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The valid generic name for red-backed voles (Muroidea: Cricetidae: Arvicolinae): restatement of the case for *Myodes* Pallas, 1811

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In view of contradictions in the recent literature, the valid genus-group name to be applied to northern red-backed voles—*Myodes* Pallas, 1811, or *Clethrionomys* Tilesius, 1850—is reviewed. To develop the thesis that *Myodes* (type species, *Mus rutilus* Pallas, 1779) is the correct name, our discussion explores the 19th-century taxonomic works that bear on the relevant taxa, the transition in zoological codes apropos the identification of type species, and past nomenclatural habits in cases where no type species was originally indicated. We conclude that *Myodes* is the senior name to use for the genus-group taxon that includes the Holarctic species *rutilus* and frame this conclusion within a synonymy of the genus.

Key words: *Clethrionomys*, *Evotomys*, *Lemmus*, nomenclature, taxonomy

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New genera of muroid rodents continue to be discovered and named in our modern era of systematic study, impelled in large measure by the improved understanding of phylogenetic relationship gained through gene-sequence analysis (e.g., Heaney et al. 2005; Weksler et al. 2006; Percequillo et al. 2011; Balete et al. 2012; Fabre et al. 2013), but an oversupply of old names has burdened the taxonomy of red-backed voles, a small group of Holarctic rodents (Cricetidae: Arvicolinae). The group has been recognized as distinct either at the subgeneric or generic rank since the middle 1800s (Sélys-Longchamps 1839; Keyserling and Blasius 1840; Baird 1857; Coues 1874), and its taxonomic circumscription within the arvicoline radiation receives endorsement from recent phylogenetic studies that employ gene-sequencing methodologies (Conroy and Cook 1999; Cook et al. 2004; Galewski et al. 2006; Lebedev et al. 2007; Buzan et al. 2008; Robovský et al. 2008; Abramson et al. 2009). However, certain reports in this same body of molecular research pointedly reveal that the subgenus or genus known to writers of the middle 1800s is more or less equivalent to an arvicoline tribe of closely related, morphologically similar genera (e.g., Cook et al. 2004; Lebedev et al. 2007). "Red-backed voles," as a loosely applied vernacular, is semantically a paraphyletic, if not polyphyletic, aggregation. Therefore, the following discussion strictly focuses on the valid genus-group name that should be applied to the clade that includes the northern red-backed vole, *rutilus*, and closely related species.

Three genus-group names are prominent in the early taxonomic history of red-backed voles, and all are based on the same type species, *Mus rutilus* Pallas, 1779. They are *Myodes* Pallas, 1811, type species as subsequently designated by Lataste (1883d); *Clethrionomys* Tilesius, 1850, type species as subsequently designated by Palmer (1928); and *Evotomys* Coues, 1874, type species as originally designated by Coues. The 3 genus-group taxa must be regarded as objective synonyms because they share the same type species (International Commission on Zoological Nomenclature [ICZN] 1999: Article 61.3.3), and *Myodes* Pallas, 1811, which is the senior name among them, assumes precedence following stipulations of priority (ICZN 1999: Articles 23.1, 23.3).

Both Carleton et al. (2003:96) and Pavlinov (2006:667) drew upon those nomenclatural canons to sustain their

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Table 1.—Original nominal species of generic constructs important in the early taxonomic history of lemmings and red-backed voles.

Lemmus[a] Link, 1795	*Hypudaeus*[b] Illiger, 1811	*Myodes*[c] Pallas, 1811	*Clethrionomys*[d] Tilesius, 1850	*Evotomys*[e] Coues, 1874	Current status
L. lemmus	*H. lemmus*	*M. lemmus*	—	—	*Lemmus lemmus* (Linnaeus, 1758)
L. torquatus	—	*M. torquatus*	—	—	*Dicrostonyx torquatus* (Pallas, 1779)
L. hudsonius	—	—	—	—	*Dicrostonyx hudsonius* (Pallas, 1779)
L. lagurus	—	*M. lagurus*	—	—	*Lagurus lagurus* (Pallas, 1773)
—	*H. amphibius*	—	—	—	*Arvicola amphibius* (Linnaeus, 1758)
—	*H. arvalis*	*M. arvalis*	—	—	*Microtus arvalis* (Pallas, 1779)
—	—	*M. gregalis*	—	—	*Microtus gregalis* (Pallas, 1779)
—	—	*M. oeconomus*	—	—	*Microtus oeconomus* (Pallas, 1779)
—	—	*M. saxatilis*[f]	—	—	*Microtus saxatilis* (Pallas, 1779)
L. socialis	—	*M. socialis*	—	—	*Microtus socialis* (Pallas, 1773)
—	—	*M. alliarius*[f]	—	—	*Alticola alliarius* (Pallas, 1779)
—	—	*M. rutilus*	*C. rutilus*	*E. rutilus*[g]	*Myodes rutilus* (Pallas, 1779)
L. glareolus	—	—	*C. glareolus*	—	*Myodes glareolus* (Schreber, 1780)

[a] Type species *Mus lemmus* Linnaeus, 1758, as originally fixed by absolute tautonomy (International Commission on Zoological Nomenclature 1999: Article 68.4), a rationale first appreciated and explicitly stated by Miller (1912:614), not "type by elimination" as earlier deduced by Miller (1896:36).

[b] Type species *Mus lemmus* Linnaeus, 1758, as subsequently indicated by Kretzoi and Kretzoi (2000), not *Mus glareolus* Schreber, 1780, as mistakenly listed by Coues (1877), Miller (1896), and others (see "Remarks" under "Taxonomic Summary").

[c] Type species *Mus rutilus* Pallas, 1779, as subsequently designated by Lataste (1883d).

[d] Type species *Mus rutilus* Pallas, 1779, as subsequently designated by Palmer (1928).

[e] Type species *Mus rutilus* Pallas, 1779, as originally designated by Coues (1874).

[f] These 2 species-group taxa, described by Pallas (1779) from the Lake Baikal region of south-central Russia (see Ognev 1950), have been overlooked in recent systematic compendia and faunal works (Gromov and Polyakov 1977; Corbet 1978; Corbet and Hill 1980, 1986, 1991; Honacki et al. 1982; Musser and Carleton 1993, 2005; Pavlinov and Rossolimo 1998; Abramson and Lissovsky 2012). Hinton (1926) assigned *alliarius* to *Alticola* (*Platycranius*), an allocation followed by Ellerman (1941) and Ellerman and Morrison-Scott (1951); in the account of *Alticola strelzowi strelzowi*, the latter authors (1951:674) suggested that "Possibly *Mus alliarius* Pallas … should replace this name." Kastschenko (1901) considered *alliarius* a nomen dubium (name of doubtful application), as did Ognev (1950). *Mus saxatilis* Pallas was maintained as a species of *Microtus* by Ellerman (1941) and Ellerman and Morrison-Scott (1951); in contrast, Ognev (1950) affiliated *saxatilis* with *Alticola*, provisionally placing it in synonymy under *A. macrotis*. Pavlinov and Rossolimo (1987:285) listed both names as Arvicolinae incertae sedis and characterized each as a nomen dubium. Although their equivalence to currently recognized species remains uncertain, the treatment of *alliarius* and *saxatilis* as nomina oblita seems reasonable.

[g] In his generic description, Coues (1874:187) listed *gapperi* as a variety of *Evotomys rutilus*, but subsequently (1877:142) recognized it as a subspecies.

declaration that "*Myodes* Pallas, 1811, is the valid name for the genus of red-backed voles." More recently, Tesakov et al. (2010:83) instead asserted that "*Clethrionomys* Tilesius, 1850 is the valid generic name for red-backed voles …." Their opposite conclusion rested upon the earlier usage of *Myodes* by Coues (1877), whose taxonomic treatment of North American lemmings was interpreted by Tesakov et al. (2010) as designating *Mus lemmus* Linnaeus, 1758, as the type species of *Myodes*. According to their view, *Myodes* Pallas, 1811, and *Lemmus* Link, 1795, were founded on the same type species and therefore became objective synonyms as a result of Coues's action; *Myodes* is necessarily relegated to the synonymy of the older genus-group taxon *Lemmus*; and *Clethrionomys* Tilesius, 1850, should resume its status as the senior name and valid genus for red-backed voles.

We disagree and herein restate the case for *Myodes* Pallas, 1811.

