 1); consequently, the pattern and timing (or relative levels) of nuclear and mitochondrial divergence offer clues to identify introgression. For example, Good et al. (2008) documented hybridization as a cause for mitochondrial introgression in chipmunks, contrasting the pattern of mtDNA variation with that of four nuclear loci. Genomic data indicate that species remained distinct in spite of incomplete reproductive isolation and multiple cases of hybridization, and that introgression is largely restricted to the mitochondrial genome and resulted from historical, not ongoing, hybridization (Good et al. 2015).

Although introgression may be uncovered in comparative studies of variation within and between species, the processes leading to introgression are best studied in hybrid zones. In a recent review of mammalian hybrid zones, Shurtliff (2013) concludes that hybridization is more common than previously recognized and is often asymmetrical for multiple reasons, including relative abundances of species in contact areas, asymmetric mate preferences, and other genetic and ecological interactions. An example in pocket gophers is offered by Ruedi et al. (1997), who show mitochondrial introgression extending well beyond the limits of an otherwise narrow hybrid zone.

The classical hybrid zone formed by *Mus musculus musculus* and *M. m. domesticus* in central Europe has served to document how genetically based mate preferences, hybrid sterility, and positive natural selection interact in determining the local dynamics of hybridization and the direction and magnitude of

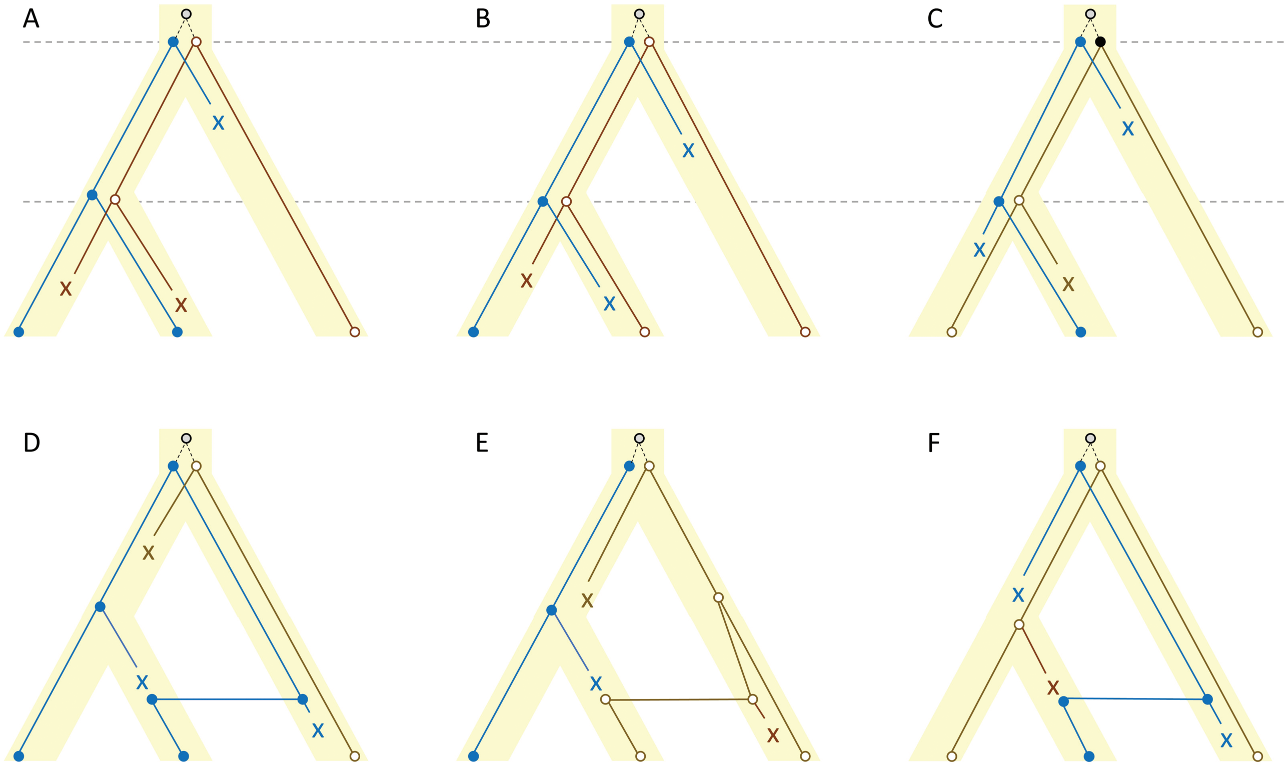

Fig. 1.—Relationships between gene (allele) trees (lines) and species trees (shaded area). The ancestry of alleles (circles) of three species, resulting from two successive speciation events, is tracked to two ancestral alleles. The symbol X signals allele extinction. A) a gene tree congruent with the species tree. B, C) gene trees incongruent as a result of incomplete lineage sorting. D–F) the same gene tree topologies of A–C, but resulting from introgression.

introgression of genes away from the hybrid zone (Geraldes et al. 2008). Introgression of a chromosomal segment into the native genome of a species requires recombination. Studies of *Mus* have shown that centromeric regions, which have reduced recombination, are less likely to introgress than other regions of the same chromosomes (Payseur 2016). There appears to be stronger selection against introgression in the X chromosome than in autosomal loci (Geraldes et al. 2008). There are also known cases of Y-chromosome introgression (Geraldes et al. 2008, and references therein), but the frequency of this phenomenon is unknown at this point. Ongoing studies of hybridization in woodrats (*Neotoma*) illustrate the roles of mate choice in asymmetrical hybridization (Coyner et al. 2015). Additionally, ecological segregation of species and selection against hybrids also play a role in limiting hybridization (Shurtliff et al. 2014).

The net result of these complex interactions is that introgressed segments usually represent a small fraction of the genome, whose long-term success greatly depends on their effects on fitness in the recipient species (White et al. 2009). A potential illustration is warfarin resistance in the house mouse (*M. m. domesticus*), which seems to be based on introgression of a relevant allele from *M. spretus*. Hedrick (2013) reviewed this and other cases of introgression and concluded that introgression may be a source of adaptive evolution of recipient species (see also Mallet et al. 2016).

In sum, introgression may be important for fueling adaptive evolution but appears to be restricted to relatively minor segments of the genome. For the practice of taxonomy at the species level, however, it may introduce a bias in species delimitation given the widespread use of mtDNA data and the far more limited use of nuclear DNA loci and other relevant (e.g., chromosomal) data in species discovery and delimitation.

Incomplete lineage sorting.—It has long been recognized that incomplete lineage sorting between successive speciation events is a major source of incongruence between gene trees and species trees (Pamilo and Nei 1988). Briefly, species trees condition, but do not determine, gene trees. Even in the absence of introgression, incomplete sorting of ancestral polymorphisms allows different loci to have different genealogical topologies (Fig. 1). This is well illustrated by the human–chimp–gorilla genomes, in which most genes reflect the accepted species tree (humans and chimps closer to each other than either is to gorillas), but the other two possible topologies are also represented in the genomes; in fact, segments representing each of the topologies are interspersed along chromosomes (Pääbo 2003; Ebersberger et al. 2007).

Under neutrality, the opportunity for a gene tree to depart from the species tree due to incomplete lineage sorting is directly related to effective population size, and is consequently highest in autosomal loci, intermediate in X-linked loci, and lowest in Y-linked or mitochondrial genes. In addition, incomplete lineage sorting requires that a given polymorphism survives through two speciation events; therefore, it is more likely to occur in cases of rapid diversification (i.e., short times between successive speciation events). Incomplete lineage sorting may be common in groups that have undergone rapid diversification, especially in autosomal loci.