Literature Background and Nomenclatural Resources

The review by Tesakov et al. (2010) of the 19th-century literature that bears on the genus-group names applied to red-backed voles is quite good and does not warrant repetition here (also see Musser and Carleton 2005:1020–1021). See Table 1 as a reminder of the genera critical to this discussion, their authors, original specific contents, and type species. Our essay throughout references the *International Code of Zoological Nomenclature*, 4th edition (International Commission on Zoological Nomenclature 1999), hereafter contracted to the "*Code*," its authorship abbreviated as ICZN, together with the year and relevant article. The *Mammalian Species* account on constructing synonymies (Gardner and Hayssen 2004) provides a highly readable introduction to many of the nomenclatural issues covered herein, especially their lucid summary of type species. We also consulted earlier nomenclatural works to gain insight to the criteria that may have guided our 19th-century predecessors in rendering their taxonomic decisions. The Stricklandian or British Association Code (Strickland et al. 1843), formulated by a committee impaneled by the British Association for the Advancement of Science; a French code, *De la nomenclature des êtres organisés*, sponsored by the Société Zoologique de France (Chaper 1881); the initial Code of Nomenclature adopted by the American Ornithologists' Union (Coues et al. 1886); and the *Règles internationales de la Nomenclature zoologique* (ICZN 1905, 1926), adopted by the 5th International Congress of Zoology, proved most helpful. The *Règles internationales*, supplemented by interim amendments, was the forerunner to the extensively altered 1st edition of the *International Code of Zoological Nomenclature* (ICZN 1961). We cannot interview Elliott Coues (1842–1899), but some understanding of his nomenclatural and taxonomic approach can be gleaned from

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his official writings on the topics. Coues was chair of the committee that produced the American Ornithologists' Union Code of Nomenclature (Coues et al. 1886), and he was an editorial contributor to *The Century Dictionary* (Whitney 1889–1891; hereafter abbreviated *TCD*). This monumental work served not only as a dictionary of the English language, but also, as noted in the Preface (Whitney 1889, Vol. I:v), "a more complete collection of the technical terms of the various sciences, arts, trades, and professions." Specifically, Dr. Coues is credited (Whitney 1889, Vol. I:xiii) for terms and definitions relating to the biological sciences, "including systematic zoology" and "new Latin names of classificatory groups as are essential to a serviceable presentation of zoölogy and botany."

The Central Argument of Tesakov et al. (2010)

Tesakov et al. (2010:85) framed their essential argument as follows (boldfaced and italicized emphases are theirs): "He [Coues 1877] gave a detailed description of the genus *Myodes* and noted that the '*... foregoing diagnosis, so drawn as to exclude Cuniculus* [=*Dicrostonyx*], *is based on Mus lemmus of Linnaeus, and indicates a perfectly natural generic group of Arvicolinae*,'" and in consequence "**this action of Coues (1877: p. 239) constitutes a subsequent designation of *Mus lemmus* as the type species of the genus *Myodes***." The italicized quotation from Coues (1877) exemplifies but one among many of the taxonomic puzzles and knotty nomenclatural decisions that he and Joel Asaph Allen faced in composing their several *Monographs of North American Rodentia* (Coues and Allen 1877). However, Coues's statement cannot be construed as a subsequent designation of a type species for *Myodes*, and we are uncertain about what word choice in Coues's expression led the authors to their boldfaced, albeit mistaken, conclusion.

Coues's deliberate employment of the term "diagnosis" and pointed comparative discrimination must be understood within the historical context of the taxonomic changes that he was proposing. At the time, comprehension and classification of North American mammals rested upon Spencer F. Baird's (1857) magnum opus, which Coues regularly acknowledged as the starting point for his own taxonomic interpretations. Writing 20 years later, Coues (1874, 1877) was instituting certain radical departures, particularly at the genus-group ranks, from Baird's taxonomy of "Muridae," which then contained elements of the Arvicolinae, Neotominae, and Sigmodontinae, 3 subfamilies now placed in the family Cricetidae (e.g., see Musser and Carleton 2005). Whereas Baird grouped North and Central American harvest mice in *Reithrodon*, Coues (1874) placed them in his newly created genus *Ochetodon* (now a synonym of *Reithrodontomys* Giglioli, 1874) and differentially diagnosed it (Coues 1877:120–121) to exclude the South American taxa *Reithrodon* and *Euneomys*. Whereas Baird treated deermice as species of *Hesperomys*, without distinction from South American groups, Coues (1874) circumscribed North American deermice within his new subgenus *Vesperimus* (its synonymy with *Peromyscus* Gloger, 1841, was then unappreciated). Whereas Baird maintained the brown, collared, and bog lemmings within the single genus *Myodes*, citing the classification of Keyserling and Blasius (1840) for European forms, Coues (1874, 1877) elevated both the bog lemmings (*Synaptomys*) and collared lemmings (*Cuniculus* [= *Dicrostonyx* Gloger, 1841]) to separate genera and accordingly emended their diagnoses with respect to brown lemmings, which he placed in the genus *Myodes*. Whereas Baird classified red-backed voles under *Arvicola* (*Hypudaeus*), again following Keyserling and Blasius (1840), Coues (1874) erected the new genus *Evotomys* and later expanded his generic diagnosis (1877:132) to segregate them from meadow voles, genus *Arvicola* (equivalent to *Microtus* as now recognized). Coues's taxonomic changes collectively provided the earliest glimpse into the level of endemism that characterized North American Rodentia and brought some taxonomic empiricism to the notion of a biogeographic division between Nearctic and Neotropical rodent assemblages.

Coues (1877) used the term "diagnosis," for example, as quoted above apropos *Myodes*, consistent with the definition supplied in the Glossary to the *Code* (ICZN 1999:103):

> **diagnosis**, *n*. A statement in words that purports to give those characters which differentiate the taxon from other taxa with which it is likely to be confused.

The *Code*'s definition of diagnosis entirely concords with Coues's own, which he formulated a century earlier in *TCD* (Coues in Whitney 1889, Vol. II:1588; his crisp remarks on "description," "definition," and "diagnosis" and their shades of meaning in systematic discourse are still insightful, if somewhat dated). Although the *Code* now prescribes that a diagnosis should accompany the naming of new taxa (ICZN 1999: Article 13, Recommendation 13A), the word's utility in systematic study is by no means limited to such a role. To allocate the collared lemmings (*Cuniculus*) to a genus distinct from brown lemmings (*Myodes*), Coues (1877:239) was careful to substantiate their differentiating traits—a "diagnosis, so drawn as to exclude *Cuniculus*"—and quite naturally used *Mus lemmus* Linnaeus, 1758, then a commonly known member of *Myodes* (Table 1), as his standard for morphological comparisons. In fact, he sedulously presented either essential characters or a literal "diagnosis" at the beginning of each of his generic and specific treatments throughout his monograph on North American Muridae, often giving the specific "Diagnosis" in Latin as was conventional for the era. Given the standard format of his taxonomic accounts, therefore, Coues's representation of the differentiating characters for *Myodes* as a "diagnosis" is unremarkable, hardly interpretable as a purposeful "action" for type-species fixation as maintained by Tesakov et al. (2010). Taxa such as *Myodes*—or *Neotoma*, or *Sigmodon*, *Synaptomys*, *Cuniculus*, *Evotomys*, etc.—had already been described (at least in some nominal fashion), published upon as far as the early codes were concerned

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(Strickland et al. 1843; Coues et al. 1886), and were properly available for classificatory purposes. Coues's intent was to encapsulate the differentiating traits of (i.e., diagnose) those North American taxa that he regarded as valid genera and species. In so doing, he substantially improved the morphological definitions of North American rodents and brought much-needed clarity to their taxonomic recognition compared with the 1857 classification of his mentor and close friend Spencer Baird (Coues christened his firstborn son Elliott Baird Coues—Allen 1909).

Although Coues's 1877 synopsis is a hallmark achievement in systematic comprehension of North American rodents, his thorough account of *Myodes* is insufficient for subsequent designation of a type species, nor do we believe that he ever intended to do so. Pallas (1811) did not indicate a type species when he named the genus *Myodes* (i.e., an original designation of the type—ICZN 1999: Article 68.2), a common omission for that era of zoological investigation but an omission no longer permissible in genus-group descriptions (i.e., after 1930 per Article 67.4.1). Consequently, retention and application of Pallas's genus became acceptable only through a subsequent designation of the type species (ICZN 1999: Article 69.1), one chosen among the nominal species originally included within it (ICZN 1999: Article 67.2). Today the 10 nominal species that Pallas (1811) originally arranged within *Myodes* represent 6 genera according to current taxonomic consensus (Table 1); absent clear attachment to a single species, definition of the taxon would be nonsensical and its meaningful usage in systematic investigation impossible. The *Code* intends that "designation" be understood in a rigid sense (ICZN 1999: Article 67.5): It requires that an author explicitly state that some original nominal species is the "type or type species, or uses an equivalent term, and if it is clear that that author accepts it as the type species" when providing a subsequent designation (ICZN 1999: Article 69.1.1). Coues's (1877) provision of a diagnosis for *Myodes*—based on the exemplar species *Mus lemmus* and expressly crafted to dispel confusion with the morphologically similar *Cuniculus*—does not equate to fixation of a type species according to the narrow strictures laid out by the *Code*. Although Tesakov et al. (2010) linked the words "*Mus lemmus*" and "type species" of *Myodes* in their own sentences, Coues (1877) himself did not, nor did he mention the words "type" or "type species" anywhere in his account of *Myodes*. That basic fact embodies the crux of the argument for dismissing Coues's (1877) treatment of *Myodes* as a clear and deliberate action to designate *Mus lemmus* as the type species.

Coues was wholly conversant with the notion of types and a capable practitioner of the concept in acknowledging or designating type species in his own taxonomic contributions (also see Coues's extended explanation of type species in *TCD* [Whitney 1891, Vol. VI:6562]). His 1877 classic is replete with acknowledgments of type specimens, type species, and type genera in his accounts of species and subspecies, genera and subgenera, families and subfamilies, respectively. Sometimes Coues (1877:132) isolated the type species as a subheading in a taxonomic account, for example, "Type.—*Mus rutilus*, Pallas" for the genus *Evotomys*. More commonly, Coues listed the type species within a subgeneric or generic synonymy, such as "*Neotoma*, Say & Ord, Journ. Acad. Nat. Sci. Phila. iv, pt ii, 1825, 346 (type, *N. floridana*)"—p. 7; "*Onychomys*, Baird, M[ammals of]. N[orth]. A[merica]. 1857, 458 (type, *Hypudaeus leucogaster*, Max[imillian zu Wied-Neuwied].)"—p. 105; "*Oryzomys* Baird, M. N. A. 1857, 458; type, *Mus palustris*, Harl[an]."—p. 111. In discussing Waterhouse's (1839) creation of *Hesperomys*, Coues (1877:44) even used "type" in an explicit statement that legitimately serves as a subsequent designation: "We may therefore, with entire propriety, elect *Mus bimaculatus* as technically the type of *Hesperomys*." Measured against this abiding concern for taxonomic foundation that permeates the 1877 publication, the absence of a type within the synonymy of *Myodes* (Coues 1877:237) or mention of type species within the generic account is instructive. Note that Coues (1877:243) did indicate a type for *Cuniculus* ("Type, *C. groenlandicus* = *C. torquatus*"), the generic construct he accepted for the collared lemmings that he isolated from *Myodes*, contra Baird (1857). Although Tesakov et al. (2010:85) might affirm that "There is no doubt that Coues regarded *Mus lemmus* as the type species of the genus *Myodes*," Coues's own taxonomic habit casts substantial doubt on their affirmation. Where is the clarity that an author, in this case Coues (1877), has accepted a particular species that he/she subsequently designated as the type species as stipulated by the *Code* (ICZN 1999: Article 69.1.1): ". . . and if it is clear that that author accepts it as the type species"?

We believe that Coues (1877) exercised reasoned restraint and purposely omitted a type species in the *Myodes* account because he lacked access to critical older literature that might have illuminated the issue. He (1877:240) was appropriately aware that, "Like that of other genera known in early zoological times, the synonymy of *Myodes* is involved." With regard to which genus had priority for North American brown lemmings, Coues (1877:240) further supposed that "The choice, then, narrows to *Myodes* and *Lemmus*; *we have not the authorities at hand to decide the case* [italics ours], but the balance of opinion is in favor of *Myodes*." Instead, the balance of evidence, not opinion, as supplied by later systematists has swung to *Lemmus* Link, 1795 (Table 1), a genus and publication date unfamiliar to most naturalists in the middle 1800s. Oldfield Thomas (British Museum of Natural History, London) had alerted Gerrit S. Miller (United States National Museum, Washington [USNM]) to the seniority of *Lemmus* (type species = *Mus lemmus* Linnaeus, as fixed by absolute tautonomy—ICZN 1999: Article 68.4), the genus that Miller (1896:13–14) adopted in his pivotal work entitled "The genera and subgenera of voles and lemmings" and cemented its usage thereafter in mammalian systematics (e.g., Trouessart 1898; Hinton 1926; Ellerman 1941; Simpson 1945). At the species level within *Myodes*, Coues (1877:240) demonstrated similar reserve, accepting Middendorff's (1853) recognition of valid species and applying a name based on an Asian taxon, *M. obensis*, as senior synonym for North American forms (e.g.,

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trimucronatus): "But this [synonymy of Old and New World brown lemmings] is a question we do not propose to enter upon here; our business being simply the determination of the North American species."

We grant that our attribution of intent to Coues's treatment of *Myodes* in this particular regard, like that of Tesakov et al. (2010), ultimately hinges on conjecture (although we believe that our inference is more firmly grounded). Ineradicable aspects of ambiguity or uncertainty are regrettably inherent in many generic descriptions of the early 1800s, a circumstance that precisely underscores why recent codes have hewn to ever more rigid standards for interpreting subsequent designation and for requiring direct mention of "type or type species," conditions not met in Coues's account of *Myodes*.

Coues's (1877) uncertainty over the priority of *Myodes* versus *Lemmus* echoed the nomenclatural dilemma that confronted his predecessor Spencer Baird, who explained (1857:554), "Not having access to all the authorities, I am unable to say whether the name of *Myodes* or *Lemmus* should be retained for this group [North American lemmings sensu lato]." Baird ultimately accepted *Myodes* and the generic scope adopted by Keyserling and Blasius (1840) in their faunal compendium of European vertebrates. Baird (1857:554) continued, "In the absence of any specimens of typical *Myodes* from America, I am obliged to select one of the European species for the illustration of the genus. Of the four species in the collection of the Smithsonian Institution, *M. lemmus*, *torquatus*, *obensis*, and *schisticolor*, I choose the first mentioned as the best known type." Baird's usage of "type" in this context does not carry a binding nomenclatural connotation, but rather is intended in the sense of "kind," "form," or "exemplar," as he made clear in his prefatory remarks on comparative and descriptive procedures (Baird 1857:xxvii):

> A few words of explanation of the plan adopted in preparing the articles of the present report may not be out of place. I have usually made the entire detailed description of the species from one particular specimen (often indicating it by number), mentioning afterwards the variations presented from this type by the others before me. The specific diagnoses alone contain a combination or selection of the characters of several specimens.

Examples of Baird's (1857) comparative usage of "type" follow (emphases ours).

- P. 81—"Taking the panther or cougar (*Felis concolor*) as the *type* of the American cats, the dental formula is as follows:"
- P. 217—"In describing the skulls of the bears it will be better to select as the *type* one of middle age, and afterwards indicate the variations in the very old and the very young ones."
- P. 226 (under *Ursus americanus*)—"The specimen selected as the *type* of the skull in this species is No. 897, from St. Lawrence county, New York."
- P. 461 (introduction to *Hesperomys leucopus*)—"I have taken the white-footed mouse of Massachusetts as my *type* in describing the species on account of the very large series of specimens on hand ...."
- P. 577 (morphological description of *Lepus glacialis*)—"Taking an adult in winter as the *type*, the head is much arched and broad."

"Type" in these examples, and numerous other instances in Baird's 1857 tome, is used as a standard of comparison, not the actual type specimen or type species. Compared with today's disciplined vocabulary of taxonomic description, Baird's usage of "type" is imprecise, even misleading if taken out of context, and may partially explain why Coues (1877) was so diligent in identifying actual type specimens and type species in his accounts of North American rodents. Indeed, the task would fall to Coues (1877) and later catalogers of USNM types (especially Lyon and Osgood 1909) to tidy-up the key foundational elements of Baird's species- and genus-group descriptions.