Documenting incomplete lineage sorting, however, is difficult because it requires sampling multiple loci. Finding diagnostic sites to document incongruence between gene trees is difficult in autosomal loci, which in closely related species usually have limited variation. Finally, topological differences in gene trees may not suffice to distinguish introgression from incomplete lineage sorting (Fig. 1). In sum, detecting incomplete lineage sorting often requires substantial autosomal gene sampling; consequently, such efforts are restricted to a relatively small number of case studies (e.g., *Rattus* in Pagès et al. 2013).

Tucker et al. (2005) analyzed the phylogeny of the genus *Mus* using two mitochondrial fragments and six nuclear loci. They found statistical support for mito-nuclear incongruence but could not discern the possible roles of introgression or incomplete lineage sorting. In some cases, apparent incongruence between gene trees was not statistically supported, suggesting rate heterogeneity and homoplasy as potential causes for the observed topological differences. More recent analyses at the genomic scale provide multiple examples of gene tree incongruences, a fraction of which are attributable to incomplete lineage sorting (Geraldes et al. 2008; Sarver et al. 2017). Using an exome capture approach, Sarver et al. (2017) examined incongruences between gene and species trees in seven sets of mouse species, and detected introgression in two of them. In all the remaining cases, incomplete lineage sorting is a sufficient explanation for incongruences between gene and species trees. Importantly, incomplete lineage sorting is implied in all cases, a fact that may be obscured by the emphasis on statistical tests devised to detect introgression.

Integration of multiple datasets.—The joint consideration of multiple loci is not devoid of analytical dilemmas, many of which fall in the realm of molecular phylogenetics. As an example, Malaney et al. (2017) looked for overall congruence of five loci and, using several species-delimitation approaches, identified a range of possible species of jumping mice (*Zapus*). Examination of ecological variation among candidate species was done based on niche models. Overall, the number of putative species supported by the molecular and ecological data ("discovery-based" species) was much larger than the number of species recognized by current taxonomy.

However, the integration of DNA studies with other sources of relevant systematic information present substantial additional challenges that remain to be addressed. Indeed, relatively few studies incorporate multiple genetic (e.g., mitochondrial and nuclear DNA sequences, microsatellites), and qualitative morphological and morphometric approaches for an integrative assessment of species-level taxonomy. Patton et al. (2007) provide an exemplary case in the study of woodrats of the *Neotoma lepida* group. Phylogenetic criteria delineate four major units, which are recognized as species on the additional basis of consistent morphological differentiation and evidence of full reproductive compatibility within each of these units. Subspecific differentiation is also recognized in species that have substantial internal structure demonstrable, to various extents, by different data sets (see Patton and Conroy 2017 for additional discussion of subspecies delimitation).

ADVANCES IN UNDERSTANDING RODENT SPECIES DIVERSITY

We compiled a list, intended to be exhaustive, of living rodent species described from January 2000 up to December 2017 (Supplementary Data SD1). The list includes only newly proposed specific names (i.e., new subspecies are not considered); however, new names that have failed to comply with the provisions of the International Code of Zoological Nomenclature (ICZN 1999), in other words that are not available, were not included (e.g., *Ctenomys mariafarelli* Azurduy, 2005 and *Cuniculus hernandezi* Castro, López, and Becerra, 2010; see Bidau 2015 and Ramírez-Chaves and Solari 2014). The list does not include either newly considered species for which already available names apply (i.e., names rescued from the synonymy of already considered distinct species), including those elevated from subspecies to species (e.g., *Grammomys ibeanus* shown to be distinct from *G. cometes* by Kryštufek et al. (2008) or the case of *Glaucomys oregonensis* described above). Newly proposed species are considered even if they were later suggested to be synonyms (e.g., *Abrawayaomys chebezi*—see Percequillo et al. 2017). Similarly, we have not evaluated the evidence presented to sustain any new name. Finally, we have not considered changes of generic allocation of new species (e.g., the form *rupicola* was described by Granjon et al. (2002) as a species of *Gerbillus* and it was considered as a species of *Dipodillus* by Musser and Carleton 2005; see also Monadjem et al. 2015, who regard this form as a species of *Gerbillus*). A revision of the status, distinction, and relationships of the newly proposed species is out of the scope of the present paper. We expect that, even with these caveats, our list is reflective of the general trends of rodent taxonomy.

The single most important point regarding rodent taxonomy is that we are in an age of species discovery. At least 248 new rodent species have been described from January 2000 to December 2017 (Table 1; Supplementary Data SD1); of these, at least 41 have been described in the *Journal of Mammalogy* (*JM*; Table 2). Thus, an average of 13.8 new rodent species were described each year since 2000. This number is larger than the one (ca. 11.1) obtained by Reeder et al. (2008) for the period July 1992–June 2006 (with an overlap of 6.5 years with the period analyzed by us). The fact that this is an age of rodent species discovery needs to be recognized not only by the direct users of taxonomic knowledge, including ecologists, biogeographers, and conservation biologists, but also by funding agencies and officers in charge of granting collection permits. Field collection of specimens and collections-based research needs to be intensified to characterize rodent diversity.

The 248 new rodent species belong to 21 families (Table 1; Fig. 2) of the 35 living families currently recognized (Fig. 3). Most of the new rodent species belong to the families Muridae

Table 1.—Number of new rodent species per family and continent described between January 2000 and December 2017 (see text and Supplementary Data SD1 for details).

Family	Number of new species	Africa	Asia	Europe	Oceania	North America	Central America	South America
All families	248	45	73	1	14	7	4	104
Abrocomidae	1							1
Bathyergidae	5	5						
Caviidae	2							2
Chinchillidae	1							1
Cricetidae	87		7			7	3	70
Ctenomyidae	7							7
Cuniculidae	2							2
Dasyproctidae	1							1
Diatomyidae	1		1					
Dipodidae	3		3					
Echimyidae	8							8
Erethizontidae	6							6
Gliridae	1		1					
Heteromyidae	4						1	3
Muridae	99	36	48	1	14			
Nesomyidae	4	4						
Octodontidae	3							3
Platacanthomyidae	1		1					
Sciuridae	6		6					
Sminthidae	1		1					
Spalacidae	5		5					

(*n* = 99) and Cricetidae (*n* = 87), which in turn are the most diverse of the order (see current numbers in Mammal Diversity Database 2018; see also Burgin et al. 2018); the number of species described in these two families is an order of magnitude larger than the number of species described in each of the other 19 rodent families. Within Muridae and Cricetidae, most new species belong to the subfamilies Murinae and Sigmodontinae, respectively. Of particular interest is the description of the Laotian rock rat, *Laonastes aenigmamus*, which is the sole living representative of the family Diatomyidae, previously thought to be extinct since the Miocene (Jenkins et al. 2005; Huchon et al. 2007). Also remarkable is the recent description in the *JM* of the third living species of Platacanthomyidae, the blind mouse, *Typhlomys nanus* (Cheng et al. 2017). Finally, the families Aplodontiidae, Diatomyidae, Dinomyidae, Heterocephalidae, Petromuridae, and Zenkerellidae remain formed by a single living species each (Burgin et al. 2018).