Contrast the equivocal case for identifying a type species of *Myodes* as the genus was reported by Baird (1857) or Coues (1877) with the manifestly interpretable action implemented by Fernand Lataste (1883d). In a review of French voles, Lataste (1883a) supplied a key to the 7 species he recognized, apportioned among 4 subgenera of *Microtus*, and then reviewed past taxonomic studies, beginning with Linnaeus (1758), for the availability of names that should be applied. Common voles, red-backed voles, steppe lemmings, and lemmings were represented among the original specific contents of the genus *Myodes* as conceived by Pallas (1811; see Table 1). Lataste (1883b), however, acknowledged Sélys-Longchamps (1839) as the conceptual model for restricting *Myodes* Pallas, 1811, to red-backed voles instead of lemmings, the taxonomic signification employed by Keyserling and Blasius (1840), and gave a morphological definition of *Microtus* (*Myodes*) as he and Sélys-Longchamps recognized the subgenus (rooted molars, proportional features [ears, eyes, tail], plantar tubercle number, mammary formula, and terrestrial habit). His literature review (Lataste 1883b, 1883c) acknowledged other genus-group taxa that had been applied to red-backed voles, including *Hypudaeus* (Baird 1857 and Blasius 1857, as subgenus; Fatio 1869, as genus) and *Evotomys* (Coues 1874, 1877, as genus) and concluding with a subgeneric synonymy of *Myodes* (Fig. 1). Nevertheless, both Lataste (1883a, 1883b, 1883c, 1883d) and Coues (1877) overlooked *Clethrionomys*, named by Tilesius (1850) to embrace 2 species of red-backed voles (Table 1), but without mention of a type species, an omission later corrected by Palmer (1928). Because Lataste (1883a) was aware that many nominal species within Pallas's *Myodes* had been previously removed to other genera—namely, *Lemmus* (in this instance *Lemmus* sensu Tiedemann, 1808, not Link, 1795), *Microtus*, or *Arvicola*—he (Lataste 1883d:349) deliberately indicated *Mus rutilus* Pallas as type species in his summary table for *Myodes* (Fig. 1) to preserve the genus-group name (Lataste 1883d:348): "Je fais suivre chacun d'eux de sa synonymie, et j'indique: 1°

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LE NATURALISTE

Premier sous-genre.

MYODES

1811. < Myodes Pallas, *Zoographia*, p. 173.
1814. < Brachyurus Fischer, *Zoognosia*, ed. III, v. III, p. 55.
1839. = Myodes Sélys, *Micromammalogie*, p. 87.
1845. < Hypudæus Nillsson, *loc. cit.*, p. 34 (non Illiger, 1811).
1857. = Hypudæus Blasius, *Fauna*, p. 336.
1874. = Evotomys Coues, *Monographs*, p. 131.
Espèce type : *rutilus* Pallas.
Espèce française : *glareolus* Schreber.

Fig. 1.—Portion of Lataste's (1883d:349) classificatory table as published in *Le Naturaliste*, in which he indicated the type species, *Mus rutilus* Pallas, of his 1st subgenus *Myodes*, genus *Microtus*. Symbols employed in the subgeneric synonymy, less than (<) or same as (=), compare the taxonomic scope of *Myodes* as defined by Lataste with taxonomic arrangements of previous authors. For example, *Myodes* sensu Lataste was narrower in definition than that used by Pallas (1811), who also included species of lemmings and common voles (see Table 1), but was the same as the taxon was intended by Sélys-Longchamps (1839) or its objective junior synonym *Evotomys* (type species, *Mus rutilus*) described by Coues (1874), both of whom restricted the contents to species of red-backed voles.

son espece type; 2° ses autres espèces françaises" (= I follow each of them [the 4 subgenera] with its synonymy, and I indicate: 1st, its type species; 2nd, other species in France). Lataste's alert designation of a type species in order to anchor the taxonomic definition of *Myodes* likely stemmed from his participation on the nomenclatural committee convened by the Société Zoologique de France and chaired by his colleague Maurice Chaper. Chaper's (1881) *De la nomenclature des êtres organisés* is conceptually important in advancing the international rules of zoological nomenclature that we accept today (e.g., see Melville 1995:15–17; Dayrat 2010:210–211).

In summary, we continue to regard *Myodes* Pallas, 1811, as the proper genus for red-backed voles (i.e., *Mus rutilus* Pallas and related species) because:

A) Lataste (1883d:348) signaled his intention to indicate type species for the subgenera of voles that he considered valid, conforming to the law of priority, and did so (p. 349) by labeling *Mus rutilus* Pallas as type species of *Myodes* in his classificatory table (Fig. 1). In a broader synthesis of Old and New World voles (*Microtus* sensu lato), Lataste (1886:271) repeated his definition of the subgenus *Myodes* and reiterated *Mus rutilus* Pallas as its type species, demonstrating his acceptance of its stature and his role in fixing it as type (ICZN 1999: Article 91.1.1).
B) Coues (1877) nowhere used the words "type" or "type species" in a nomenclatural context in his treatment of *Myodes*. He formulated a diagnosis for *Myodes*, based on characters exhibited by *Mus lemmus* Linnaeus, to clarify morphological separation of brown lemmings (*Myodes*) from collared lemmings (*Cuniculus* [= *Dicrostonyx*]), a taxonomic innovation of his work in contrast to the classification of his predecessor Baird (1857). Coues's reference to "diagnosis" does not amount to an intentional nomenclatural act to designate a type in a work wherein he employed that term, as noun or verb, in the taxonomic accounts of the rodent genera and species that he considered valid. That Coues did not list a type species in his synonymy of *Myodes*, a nomenclatural detail that he commonly provided in his other generic synonymies, tellingly conveys his uncertainty regarding the applicability of this name and incomplete knowledge of earlier literature that may (or may not) have sustained its usage for the taxon including brown lemmings. Coues's account of *Myodes* fails to meet the high bar that the *Code* now sets for an unambiguous subsequent designation of a type species (ICZN 1999: Articles 67.5, 69.1.1).
C) *Myodes* Pallas, 1811, is the oldest genus-group name whose definition rests upon the type species *Mus rutilus* Pallas, 1779, according to the subsequent designation by Lataste (1883d). *Myodes* antedates *Clethrionomys* Tilesius, 1850, and *Evotomys* Coues, 1874, both taxa also having *Mus rutilus* as their type species, the former by subsequent designation (Palmer 1928) and the latter by original designation (Coues 1874). According to present understanding, the clade of red-backed voles that includes the species *rutilus* and its closest relatives takes the generic appellation *Myodes*.

Interesting but Extraneous Points

In addition to their central argument, discussed above, Tesakov et al. (2010) related ancillary information meant to amplify the case for *Myodes* as a junior synonym of *Lemmus* or to reinstate *Clethionomys* as the valid generic name for red-backed voles. Although noteworthy as historical anecdotes, these subsidiary arguments are extraneous to the criteria deemed strictly relevant according to the *Code*. Nonetheless, some merit comment for expansion, clarification, or contradiction.

In reviewing the early literature, Tesakov et al. (2010:84) remarked that "there was a long-standing, though quite regional tradition of referring red-backed voles to the genus *Myodes* Pallas, 1811 based on the informal usage of *Arvicola* (*Myodes*) by de Sélys-Longchamps (1839)." From the late 18th through the middle 19th century, ALL of our taxonomic literature was "quite regional." In an era when communication among scientists was transmitted by means of slow-speed sailing ships, not by high-speed Internet, it is understandable that provincial differences and regional viewpoints would characterize much early taxonomy and hamper integrative biological investigation. This weakness, along with myriad other taxonomic inconsistencies and eccentricities that existed

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among countries and continents, motivated early attempts to create a universally applicable, internationally acceptable system of zoological nomenclature (see overviews by Melville 1995 and Dayrat 2010). Thus, the forward-looking British Association Code would boldly suggest that new genera and species be "*extensively* circulated in the first instance [of their description]" (Strickland et al. 1843:274, Recommendation F), a suggestion only now fully realized 150 years later thanks to the worldwide Internet. Notwithstanding the regional flavor of *Myodes* as initially restricted by Sélys-Longchamps (1839), Lataste's (1883a, 1883b, 1883c, 1883d, 1886) taxonomic formalization of *Myodes*, as a subgenus of *Microtus*, satisfies current requirements of the *Code* to secure the name and individuate its taxonomic meaning; moreover, Lataste's literature review and synonymy (Fig. 1) demonstrated his broad understanding of red-backed voles as classified in other parts of the world, not simply France or western Europe.

"Their [= Carleton et al. 2003; Musser and Carleton 2005; Pavlinov 2006] premature usage of *Myodes* instead of *Clethrionomys* . . . has unfortunately led to taxonomic instability and discontinuity in scientific usage in a very widespread group of organisms" (Tesakov et al. 2010:84). For a taxon the type species of which had been designated 120 years ago (Lataste 1883d), which action was acknowledged 50 years ago (Kretzoi 1964), and which priority has been either subsequently referenced or actually employed in the literature (e.g., Kretzoi 1969; Pavlinov and Rossolimo 1987, 1998; Zagorodnyuk 1990; Kretzoi and Kretzoi 2000), return to the usage of *Myodes* seemed long overdue from our perspective, not premature. We have appreciated the opportunity to reflect further on this issue, as occasioned by the thoughtful evaluation of Tesakov et al. (2010), but as explicated above, our conviction that *Myodes* Pallas is the correct generic name to use for red-backed voles has only been reinforced as a result. In the next section, we shall address the notion of "taxonomic instability and discontinuity in scientific usage."

Tesakov et al. (2010:84) devoted a paragraph to Pallas's (1811) concept of *Myodes*, which originally embraced 10 species (Table 1), and helpfully illustrated a criterion that early taxonomists improvised to interpret "typical" when no type species was originally designated: the order of species listed by an author when the new genus was created. As elaborated by Tesakov et al. (2010:84), ". . . more typical forms were usually mentioned first. Among characteristic features of *Myodes* Pallas noted 'ear hidden in fur' and 'shortened tail.' Indeed, the two first listed species (*lemmus*, *torquatus*) have very small hidden ears, and very short tails thus strongly expressing the typical characters of the group." Or for the sake of argument, we might note that the literal meaning of *Myodes*—"mouse-like form" per *TCD* (Whitney 1890, Vol. IV:3919) or simply "mouse-like" per Palmer (1904:439)—may have guided Pallas's choice of the generic epithet based on the conspicuous pinnae and relatively long tail of the last-listed *rutilus*. Coues appropriately underscored the subjectivity inherent in this method of determining a type, dismissing it as "mere convention, which often becomes an absurdity" (Coues in Whitney 1891, Vol. VI:6562). Post hoc attempts to guess an author's meaning of "typical" are ultimately futile for many of the broad generic constructs created in the early 19th century, genera that included morphologically diverse and distantly related species as informed by subsequent decades of systematic research. To avoid inconsistency and subjectivity in taxonomic interpretation of such early names, zoological codes have mandated clear indication of a type species in any subsequent designation for older genera that lack a type (ICZN 1999: Articles 67.2, 69.1); to avert such problems from ever recurring, the *Code* now requires explicit provision of a type species for new descriptions of genus-group taxa described after 1930 (ICZN 1999: Article 67.4.1). The usage by Keyserling and Blasius (1840) of *Myodes* to contain only lemmings (*lemmus*, *obensis*, *torquatus*) and lemming-like species (*lagurus*) was plausibly based on a species-listed-first rationale and set the precedent for employing the genus in this taxonomic sense (Miller [1896] would later resurrect *Lemmus* Link, 1795, from obscurity and confirm its seniority for brown lemmings). Keyserling and Blasius, however, did not attach designation of a type species to their account of *Myodes*, nor did Baird (1857) or Coues (1877). Lataste (1883d) did, and he did so in a deliberate and unequivocal manner (see Fig. 1).

Tesakov et al. (2010:84) acknowledged Sélys-Longchamps (1839) for originating the alternative interpretation of *Myodes* variously observed during the middle 1800s when he associated the taxon with red-backed voles instead of lemmings. They emphasized that Sélys-Longchamps himself had "stressed the non-taxonomic essence of his groupings," dividing European voles among informal "sections" and "groups" within *Arvicola* instead of assigning them to formal subgenera. We hasten to point out that Sélys-Longchamps's (1839) *Études de Micromammalogie* was a mature synthesis of European shrews and rodents—authorship and issues of priority were heeded, generic and specific synonymies, together with diagnoses and morphological descriptions, were provided for taxa considered valid, measurements were supplied and crania illustrated; he simply declined to go below the rank of genus in developing his formal classification. Of course, Sélys-Longchamps's wishes on this account cannot suppress future taxonomic judgments implemented by subsequent researchers who otherwise fulfill the requirements of publication, a binomial format, attention to priority, and other nomenclatural protocols. Lataste (1883b:333) frankly admired Sélys-Longchamps and paid homage to the man's contributions for influencing his own classification of voles. Sélys-Longchamps's (1839:87) admonition apropos the future recognition of *Myodes* as a subgenus or genus is an ironic footnote in the classificatory history of red-backed voles, but it remains immaterial to the legitimate subsequent designation of a type species effected by Lataste (1883d; Fig. 1).

Conclusion 5 of Tesakov et al. (2010)

Of the 5 conclusions enumerated by Tesakov et al. (2010:85), points 1 through 4 have been addressed in our

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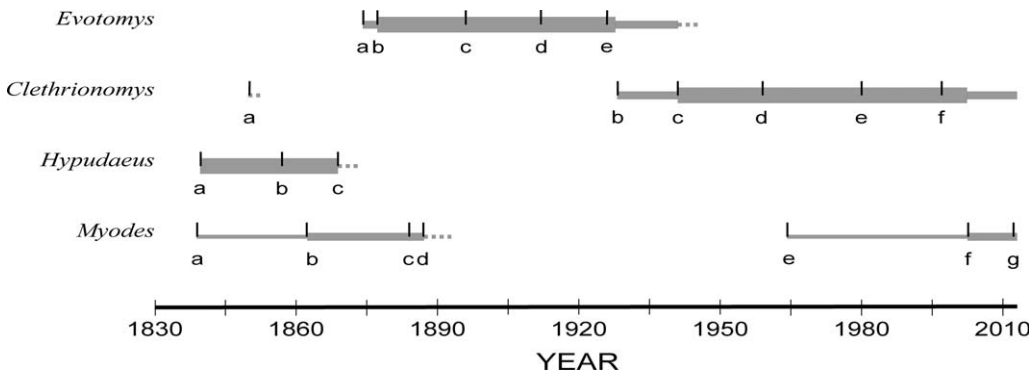


Fig. 2.—Timeline of the 4 genus-group names applied to red-backed voles over their 174-year taxonomic history. Lettered tick-marks indicate dates of important publications discussed in the text or otherwise influential works relevant to the usage of the 4 taxa: *Evotomys* (a, Coues 1874; b, Coues 1877; c, Miller 1896; d, Miller 1912; e, Hinton 1926); *Clethrionomys* (a, Tilesius 1850; b, Palmer 1928; c, Ellerman, 1941; d, Hall and Kelson 1959; e, Corbet and Hill 1980; f, McKenna and Bell 1997); *Hypudaeus* (a, Keyserling and Blasius 1840; b, Baird 1857; c, Fatio 1869); and *Myodes* (a, Sélys-Longchamps 1839; b, Fatio 1862; c, Lataste 1883d; d, Lataste 1886; e, Kretzoi 1964; f, Carleton et al. 2003 and Pavlinov 2003; g, Abramson and Lissovsky 2012). The comparative widths of the timelines represent our impression of relative usage.

foregoing section on "The Central Argument." Point 5, quoted verbatim below, is involved and deserves extended comment.

> 5. Although the validity of *Clethrionomys* follows directly from the regulations of ICZN, to avoid further instability in taxonomic usage in this group of voles, stemming from possible new discoveries in old literature, it is proposed to consider the future inclusion of the name *Myodes* with the type species *Mus lemmus* Linnaeus, 1758 in the *List of Available Names in Zoology*.

Yes, the *availability* of *Clethrionomys* Tilesius, 1850, is covered by regulations of the *Code*, and its applicability to red-backed voles issues from the subsequent designation of its type species, *Mus rutilus* Pallas, 1779, by Palmer (1928). However, its *validity* as the proper genus to embrace red-backed voles is superseded by *Myodes* Pallas, 1811, whose taxonomic definition is based on the same type, *Mus rutilus*, as subsequently designated by Lataste (1883d), as we have explained above.