In particular, new species are mostly described based on South American (*n* = 104), Asian (*n* = 73), and African (*n* = 45) specimens, representing 41.9%, 29.4%, and 18.1% of the new species, respectively. These numbers reflect the fraction of the high rodent diversity of each continent that still awaits discovery, in particular in the three continents of high overall biotic richness. In addition, these discoveries are the direct result of the research efforts conducted on the fauna of each area. Assessing the relative contribution of each of these two factors is outside the scope of this synthesis, but we suggest that the large number of new South American rodents is, in part, due to the intense taxonomic work that is being carried out on almost all South American countries (e.g., see author affiliations in the recently treatise of South American rodents edited by Patton et al. 2015). Regarding the first factor, it is noticeable that the single European species, *Mus cypriacus*, comes from the Republic of Cyprus (Cucchi et al. 2006), on the Island of Cyprus, which is closer to the Asian mainland than to the coast of Europe. Similarly, only seven species in our list were discovered in North America, all of which came from Mexico. Also of interest is the fact that all but one of the 14 new species from Oceania are from Papua New Guinea; the exception is the giant rat, *Uromys vika*, from the Solomon Islands recently described in *JM* by Lavery and Judge (2017).

Among the less explored regions on Earth is the Indo-Pacific region, where several recent discoveries have highlighted our limited knowledge of its rodent fauna. Several early explorations contributed to the knowledge of rodents in this region (e.g., Thomas 1898, 1920), but studies carried out over the last two decades have shed light on the rodent diversity of large oceanic islands such as Luzon and Sulawesi. Surveys of altitudinal gradients on Luzon (Heaney et al. 2016) have doubled the number of described endemic species since 2000 (from 28 to 56 species), with several new species of *Apomys*, *Rhynchomys*, *Archboldomys*, and other species that have prompted the creation of new genera (Heaney et al. 2009, 2016; see below for more details). A similar trend can be expected on the large oceanic island of Sulawesi, and from the Moluccas (Fabre et al. 2013c, 2018) and the large Island Shelf of Papua New Guinea, where few thorough taxonomical surveys of mammals or surveys of altitudinal gradients have been implemented. Morphological and taxonomic work based on sparse museum collections has only shed light on some endemic Papuan genera such as *Brassomys*, *Mirzamys*, or *Baiyankamys* (Helgen and Helgen 2009; Musser and Lunde 2009) or new species of *Leptomys* and *Pseudohydromys* (Musser et al. 2008; Helgen and Helgen 2009). The complementary implementation of molecular-based methods of species delimitation on complex species belonging to widespread Papua New Guinea lineages, such as the diverse genera *Melomys*, *Rattus*, or *Uromys*, might prove an important step toward the understanding of the rodent diversity of

Table 2.—Species newly described in the *Journal of Mammalogy* (January 2000–December 2017).

Species	Family	Continent	Evidence	Authors
Tapecomys primus	Cricetidae	South America	Morphology, molecular	Anderson and Yates (2000)
Akodon paranaensis	Cricetidae	South America	Morphology, karyotypes, molecular	Christoff et al. (2000)
Abrocoma uspallata	Abrocomidae	South America	Morphology, karyotypes	Braun and Mares (2002)
Oxymycterus josei	Cricetidae	South America	Morphology, molecular	Hoffmann et al. (2002)
Bullimus gamay	Muridae	Asia	Morphology	Rickart et al. (2003)
Thomasomys onkiro	Cricetidae	South America	Morphology	Luna and Pacheco (2002)
Limnomys bryophilus	Muridae	Asia	Morphology, karyotypes	Rickart et al. (2002)
Peromyscus schmidlyi	Cricetidae	North America	Morphology, karyotypes, molecular	Bradley et al. (2004)
Chrotomys sibuyanensis	Muridae	Asia	Morphology, molecular	Rickart et al. (2005)
Akodon philipmyersi	Cricetidae	South America	Morphology, karyotypes, molecular	Pardiñas et al. 2005)
Neusticolmys ferreirai	Cricetidae	South America	Morphology, karyotypes	Percequillo et al. (2005)
Rhynchomys banohao	Muridae	Asia	Morphology	Balete et al. (2007)
Rhynchomys tapulao	Muridae	Asia	Morphology	Balete et al. (2007)
Proedromys liangshanensis	Cricetidae	Asia	Morphology	Liu et al. (2007)
Hylomyscus walterverheyeni	Muridae	Africa	Morphology	Nicolas et al. (2008)
Phyllomys sulinus	Echimyidae	South America	Morphology, karyotypes	Leite et al. (2008)
Akodon viridescens	Cricetidae	South America	Morphology, karyotypes, molecular	Braun et al. (2010)
Cerradomys goytaca	Cricetidae	South America	Morphology, karyotypes	Tavares et al. (2011)
Rhipidomys itoan	Cricetidae	South America	Morphology, karyotypes, molecular	Costa et al. (2011)
Rhipidomys tribei	Cricetidae	South America	Morphology, karyotypes, molecular	Costa et al. (2011)
Ctenomys ibicuiensis	Ctenomyidae	South America	Morphology, karyotypes, molecular	Freitas et al. (2012)
Holochilus lagigliai	Cricetidae	South America	Morphology	Pardiñas et al. (2013)
Thomomys nayarensis	Geomyidae	North America	Morphology, molecular	Mathis et al. (2013)
Peromyscus carletoni	Cricetidae	North America	Morphology, karyotypes, molecular	Bradley et al. (2014)
Tympanoctomys kirchnerorum	Octodontidae	South America	Morphology, molecular	Teta et al. (2014)
Calassomys apicalis	Cricetidae	South America	Morphology, karyotypes, molecular	Pardiñas et al. (2014)
Abrothrix manni	Cricetidae	South America	Morphology, molecular	D'Elía et al. (2015)
Hyorhinomys stuempkei	Muridae	Asia	Morphology, molecular	Esselstyn et al. (2015)
Rattus detentus	Muridae	Oceania	Morphology, molecular	Timm et al. (2016)
Peromyscus gardneri	Cricetidae	Central America	Morphology, molecular	Lorenzo et al. (2016)
Gracilimus radix	Muridae	Asia	Morphology, molecular	Rowe et al. (2016)
Oecomys franciscorum	Cricetidae	South America	Morphology, molecular	Pardiñas et al. (2016)
Necromys lilloi	Cricetidae	South America	Morphology, molecular	Jayat et al. (2016)
Juliomys ximenezi	Cricetidae	South America	Morphology, karyotypes, molecular	Christoff et al. (2016)
Peromyscus kilpatricki	Cricetidae	North America	Morphology, karyotypes, molecular	Bradley et al. (2017)[a]
Neodon medogensis	Cricetidae	Asia	Morphology, molecular	Liu et al. (2017)
Neodon nyalamensis	Cricetidae	Asia	Morphology, molecular	Liu et al. (2017)
Typhlomys nanus	Platacanthomyidae	Asia	Morphology, molecular	Cheng et al. (2017)
Ototylomys chiapensis	Cricetidae	North America	Morphology, karyotypes, molecular	Porter et al. (2017)
Uromys vika	Muridae	Oceania	Morphology, molecular	Lavery and Judge (2017)
Halmaheramys wallacei	Muridae	Asia	Morphology, molecular	Fabre et al. (2017)[b]

[a] Published online in 2016.

[b] published online in 2017 and listed as 2018 in the Literature Cited.

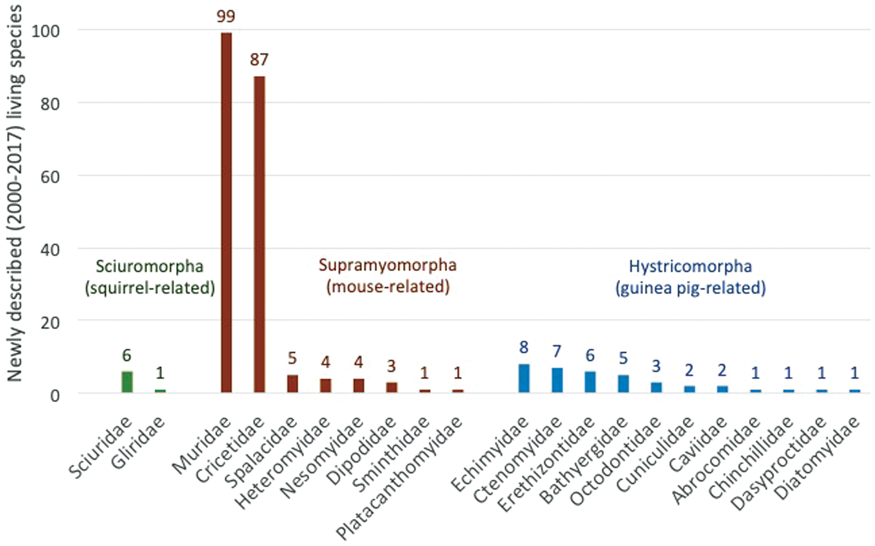

Fig. 2.—Distribution among families of 248 species of rodents newly described in the period January 2000–December 2017.

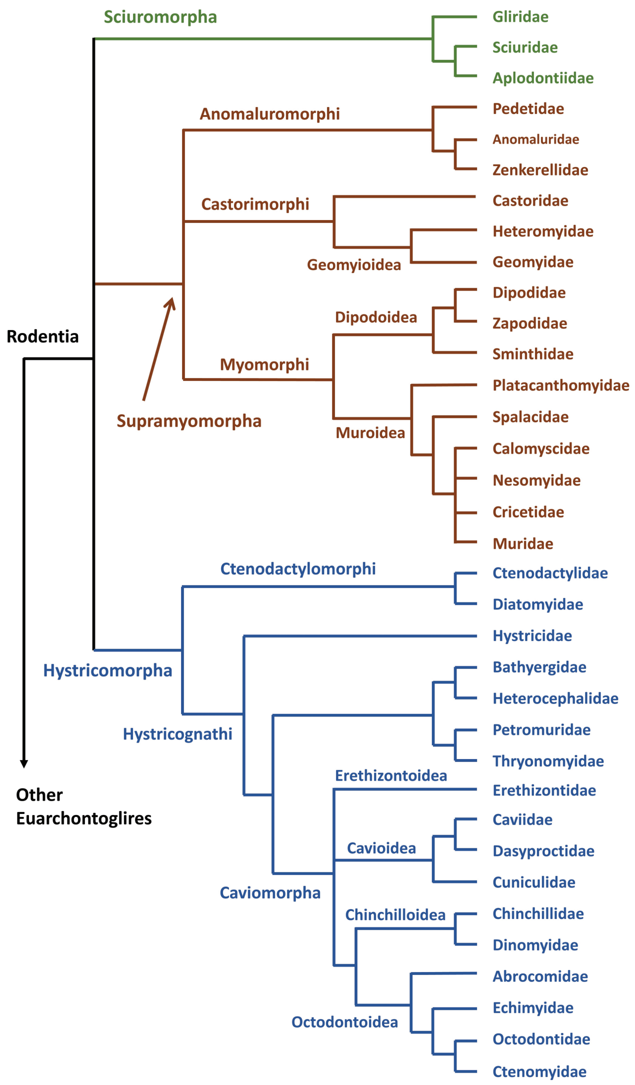

Fig. 3.—Phylogenetic relationships among rodents to the level of families. Polytomies reflect relationships whose solutions we (at times conservatively) consider to be insufficiently supported. Within Caviomorpha, there is support for a Cavioidea–Erethizontoidea (Erethizontidae) clade, but it is less supported than the Octodontoidea–Chinchilloidea (Chinchillidae) clade (see Upham and Patterson 2015). The polytomy depicted within Muroidea may be resolved with Calomyscidae as sister to the remaining three families, of which Nesomyidae may be sister to a clade formed by Cricetidae and Muridae (see Steppan and Schenk 2017).

this poorly known region. In view of the ecological threats related to nickel mining and logging in this Indo-Pacific region, more fieldwork must be undertaken in this highly threatened region where most of the murid diversity in found. Certainly, the need for integrative taxonomic approaches and further field collection applies to most areas of the world, in particular the Neotropics, Africa, and Asia.

Several new rodent species were discovered in the course of revisionary work. This is the case for Jayat's cavy, *Microcavia jayat*, whose type series members were collected in 1969, whereas the species was only recently described by Teta et al. (2017). In contrast, several other new species were described on the basis of newly collected specimens, as illustrated by Lillo's hairy-tailed akodont (*Necromys lilloi*), whose type series members were collected a year before the species was described by Jayat et al. (2016). In either case, all studies relied on collection material, reinforcing the importance of research collections and the need for sustained collecting efforts (Rocha et al. 2014; Cook and Light 2019).

An inspection of the list of 41 new species described in *JM* (Table 2) shows that 17.1% were discovered based on only morphological evidence, 12.2% on the basis of morphology and karyotypes, 29.2% based on combined morphological, karyotypic, and molecular evidence, and 41.5% based on both morphological and molecular data. Combining these numbers indicates that morphological information was taken into account in all cases, whereas molecular and karyotypic data were used in 70.7% and 41.4% of the cases, respectively. Interestingly, in the span of time analyzed (2000–2017), there is no apparent trend toward the usage of a particular type of evidence.

A combination of two of the about 30 delimitation criteria that have been proposed (Sites and Marshall 2003) appears to dominate current taxonomic practice, at least in the case of rodents. First, monophyletic groups are identified in a genealogical analysis based on mtDNA sequences alone or in conjunction with one or a few nuclear loci. Second, the existence of qualitative or quantitative morphological discontinuities, and in some cases, chromosomal discontinuities, among the identified monophyletic groups is assessed. If clades are morphologically (or chromosomally) distinct, they are considered distinct species. Most of the recently described new rodent species have been delimited using this approach (Table 2; Supplementary Data SD1). One of the main drawbacks of this scheme is that it requires a threshold of genetic divergence to distinguish between intra- and interspecific variation (Knowles and Carstens 2007). Additional problems arise because, as mentioned above, gene trees can differ from species trees. The application of multilocus-multispecies coalescent-based approximations advanced to face these limitations (Knowles and Carstens 2007; Fujita et al. 2012; Edwards et al. 2016) is, for the moment, far from being a common practice in rodent taxonomy. Single- and multilocus coalescent methods are starting to be used in rodent species discovery, as exemplified, respectively, in the case of the two new vole species of the genus *Neodon* described in *JM* by Liu et al. (2017) and the evaluation of species limits of ground squirrels of the genus *Otospermophilus* by Phuong et al. (2014). We anticipate that coalescent-based approaches will rapidly become incorporated in rodent species discovery and validation (e.g., da Cruz and Weksler 2018).