The *Code* too is concerned with stability. Adherence to the Principle of Priority (ICZN 1999: Article 23) to adjudicate the valid name of taxa considered to be synonyms is generally preferred, but not mandated as absolute and forever inviolable. Familiar junior synonyms in prevailing usage can be maintained when both conditions of Article 23.9.1 are jointly satisfied to reverse the principle of priority: The senior synonym cannot have been used as a valid name after 1899 (nomen oblitum), and the junior synonym must have been used extensively as the prevailing name. In 1964, Kretzoi reminded the systematic community of Lataste's (1883d) type-species selection, reasserted the priority of this narrower definition of *Myodes* Pallas, 1811, and allocated *Clethrionomys* Tilesius, 1850, and *Evotomys* Coues, 1874, among its junior synonyms. In the middle to late 1900s, *Myodes* was infrequently, never predominantly, recognized as the valid genus of red-backed voles (see references in Musser and Carleton 2005). Past nomenclatural panels and commissions have uniformly encouraged the propriety of crediting our predecessors for their taxonomic contributions, taking the form of the "law" of priority, and authors of the current *Code* have allowed a century-wide window for taxonomists to express retrospective judgment before a taxon can be declared a nomen oblitum (forgotten name). Personally, we would find it illogical to label *Myodes* as a "forgotten name" when it was adopted as a valid name of lemmings (incorrectly in hindsight) over much of the 19th century, when it has been regularly listed in generic synonymies throughout the 20th century, and when subsequent designation of its type species resulted from a carefully considered, purposeful nomenclatural decision (Lataste 1883a, 1883b, 1883c, 1883d). Our personal views aside, *Myodes* cannot be legitimately discarded as a nomen oblitum because of Kretzoi's 1964 contribution and the sporadic usage of *Myodes* as the valid senior synonym that followed (ICZN 1999: Article 23.9.1.1). We find it ironical that were current regulations of the *Code* operational at the time Palmer (1928) lifted *Clethrionomys* from obscurity, that name may well have been suppressed as a nomen oblitum, and mammalogists today would be using *Evotomys* Coues.

In an engaging overview of nomenclatural debates that have unfolded since Linnaeus (1758), Dayrat (2010:218) observed that "one of the reasons that nomenclature is unstable is that the history of taxon names is highly complex in all taxa ...." His observation aptly characterizes the instability that has marked the 174-year taxonomic history of red-backed voles and the variety of genus-group names applied to them over the course of that history (Fig. 2). Since Sélys-Longchamps (1839) circumscribed red-backed voles as the "Group" *Myodes* within a broadly conceived *Arvicola*, 2 or 3 names have been used simultaneously for the genus-group taxon. Three of those names have enjoyed serially prevailing usage—beginning with *Hypudaeus* (approximately 30 years), followed by *Evotomys* (approximately 50 years), and then *Clethrionomys* (approximately 65 years)—and *Myodes* has overlapped all 3 as it has

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been doggedly recognized as valid by some systematists. The long interruption in employment of *Myodes* for designating red-backed voles approximates the barren span in usage of *Clethrionomys* (Fig. 2). Before Palmer (1928) uncovered *Clethrionomys* Tilesius, 1850, the name had demonstrably disappeared from taxonomic dialogue (e.g., not mentioned by Baird 1857; Coues 1877; Lataste 1886; Miller 1896, 1924; Trouessart 1898; Hinton 1926). *Myodes*, on the other hand, continued to be recognized, albeit erroneously as a synonym of *Lemmus* because the subsequent type designation by Lataste (1883d) had been overlooked, ignored, or unappreciated (see "Remarks" below in the "Taxonomic Summary"). To be sure, the zoological community's attitudes about absolute priority, conservation of junior names, and statutes of limitation for declaring nomina oblita have varied over the decades as reflected in past zoological codes (see review in Dayrat 2010:216–218). Our understanding of these matters and restatement of the case for *Myodes* Pallas accord with articles and definitions found in the current *Code* (ICZN 1999), which supersedes all early codes and previous editions of this *Code* (ICZN 1999: Article 86).

Because we humans are a social species, there is, expectedly, a normative generational view inherent in complaints about taxonomic instability. We empathize with Tesakov et al. (2010) and their concern on this account. The four of us are old enough (Yikes!) to remember the disgruntlement voiced by our major professors over the replacement of the long-familiar name for ground squirrels, *Citellus*, by *Spermophilus*. Nowadays, mammalogists worldwide use *Spermophilus* without giving any thought to the immemorable nomenclatural reasons for the change (see ICZN 1956). Researchers know that published data on ground squirrels must be sought under the generic tags of *Citellus* and *Spermophilus* (or now 8 genera fide the revision of Helgen et al. 2009). This is just an elementary requisite of doing research, a requirement made vastly easier with the advent of the Internet, the powerful search engines at hand, and rapid progress in digitization of the legacy literature of taxonomy. Raw results returned from literature searches of Google Scholar (http://scholar.google.com, accessed October 2013) for *Clethrionomys* and *Myodes* show that the former genus has remained in prevailing usage over the past decade, although the latter's global acceptability has risen to about 50% of articles published in 2011–2012 (Fig. 3). The slow pace of change in these trend-lines may reflect the inertia against changes in taxonomic habit within large and heterogeneous populations of scientists. The majority of scientists who happen to study red-backed voles will care little about the nomenclatural contretemps of *Clethrionomys* vis-à-vis *Myodes* covered herein. They just want to employ the correct name, one that will satisfy journal editors and reviewers.

We do not share the worry of Tesakov et al. (2010:85) that "possible new discoveries in old literature" will emerge to once again unsettle the taxonomy of red-backed voles. Coverage of the literature that addresses the taxonomy of these voles, especially formerly obscure publications of the 19th century, strikes us as exceptionally thorough. The present *Code*, and

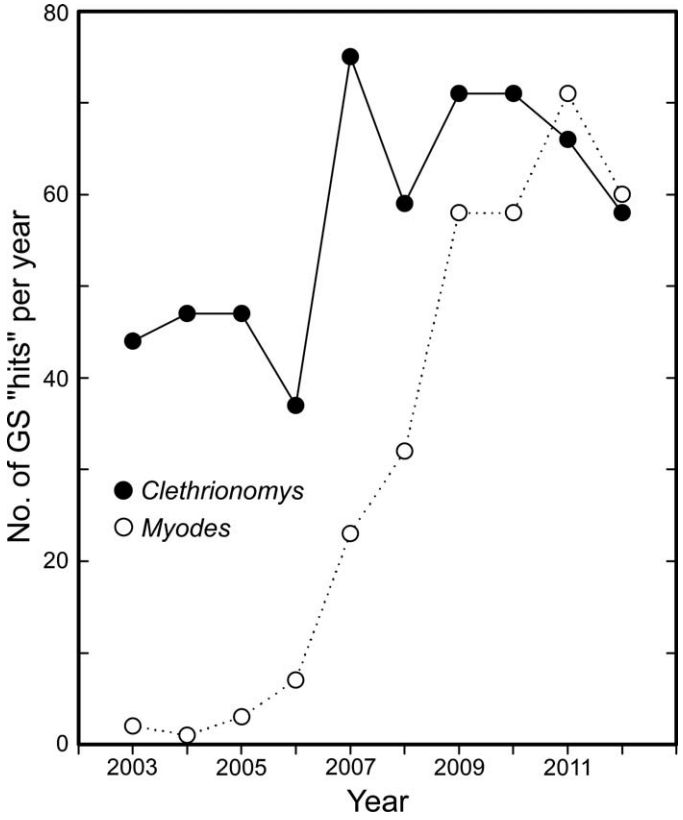


Fig. 3.—Plot of articles published per year that employed either *Clethrionomys* or *Myodes* as the genus of red-backed voles since the appearance of Carleton et al. (2003), who reinstated *Myodes* as the valid genus. Based on search results of Google Scholar (GS; http://scholar.google.com, accessed October 2013); results are raw counts using the search terms [Arvicolinae, *Clethrionomys*] or [Arvicolinae, *Myodes*] to eliminate incidental output for other organisms with "*myodes*" as the species epithet.

most of its predecessors, has drawn a line in the sands of time, namely Linnaeus's 10th Edition of *Systema Naturae*, 1758, a date before which older names cannot be resurrected (ICZN 1999: Article 3). Since then, only 4 genus-group names have been used to taxonomically circumscribe red-backed voles as a "natural" or phyletic grouping in the strict sense (Fig. 2): *Hypudaeus* Illiger, 1811; *Myodes* Pallas, 1811; *Clethrionomys* Tilesius, 1850; and *Evotomys* Coues, 1874. The last 3 genera have the same type species (*Mus rutilus* Pallas, 1779), a fact that solidifies their status as objective synonyms (Article 61.3.3) and invites the application of priority to decide among them (Articles 23.1, 23.3). With regard to the first, *Hypudaeus*, Coues (1874) had rightly exposed the inappropriateness of its usage, in part because Illiger's original generic contents contained no species of red-backed vole (Table 1); Coues (1874) artfully created the new genus *Evotomys* as a nomenclatural remedy and as introduction to his generic sequestration (1877) of red-backed voles from common voles, genus *Arvicola*. Thanks to Coues, and according to current rules (ICZN 1999: Articles 67.2.1, 69.2), the mistaken application of *Hypudaeus* to red-backed voles that transpired

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in the middle 1800s can never again materialize. And should a heretofore unknown genus-group name emerge from some long-hidden, pre-1900 systematic work, the invocation of nomen oblitum would be patently justifiable and incontestable.

To place *Myodes* Pallas, 1811, in the *List of Available Names in Zoology*, with its type fixed as *Mus lemmus* Linnaeus, 1758, would require that the type species be designated through use of the Commission's plenary powers (ICZN 1999: Article 81) in response to a petition expressly requesting such action. As a visceral reaction, this tactic troubles us based on an underlying principle long articulated by all of our zoological codes, past or present, to refrain from infringing upon taxonomic judgment (that is, the judgments rendered by Sélys-Longchamps, Lataste, Kretzoi, and others, not our own). More to the point, the ICZN's official intercession is wholly unnecessary because the articles that speak to this particular instance of nomenclatural disagreement are already provided in the present *Code*. Taxonomic instability is not at issue here. The question is straightforward: Did a particular author, Coues (1877), subsequently designate a type species of *Myodes* in a direct and unambiguous manner (he did not—see above)? The proposal by Tesakov et al. (2010:85) to have the ICZN intervene belies the authors' conviction that Coues's "actions constitute a valid designation of *Mus lemmus* as the type species for the genus *Myodes*." Instead of appealing to the ICZN to invoke its plenary power to fix the type species of *Myodes* and thereby decree its synonymy with *Lemmus*, we invite readers to consult their copy of the *Code*, apply its principles to Coues's (1877) account of the genus *Myodes* as represented by Tesakov et al. (2010) and by us, and reach their own judgment.

A Brief Retrospective

The foregoing exposition will sound a disagreeable, tediously lawyerlike tone to many: "But it isn't science!" Well, yes it is. Science stumbles forward through a dynamic tension between order and anarchy. In systematic biology, our nomenclatural rules and codes operate necessarily within the sphere of order, striving to minimize, ideally to eliminate, semantic differences in the proper names (taxa) we employ in formulating our taxonomic hypotheses, and, by so doing, focusing attention on the verbs embodied in relational statements about phylogeny, zoogeography, and ecology. The coherent thread in the evolution of our nomenclatural guidelines, from the Stricklandian Code (Strickland et al. 1843) through the 4th edition of the *International Code of Zoological Nomenclature* (ICZN 1999), is one of lessening ambiguity and strengthening objectivity at all steps in the creation and application of scientific names.

Such a progression is evidenced by the type species and its critical role as name-bearing type to anchor the definition of genus-group taxa and to clarify the applicability of their names. Provision of a type species rarely accompanied the description of new genera in the late 18th or early 19th centuries, and the nomenclatural awareness to provide one emerged only as a recommendation in the early codes (e.g., Strickland et al. 1843: Recommendation G). Although not required, original designation of the type species became a regular practice in generic descriptions toward the end of the 19th century and thereafter (e.g., see Dayrat 2010:218–219). Unfortunately for systematic mammalogy, like all branches of zoological study, a substantial proportion of our current classification rests on genera described before 1840, many of those based on multiple species and lacking any indication of type species. To apply such names, zoologists creatively resorted to various ad hoc methods for identifying the type, for example: arbitrary acceptance of the 1st-listed species, the criterion mentioned by Tesakov et al. (2010); estimation of which species seemed to most closely fit the author's diagnosis; use of the oldest, or the best known, or the most characteristic of the species originally included; or type restricted by the process of elimination as constituent species of the old genus were transferred to newly described genera. Over the middle 19th through the early 20th century, such approaches were informally followed and either formally advised or specifically rejected in approved zoological codes, such as the American Ornithologists' Union Code (Coues et al. 1886) and even the 1st international code, the *Règles internationales* (ICZN 1905, 1926).

Zoologists have long espoused the Principle of Priority, in some stated form ("law of priority," "loi de priorité"), since formulation of the earliest codes (Strickland et al. 1843; Chaper 1881; Coues et al. 1886), and it has remained a cornerstone of subsequent international codes (ICZN 1905, 1961, 1999). The type concept or Principle of Typification, on the other hand, did not emerge in its definitive form until much later codes, to wit: "Each nominal taxon in the family, genus or species groups has actually or potentially a name-bearing type" (ICZN 1999: Article 61). The turning point occurred during the 1930 XI International Congress of Zoology (Padua, Italy), which authorized amendments to the *Règles internationales* that required explicit fixation of the type species for genera described after 1930 (eventually incorporated as Article 13b, ICZN 1961) and formulated strict criteria to interpret subsequent designation of a type species (incorporated as Articles 68 and 69, ICZN 1961). Coalescence of the Principle of Typification ultimately brought much-needed nomenclatural objectivity, per the device of name-bearing types, to the application of priority and as arbiter in complicated issues of genus-group synonymy.

The taxon of interest here, *Myodes* Pallas, whether a junior synonym of *Lemmus* Link or the oldest available generic name for red-backed voles (*Mus rutilus* Pallas and its closest relatives), is a microcosm that exemplifies the need for these broad historical changes in our codes of zoological nomenclature. The rules and recommendations found in the current *Code* (ICZN 1999) are sufficient to resolve the issue.

Taxonomic Summary

We present our conclusion regarding the validity and seniority of *Myodes* within a formal generic synonymy, a

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useful taxonomic tool whose multiple functions were encapsulated by Gardner and Hayssen (2004:2).

> A synonymy provides a historical chronology of names that have been applied to the taxon (genus, species, or subspecies) under study. A well-constructed synonymy identifies available names, emendations, variant spellings, unavailable names, misidentifications, and nomenclatural acts that influence the taxonomist when determining the valid name for the subject taxon. A synonymy also facilitates compilation and synthesis of information from earlier literature when that information was provided under name combinations no longer current for the subject taxon.

The synonymy of our subject taxon, the genus *Myodes*, is here developed according to the classifications of Pavlinov (2003) and Musser and Carleton (2005). The generic boundaries as recognized by those authors will undoubtedly need adjustment, as indicated by recent molecular studies, in particular those of Cook et al. (2004), Lebedev et al. (2007), and Buzan et al. (2008). Their gene-sequencing results, based on cytochrome *b*, bear on the relationships among forms such as *Aschizomys* Miller, 1898, *Craseomys* Miller, 1900, and *Phaulomys* Thomas, 1905, and the rank to be accorded to each, for example, as generically distinct from, or synonyms of, *Myodes* or *Alticola*; indeed, Abramson and Lissovsky (2012) have recently employed *Craseomys* as a genus distinct from *Myodes* sensu stricto. Unlike the nomenclatural complications that have historically attended the recognition of *Myodes* Pallas, 1811, we can thank the authors of these genus-group taxa for designating a type species in their original description—*rufocanus* Sundevall, 1846, for *Craseomys*; *Aschizomys lemminus* Miller, 1898, for *Aschizomys*; and *Evotomys* (*Phaulomys*) *smithii* Thomas, 1905, for *Phaulomys*—an advantage that immeasurably simplifies decisions affecting synonymy and the application of names. Broadening the taxon sampling among "red-backed voles," perhaps with expanded integration of results based on morphological characters and nuclear genes (e.g., see Robovský et al. 2008), should reinforce our understanding of cladistic relationship among these taxa and encourage adoption of a stable generic classification of Myodini.

Myodes Pallas, 1811

Myodes Pallas, 1811:173; type species *Mus rutilus* Pallas, 1779, by subsequent designation (Lataste 1883d:349).