As mentioned, the majority of descriptions of new rodent species now take advantage of the power of the genealogical analysis of DNA sequences to discover and delimit species-level lineages, although coalescent-based analyses (e.g., Zhang et al. 2011; Carstens et al. 2013; Sukumaran and Knowles 2017) are seldom implemented. However, with a few exceptions, even today, most species have only been examined for sequence variation in mtDNA. A much smaller number of species is represented by (usually a few) nuclear DNA loci. This situation is expected to rapidly change as costs of enrichment (e.g., capture systems) and reduced representation (e.g., RAD-seq) methods for high-throughput sequencing decrease and coalescent-based methods for species discovery and validation become widely adopted. Finally, it is also of interest that only a handful of studies (e.g., Jayat et al. 2010) have provided molecular synapomorphies for the newly delimited species. Instead, most studies using DNA sequences to delimit species have used the criterion of monophyly and have ignored molecular characters themselves in the diagnosis of newly delimited species.

PROPOSED NEW RODENT GENERA

At least 32 new rodent genera have been proposed between 2000 and December 2017 (Supplementary Data SD1). As in the case of species, the number of recognized genera increases if genera based on already available names are also considered (e.g., *Gerbilliscus* Thomas, 1897, long regarded as a subgenus of *Tatera* Lataste, 1882, is now considered a genus, following Musser and Carleton 2005). In parallel, some of the newly proposed genera listed here have been recently synonymized (e.g., *Pipanacoctomys* and *Salinoctomys* are now considered part of *Tympanoctomys*—see Díaz et al. 2015). Newly described genera belong to the families Bathyergidae, Cricetidae, Echimyidae, Muridae, and Octodontidae. However, by far most of them belong to the New World subfamily Sigmodontinae of Cricetidae.

Most of the new genera recognized and named as results of revisionary work were previously recognized genera that were shown to be polyphyletic (e.g., the murid *Soricomys* was proposed to allocate species previously placed into *Archboldomys*—see Balete et al. 2012). Paradigmatic in this sense is the case of the sigmodontine *Oryzomys*; species traditionally allocated to it (e.g., Musser and Carleton 2005) are now placed in 12 genera, of which 11 were proposed since 2006 (the 12th being a much less diverse *Oryzomys*). Remarkably, 10 of the new genera were proposed in a single paper by Weksler et al. (2006; see also D'Elía and Pardiñas 2007); the 11th was proposed by Pine et al. (2012). At the same time, some new genera have been proposed on the basis of newly discovered species based, in turn, on newly collected specimens. This is the case of the murid genus *Tonkinomys*, and its single species *daovantieni*, described by Musser et al. (2006) on the basis of specimens collected 2 years earlier. Similar is the case of *Saxatilomys*, a genus described to encompass the newly described species *paulinae* that is based on specimens collected in 1998 and 1999 (Musser et al. 2005).

Remarkably, some diverse genera still have unclear boundaries. The New World cricetid *Peromyscus* exemplifies this scenario. *Peromyscus*, the *Drosophila* of North American mammalogy (Musser and Carleton 1993), as delimited by Musser and Carleton (2005; see Carleton 1980), encompasses a large array of deer mice that form a paraphyletic group with respect to other clades traditionally recognized as genera (as *Megadontomys*, *Osgoodomys*, *Neotomodon*, *Podomys*, and *Habromys*—see Miller and Engstrom 2008, and references therein). Two alternative options have been presented for classification to reflect the phylogeny (somewhat intermediate schemes are also possible). The first would include the other genera in the synonymy of *Peromyscus*, which would become a large and morphologically diverse genus. The second classificatory option is, as was done with *Oryzomys* (see above), to split *Peromyscus* into distinct genera (mostly by elevating already recognized species groups to genera—see Carleton 1980 and Musser and Carleton 2005). Additional systematic work is needed to render a stable species tree of all involved taxa, but also to revise the diagnosis of *Peromyscus* (and diagnose additional genera as needed).

As the era of new species discovery and revisionary work continues, we expect new genera to continue to be proposed in the next few years. A large fraction (approximately 65 %) of the genera described since 2000 have been erected primarily on the basis of phylogenetic analyses showing that an already recognized genus was not monophyletic (e.g., *Neomicroxus* was proposed to accommodate species formerly placed in *Akodon*—Alvarado-Serrano and D'Elía 2013); i.e., lineages of genus level identified via phylogenetic analyses were later diagnosed by the presence or absence of "trenchant" character states. It is now less common to delimit new genera only on the basis of the presence or absence of trenchant character states, as was the case for the sigmodontine *Juliomys* (González 2000). This trend is in line with what is seen in other groups; we expect it will persist and increase in the future.

PHYLOGENETICS AND CLASSIFICATION

High species richness and morphological diversity have prompted researchers to propose several classifications to organize rodent diversity. Functional constraints related to diprotodonty (Druzinsky 2015), a high degree of functional convergence and morphological versatility at different hierarchical levels (e.g., D'Elía 2003; Mercer and Roth 2003; Steppan et al. 2004; Fabre et al. 2012), and the rapid diversification of several major rodent groups (Steppan et al. 2004; Fabre et al. 2012; Steppan and Schenk 2017) have resulted in a wealth of phylogenetic hypotheses that have been in part stabilized by phylogenies based on molecular data (Huchon et al. 1999; Adkins et al. 2001; Fabre et al. 2015).

Here, we address progress in rodent phylogenetics, roughly since the publication of Luckett and Hartenberger (1985). We begin by providing a brief overview of the history of high-level rodent classification and phylogenetics preceding that volume. We then examine the impact of DNA-based phylogenetic studies (with reference to morphological data as needed), and provide a summary of issues that we consider to be resolved, as well as outstanding issues that are expected to be tackled in the near future with a combination of genomic- and phenomic-scale data.

Rodent Classification: A Brief Historical Overview

A recent summary of the history of rodent classification is provided by Fabre et al. (2015). We restrict this section to a very succinct overview. Blainville De (1816) was the first to propose a classification of Rodentia into three eco-morphological groups based on their lifestyles: "fouisseurs" (burrowers), "grimpeurs" (climbers), and "marcheurs" (walkers). This ecological classification was quickly abandoned in favor of an arrangement primarily based on cranio-mandibular (Waterhouse 1839) and associated myological (Brandt 1855) characteristics. Three suborders were recognized by these authors based on the origin on the skull and insertions on the jaws of the masseter and temporalis jaw adductor muscles: Sciuromorpha, Hystricomorpha, and Myomorpha. This scheme remained in use for most of the 20th century (e.g., Simpson 1945). A related dichotomic classification was proposed by Tullberg (1899), who considered the position of the angular process relative to the incisor plane to divide rodents in two groups, the Sciurognathi and the Hystricognathi. This subdivision was also used during the last century (e.g., Chaline et al. 1977; Wilson and Reeder 1993; Landry 1999). Of these two large groups, only Hystricognathi forms a strongly supported clade in phylogenies based on molecular data (e.g., Huchon et al. 2000, 2007; Fabre et al. 2013a) and also is supported by morphology (Vianey-Liaud 1974; Bugge 1985; Luckett and Hartenberger 1985; Woods and Hermason 1985; Landry 1999). Also, whereas these classifications were convenient, several rodent lineages could not be confidently placed into these suborders (see discussion in Simpson 1945). More generally, many aspects of rodent phylogenetics were being heatedly debated at the time of publication of Luckett and Hartenberger (1985). Chief among these was whether extant Old World hystricomorphs, including mole-rats (Bathyergidae), porcupines (Hystricidae), and allied taxa, were closely related to the New World caviomorphs suggesting, in turn, an African origin of the latter. Several other high-level problems involving distinct families arose—for instance, the unclear position of Platacanthomyidae, either placed into Gliridae due to their dental characters or into Myomorpha due to their muscle and jaw morphology (Jansa et al. 2009). Studies on rodent cranio-mandibular anatomy had also revealed a new type of muscle morphology, namely protrogomorphy, in the monotypic family Aplodontidae and some extinct rodent families (Wood 1955). Other families, such as Anomaluridae, had unclear phylogenetic position within the rodent radiation. Similarly, classifications of some fossil forms (including the families Theridomyidae, Diatomyidae, and stem cricetids), mainly based on tooth morphology, also generated controversies.

Molecular Phylogenetics: Major Rodent Clades

Early applications of DNA-based phylogenetics (Graur et al. 1991; D'Erchia et al. 1996) questioned rodent monophyly, but these claims turned out to be marred by methodological issues (e.g., Cao et al. 1994; Frye and Hedges 1995; Philippe 1997; Huchon and Douzery 2001; Adkins et al. 2003; Rowe et al. 2010). Both morphological and molecular synapomorphies (e.g., Hartenberger 1985; Huchon et al. 1999; Montgelard et al. 2008; Blanga-Kanfi et al. 2009; Churakov et al. 2010; Esselstyn et al. 2017) strongly support rodent monophyly, validate the combination of rodents and lagomorphs into Glires (Hartenberger 1985; Douzery and Huchon 2004), and firmly place this group within the Euarchontoglires, a major placental clade that also includes Scandentia, Primates, and Dermoptera (Murphy et al. 2001; Springer et al. 2001; Meredith et al. 2011; Esselstyn et al. 2017).

Molecular phylogenies (e.g., Huchon et al. 1999; Smith and Patton 1999; DeBry and Sagel 2001; Adkins et al. 2003; DeBry 2003; Douzery et al. 2003; Steppan et al. 2004; Montgelard et al. 2008; Blanga-Kanfi et al. 2009; Churakov et al. 2010; Meredith et al. 2011; Fabre et al. 2013b) have greatly contributed to convergence to a new rodent classification (summarized in Table 3) and lead to the abandonment of previous ones. From these studies, based on both mitochondrial and nuclear DNA sequences, a new picture of family delimitation (e.g., placement of Lophiomyinae within Muridae and not Cricetidae—Schenk et al. 2013; the recognition of Sminthidae as a distinct family—Lebedev et al. 2013) and suprafamilial relationships has emerged (Fig. 3). Currently 35 living rodent families are recognized and form three well-supported main lineages of Rodentia: 1) a squirrel-related clade, comprising three families; 2) a mouse-related clade that includes 15 families; and 3) a guinea pig-related clade, comprising 17 families (Table 3). However, relationships among these three clades remain unresolved; currently, there is no strong statistical support to rule out any of the alternatives (Montgelard et al. 2008; Blanga-Kanfi et al. 2009; Churakov et al. 2010; Fabre et al. 2015; but see Marivaux et al. 2004 for a possible resolution).

Squirrel-related clade.—This compact group, Sciuromorpha, comprises three families: Sciuridae, Aplodontidae, and Gliridae; there is good support for a sister relationship between the first two (Mercer and Roth 2003; Montgelard et al. 2008; Blanga-Kanfi et al. 2009).

Mouse-related clade.—This diverse rodent group is composed of three major clades, namely 1) the anomaluromorphs, including Pedetidae, sister to the clade formed by Anomaluridae and Zenkerellidae (Heritage et al. 2016); 2) the castorimorphs, including Castoridae as sister to the clade formed by Geomyidae and Heteromyidae (Doronina et al. 2017); and 3) the highly diverse myomorphs, collectively representing nine families distributed between the superfamilies Dipodoidea and Muroidea (Table 3). Although analysis of complete mitochondrial protein-coding genomes (Horner et al. 2007) and a structural analysis of B1 retroposon elements (Veniaminova et al. 2007) have not recovered the mouse-related clade, this large rodent clade is found in the vast majority of phylogenetic studies focused on rodent relationships. Studies corroborating the mouse-related clade vary in the type evidence analyzed (distinct gene datasets and morphology) and in their taxonomic coverage (including fossil taxa), thus representing independent tests of the monophyly of this rodent lineage (Michaux and Catzeflis 2000; Huchon et al. 2002; Adkins et al. 2003; DeBry 2003; Marivaux et al. 2004; Steppan et al. 2004; Farwick et al. 2006; Montgelard et al. 2008; Blanga-Kanfi et al. 2009; Churakov et al. 2010; Fabre et al. 2012; Steppan and Schenk 2017).

The relationships among the three main lineages of the mouse-related clade remain essentially unresolved (Fabre et al. 2013b, 2015, and references therein). One understudied issue

Table 3.—Current rodent classification to the level of families. Comments include changes since Wilson and Reeder (2005), and selected references. The extinct family Heptaxodontidae is not considered.

Suborder	Infraorder	Superfamily	Family	Comments
Sciuromorpha				
			Aplodontidae	
			Gliridae	
			Sciuridae	
Supramyomorpha				New suborder (this paper)
	Anomaluromorphi			Treated as suborder in Wilson and Reeder (2005)
			Anomaluridae	
			Pedetidae	
			Zenkerellidae	Separated from Anomaluridae (Heritage et al. 2016)
	Castorimorphi			Treated as suborder in Wilson and Reeder (2005)
			Castoridae	
			Heteromyidae	May be paraphyletic with respect to Geomyidae (Fabre et al. 2012)
			Geomyidae	
	Myomorphi			Treated as suborder in Wilson and Reeder (2005)
		Dipodoidea		
			Dipodidae	
			Sminthidae	See Rusin et al. (2016)
			Zapodidae	See Lebedev et al. (2013) and Pisano et al. (2015)
		Muroidea		
			Calomyscidae	
			Cricetidae	
			Muridae	Includes Lophiomyinae; see Jansa and Weksler (2004)
			Nesomyidae	
			Platacanthomyidae	
			Spalacidae	
Hystricomorpha				
	Ctenodactylomorphi			
			Ctenodactylidae	
			Diatomyidae	See Jenkins et al. (2005) and Dawson et al. (2006)
	Hystricognathi			
			Bathyergidae	
			Heterocephalidae	See Patterson and Upham (2014)
			Hystricidae	
			Petromuridae	
			Thryonomyidae	
		Erethizontoidea		
			Erethizontidae	
		Chinchilloidea		
			Chinchillidae	
			Dinomyidae	
		Cavioidea		
			Caviidae	
			Dasyproctidae	
			Cuniculidae	
		Octodontoidea		
			Abrocomidae	
			Ctenomyidae	
			Echimyidae	Includes Myocastorinae and Capromyinae (Fabre et al., 2014, 2016)
			Octodontidae	

is the relationship between Geomyidae and Heteromyidae; indeed, Heteromyidae might be paraphyletic to Geomyidae (DeBry 2003; Hafner et al. 2007; Fabre et al. 2012). Within the Muroidea, a superfamily that includes most rodent species, the inter-relationships among families of Eumuroidea (i.e., Calomyscidae, Nesomyidae, Cricetidae, and Muridae) are still unclear. The same is true of the subfamilies of Cricetidae. Similarly, the phylogenetic position of the murid genus *Leimacomys* remains uncertain; a cladistics analysis of craniodental and external characters indicates that it is not related to dendromurines as previously thought, and may, rather, represent one of the main lineages of murids (Denys et al. 1995). Musser and Carleton (2005) erected a new subfamily, Leimacomyinae, to place this genus. Currently, there are no molecular data for the sole member of this subfamily, the groove-toothed forest mouse *Leimacomys buettneri*.

Guinea pig-related clade.—This clade constitutes the suborder Hystricomorpha and includes the infraorders Hystricognathi and the Ctenodactylomorphi. The Hystricognathi is a taxonomically diverse group, including the families Hystricidae, Bathyergidae, Heterocephalidae, Petromuridae, Thryonomyidae, and 10 families of New World caviomorphs, a monophyletic group that receives strong molecular (e.g., Huchon et al. 2000, 2007; Fabre et al. 2013a) and morphological (Bugge 1985; Luckett and Hartenberger 1985; Woods and Hermason 1985; Landry 1999; Marivaux et al. 2002, 2004) support, which in turn effectively settled the controversy concerning the African origin of caviomorphs. On the other hand, Ctenodactylomorphi includes the families Ctenodactylidae and Diatomyidae (Jenkins et al. 2005; Dawson et al. 2006; Huchon et al. 2007). Major recent advances in the understanding of Hystricomorpha include evidence for a sister relationship of the superfamilies Octodontoidea and Chinchilloidea, as well as expansion of the highly diverse Echimyidae to include two groups traditionally considered distinct families, the capromyids and the myocastorids. Whereas the placement of myocastorids within Echimyidae appears clear, that of the capromyids needs further testing (Fabre et al. 2016). Also noteworthy is the publication of a comprehensive multilocus phylogenetic analysis of almost all genera of caviomorphs (Upham and Patterson 2015). Similarly, naked mole-rats are placed into their own family (Heterocephalidae), rather than within Bathyergidae (Patterson and Upham 2014; see also Landry 1957). As noted above, the discovery of the Laotian rock rat (*Laonastes aenigmamus*) represented the addition of a new extant family (Diatomyidae), previously known only from fossils, to the group of living hystricomorphs (Jenkins et al. 2005; Dawson et al. 2006). However, several higher-level relationships within Hystricomorpha remain unclear, including the position of Hystricidae within the suborder and of Erethizontoidea within Caviomorpha.

The future analysis of genomic datasets, as well as the implementation of probabilistic methodologies that could better take into account molecular evolutionary biases using sophisticated models (Lartillot and Philippe 2004; Delsuc et al. 2005; Blanquart and Lartillot 2008), together with the analysis of phenomic matrices, should help to further elucidate current competing alternatives and gaps in our understanding of the rodent tree.

Cranio-Mandibular Variation Revisited

The new higher-level phylogenetic results imply the existence of rampant convergence in the rodent cranio-mandibular system. Jaw muscle classifications were based primarily on the presence or absence of enlarged skull foramina (the infra-orbital foramina). Hystricomorph rodents have a very large infra-orbital foramen that allows the passage of the large infra-orbital part of the zygomatico-mandibularis muscle (Fig. 4). In myomorphs, the infra-orbital foramen is reduced, but still present and intermediate in size between sciuromorph and hystricomorph morphologies (Fig. 4). Both protogomorphs and sciuromorphs lack enlarged infra-orbital foramina. In sciuromorphs, a deep masseter extends over a wide zygomatic plate and the infra-orbital part is absent (Thorington and Darrow 1996; Druzinsky 2010a; Cox and Jeffery 2011). The mountain beaver was classified into Protogomorpha on the basis of its lacking both a large infra-orbital foramen and a large zygomatic plate (Wood 1962; Druzinsky 2010a, 2010b). The apparent simplicity of infra-orbital anatomy is deceiving, and its diversity is poorly known. Several new descriptions of this system have uncovered previously unknown internal structures (e.g., Cox and Faulkes 2014; Cox and Baverstock 2016). For instance, the naked mole rat, *Heterocephalus glaber*, appears to have converged to protogomorphy in that the infra-orbital part of the zygomatico-mandibularis is not going through the infra-orbital foramen, but instead remains posterior to the lachrymal notch (Cox and Faulkes 2014). Morphological variation in the cranio-mandibular system, as reported in the naked mole rat, might be more common than expected. Indeed, pseudo-myomorphy was described on the skull of Gliridae (*Graphiurus*—Vianey-Liaud

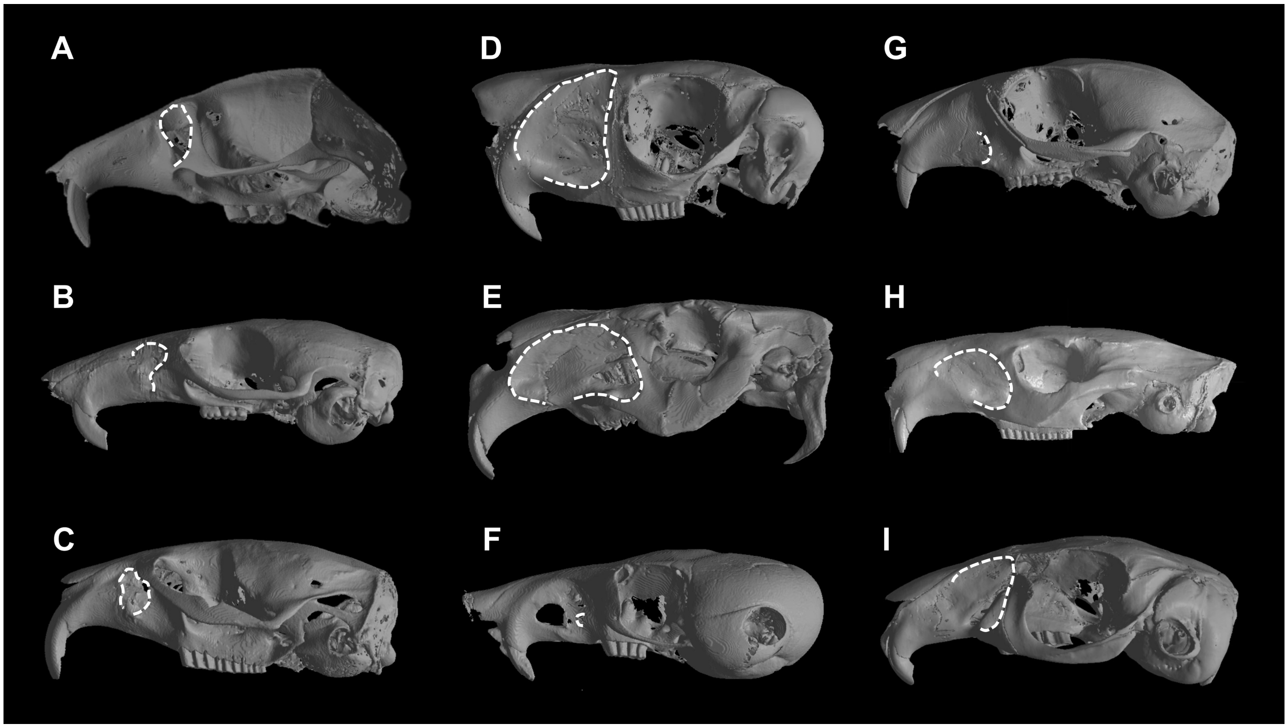

Fig. 4.—Lateral view of skulls of selected rodent species, with the area of insertion of the anterior zygomatic muscle highlighted. A) Spalacidae; B) Nesomyidae; C) Arvicolinae; D) Pedetidae; E) Caviidae; F) Heteromyidae; G) Sciuridae; H) Capromyinae; I) Ctenodactylidae.

1974; Hautier et al. 2008); an intermediary jaw between the typical hystricognath and sciurognath conditions was found in recently discovered *Laonastes aenigmamus* (Hautier and Saksiri 2009).

Despite the fact that classifications based on seemingly trenchant cranio-mandibular conditions have been used for more than a century, there have been surprisingly few studies of these traits. Among them, Woods (1972), Thorington and Darrow (1996), Hautier et al. (2011), Druzinsky (2010a, b), and Cox and Jeffery (2011) have explored the diversity of this complex system across rodent diversity. Surprisingly, the zygo-masseteric anatomy of muroids, a group that includes a large number of wild mammals as well as laboratory organisms, has barely been described (Hiiemae 1971; Satoh 1997; Cox and Jeffery 2011; Fabre et al. 2017). Recent work using dissections (Ginot et al. 2018) and new anatomical techniques, such as DICECT (Gignac et al. 2016), have opened new ways to study the cranio-mandibular apparatus, allowing inferences of masticatory biomechanical performances (Cox et al. 2012, 2013; Fabre et al. 2017), and also to explore connections between muscles and bones. Comparative anatomy has shown that homology among muscles is currently not well understood (e.g., Voss 1988:385, table 38). For example, the masseter is usually split into three layers (superficial, deep, and zygomatico-mandibularis masseters), but new parts such as the posterior temporalis (Woods 1972:129, figure 3) and the posterior masseter (Druzinsky 2010a; Cox and Baverstock 2016), that are likely to represent a structure similar to the posterior part of the zygomatico-mandibularis muscle, have been described. Future work on the cranio-mandibular system must include developmental series in order to identify muscle homologies and apomorphic character states to properly understand the evolution of this complex system.

Current Classification

The main clades detailed above falsify classifications that divide Rodentia into Sciurognathi and Hystricognathi, as the former does not form a monophyletic group. At the same time, the five main clades currently delimited by phylogenetic analyses (Fig. 3; Table 3) are mostly mirrored by the classification provided by Carleton and Musser (2005). The squirrel-related clade neatly corresponds to the suborder Sciuromorpha. Also, the three main clades within the large mouse-related clade match three of the suborders in Carleton and Musser (2005): Anomaluromorpha (Pedetidae, Anomaluridae, and Zenkerellidae), Castorimorpha (Castoridae, Geomyidae, Heteromyidae), and Myomorpha (Dipodoidea and Muroidea). Finally, the guinea pig-related clade corresponds to the suborder Hystricomorpha. Huchon et al. (2000) named this clade as the Ctenohystrica and provided molecular and morphological synapomorphies that define it. Carleton and Musser (2005) noted that, a year earlier, "Landry (1999) introduced the name Entodacrya (reflecting the internal course of the nasolacrimal duct) to identify the Ctenodactylidae-Hystricognathi clade." Carleton and Musser (2005) argued that there is no need for an exact match between the logical connotation of a taxon's name and its taxonomic intention; for instance, not all members of Carnivora are carnivorous, and neither are all Afrotheria native of Africa. Moreover, as also noted by Carleton and Musser (2005), in the majority of rodent classifications, there is an implicit distinction between taxa (e.g., Myomorpha) and the morphological condition (e.g., myomorphy) that prompted those names, which explains why Dipodidae have been nearly always placed in Myomorpha. Therefore, following Carleton and Musser (2005), we prefer to use Hystricomorpha for the guinea pig-related clade (rather than the almost ignored Entodacrya or Ctenohystrica, which in the recent literature has gained some momentum).

As a last point, the large mouse-related clade, which encompasses the anomaluromorphs, castorimorphs, and myomorphs, lacks a formal name. Recognizing the importance of formally naming large lineages to ensure rigorous scientific communication, we here erect the new suborder Supramyomorpha, and define it as the group of taxa more closely related to *Anomalurus*, *Castor*, and *Mus* than to *Cavia* or *Sciurus*. At the same time, we retain the three major groups within Supramyomorpha as the infraorders: Anomaluromorphi, Castorimorphi, and Myomorphi (Table 3).

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Concluding Remarks

A review of the recent literature shows that research at both of the main levels of rodent systematics, i.e., taxonomy and phylogenetics, is active and dynamic. First, we are in an era of species discovery that is expected to continue during the upcoming years as a result of much-needed field surveys (particularly in Africa, Asia, and South America) and revisionary work. Studies of rodent taxonomy are in particular need of multigene data and coalescent-based approaches that make use of our current understanding of species divergence processes. Certainly, the criterion of reciprocal monophyly (even for the mitochondrial genome) may be too restrictive to identify independently evolving lineages of species rank. We predict that quantifying the relative roles of incomplete lineage sorting and secondary introgression will become central issues for species delimitation, placing the more restricted concern of mito-nuclear incongruence into a broader context. At this point, it appears that, outside contact zones, incomplete lineage sorting is a more pervasive issue than secondary introgression, but studies in this respect are still insufficient.

Our review of rodent phylogenetics and classification emphasizes studies above the family level, but multiple problematic cases remain to be tackled within families. These include subfamilial relationships (e.g., those within the family Cricetidae), as well as species-dense studies of very large genera (e.g., *Rattus*, *Proechimys*, *Ctenomys*). Reduced representation and targeted enrichment methods (e.g., RAD-seq, ultra-conserved elements, exome capture, transcriptome sequencing) and full genome sequences have begun to impact areas of the rodent tree that could not be satisfactorily resolved with studies of a handful of genes. Our impression is that incomplete lineage sorting and introgression will be important below the family level and become considerably less significant for establishing relationships at higher levels. We also posit that firmly establishing gene orthology will continue to present major challenges for multigene and genomic-scale studies of higher-level rodent systematics. As noted, increased sophistication in the understanding and modeling of gene divergence will become increasingly important for higher-level phylogenetics, perhaps at the expense of the demographic assumptions required by coalescent-based methods.

Integrative studies of molecular and morphological data from both extant and extinct forms are expected to provide a more comprehensive and detailed picture of rodent diversification, including aspects of morphological evolution (e.g., modularity, rates of morphological change). In this regard, it is relevant to note that past studies in paleontology and morphology have mainly focused on dental evolution (Marivaux et al. 2002, 2004; Evans et al. 2007; Lazzari et al. 2008; Gomes Rodrigues 2015), but the integration of additional sources of evidence is required. It is possible now to access several hidden morphological characters thanks to new CT scan methodologies. Some studies of both middle and inner ears have already allowed access to key characters (Ruf et al. 2009; Mason 2015, 2016), linking morphology and ecology (Mason 2001, 2015; Pfaff et al. 2015). Chiroptera, Carnivora, Artiodactyla, and Primates have been the focus of several morphological studies using different morphological proxies, such as the inner ear (Perier et al. 2016), turbinal bones (Van Valkenburgh et al. 2011, 2014; Yee et al. 2016), braincase (Ferreira-Cardoso et al. 2017), and post-cranium (Fabre et al. 2015). Rodentia has clearly been understudied on this matter, despite its diversity allowing the implementation of large-scale comparative analyses—a situation that we expect to change in the near future.

In sum, we foresee an exciting future for the study of rodent systematics at all levels.

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SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Newly described species and genera of rodents (January 2000–December 2017) and associated data. The list includes only new available names. It does not include newly considered species or genera for which already available names apply. Newly proposed species and genera are considered even if later they were suggested to be synonyms. Changes in generic allocation are not considered (species are listed in the genus they were nominated).

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