Mus: Pallas, 1779:246; part, not *Mus* Linnaeus, 1758; in combination *Mus rutilus* Pallas, 1779.

Mus: Schreber, 1780:680 and plate 190B; part, not *Mus* Linnaeus, 1758; in combination *Mus glareolus* Schreber, 1780.

Mus: Kerr, 1792:237; part, not *Mus* Linnaeus, 1758; in combination *Mus rutilus minor* Kerr, 1792 (name preoccupied by *Mus rattus minor* Kerr, 1792).

Mus: Donndorff, 1792:452; part, not *Mus* Linnaeus, 1758; in combination *Mus rutilus β minor* Donndorff, 1792 (preoccupied by *Mus rattus minor* Kerr, 1792, and *Mus rutilus minor* Kerr, 1792).

Brachyurus Fischer, 1814:vii, 55; part, proposed as a new name to replace *Arvicola* Lacépède, 1799; *Lemmus* Link, 1795; *Mus*: Erxleben, 1777; *Glis*: Erxleben, 1777; *Mus*: Pallas, 1779; and *Microtus* Schrank, 1798, as used by these authors for arvicoline rodents.

Arvicola: Vigors, in Gapper, 1830:204, footnote; not *Arvicola* Lacépède, 1799; in combination *Arvicola gapperi* Vigors, 1830.

Hypudacus: Mehlis, 1831:column 876; incorrect subsequent spelling of, but not *Hypudaeus* Illiger, 1811; in combination *Hypudacus hercynicus* Mehlis, 1831.

Arvicola: Yarrell, 1832:109; part, not *Arvicola* Lacépède, 1799; in combination *Arvicola riparia* Yarrell, 1832; preoccupied by *Arvicola riparius* Ord, 1825.

Lemmus: Baillon, 1834:53, 54; part, not *Lemmus* Link, 1795; in combinations *Lemmus pratensis* Baillon, 1834, and *Lemmus rubidus* Baillon, 1834.

Arvicola: Sélys-Longchamps, 1836:13; part, not *Arvicola* Lacépède, 1799; in combination *Arvicola fulvescens* Sélys-Longchamps, 1836.

Hypudaeus: Keyserling and Blasius, 1840:viii, 34; used as a subgenus of *Arvicola* to contain only *Arvicola glareola* (Schreber, 1780), a species not included in the original description of *Hypudaeus* by Illiger (1811:87).

Arvicola: C. F. Cuvier, 1842:4; part, not *Arvicola* Lacépède, 1799; first use of combination *Arvicola pratensis*: C. F. Cuvier, 1842 (= *Lemmus pratensis* Baillon, 1834).

Hyp[*udaeus*].: Schinz, 1845:237; part, not *Hypudaeus* Illiger, 1811; in combination *Hypudaeus nageri* Schinz, 1845.

Hypudæus: Sundevall, 1846:122; part, not *Hypudaeus* Illiger, 1811; in combination *Hypudaeus rufocanus* Sundevall, 1846.

Clethrionomys Tilesius, 1850:28; type species *Mus rutilus* Pallas, 1779, by subsequent designation (Palmer 1928:87).

Arvicola (*Hypudaeus*): Schrenk, 1859:129; not *Arvicola* Lacépède, 1799; not *Hypudaeus* Illiger, 1811; in combination *Arvicola* (*Hypudaeus*) *amurensis* Schrenk, 1859.

Arvicola (*Hypudaeus*): Radde, 1862:186; not *Arvicola* Lacépède, 1799; not *Hypudaeus* Illiger, 1811; in combination *Arvicola* (*Hypudaeus*) *russatus* Radde, 1862.

Evotomys Coues, 1874:186; type species *Mus rutilus* Pallas, 1779, by original designation.

Arvicola: Poliakov, 1881:56; not *Arvicola* Lacépède, 1799; in combinations *Arvicola wosnessenskii* Poliakov, 1881, and *Arvicola rufocanus* var. *sibirica* Poliakov, 1881.

Euotomys Barrett-Hamilton, 1896:598; incorrect subsequent spelling of *Evotomys* Coues, 1874.

Craseomys Miller, 1900:89; type species *Evotomys rufocanus* (= *Hypudaeus rufocanus* Sundevall, 1846), by original designation; described as a subgenus of *Evotomys* Coues, 1874.

Euotomys Schulze, 1900:203; incorrect subsequent spelling of *Evotomys* Coues, 1874.

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Eotomys Major, 1902:107; incorrect subsequent spelling of *Evotomys* Coues, 1874.

Phaulomys Thomas, 1905:493; type species *Evotomys* (*Phaulomys*) *smithii* Thomas, 1905, by original designation.

Microtus: Kastschenko, 1910:294; not *Microtus* Schrank, 1798; in combination *Microtus mollessonae* Kastschenko, 1910.

Euotomys Collett, 1911:78; incorrect subsequent spelling of *Evotomys* Coues, 1874.

Neoaschizomys Tokuda, 1935:242; type species *Neoaschizomys sikotanensis* Tokuda, 1935, by monotypy.

Glareomys Rasorenova, 1952:23; nomen nudum; used in combination *Clethrionomys* (*Glareomys*) *glareolus* Schreber.

Remarks.—Nomenclatural inconsistencies and contradictions were encountered in the literature during the course of composing this article on *Myodes*. In the interest of rectifying, or at least highlighting, these problems for future researchers, we mention them here.

Novae species Quadrupedum e Glirium Ordine (Pallas 1778–1779), the source of Pallas's name *Mus rutilus*, often is cited as the year 1778, the date on the title page. This work was published in 2 parts: pages 1–70 in 1778 and the remainder in 1779, which section includes the account for *M. rutilus* beginning on page 246.

Miller (1912:632) incorrectly credited Fredéric Cuvier (1842) for the name combination *Arvicola pratensis*, which was based on F. Cuvier's "Campagnol des prairies" (plate 68 and accompanying text in Geoffroy St.-Hilaire and Cuvier, 1824–1842). However, F. Cuvier used the vernacular "*pratensè*" for this species and credited Baillon (1834) for the formal name *pratensis*. The first use of *Arvicola pratensis* was by Charles F. Cuvier, F. Cuvier's son (F. Cuvier died in 1838), who employed the name combination on page 4 in the 6-page Table générale et méthodique (C. F. Cuvier 1842), which appears at the end of volume 7 of the *Histoire naturelle des Mammiferes*.

Miller's (1896) revision of "The genera and subgenera of voles and lemmings" puzzled us at the outset when tracing the taxonomic history of *Myodes* qua lemmings or red-backed voles. His study, laudable as a classic without risk of exaggeration, was expressly directed at the genus-group ranks and ostensibly represented the ideal forum in which issues of synonymy among arvicoline groups could have been resolved with final authority. As preamble to his revised classification, Miller thoroughly reviewed previously named genera (1896:11–19) and past arvicoline classifications (1896:19–24); in the latter section, Miller summarized Lataste's (1883a, 1883b, 1883c, 1883d, 1886) papers and his composition of *Myodes*, as a subgenus of *Microtus*, that included only the red-backed voles *rutilus* and *glareolus*. Miller, whose keen mind and analytic eye had early on suspected the Piltdown fraud (Miller 1915), surely would have noticed Lataste's (1883d, 1886) plain indication of *Mus rutilus* as the type species of *Myodes* (Fig. 1). Yet, no mention of a type of *Myodes* or Lataste's action is found within Miller's synonymies of *Lemmus* (1896:36) or *Evotomys* (1896:42). In curious contrast, Miller (1896:24, footnote) fully credited Lataste (1883a) for recognizing the seniority of *Microtus* Schrank, 1798, as the valid appellation of common voles and accepted Lataste's (1883d) determination of its type species as *Mus arvalis* Pallas.

Miller (1896:15) explained his disposition of *Myodes* as follows: "Since *Myodes* contained species of exactly the same modern genera as *Lemmus* Link and no groups not included in the latter, the name is a synonym of *Lemmus*." Miller was here applying another of the informal criteria operational within the late 1800s to ascertain synonymy, basing their generic equality on an author's estimation of the equivalence or scope of the original taxonomic contents. According to Miller's (1896) understanding of generic limits, the species initially allocated to both *Lemmus* Link, 1795, and *Myodes* Pallas, 1811, represented the 4 "modern genera" *Dicrostonyx*, *Evotomys*, *Lemmus*, and *Microtus*. Today, *Lemmus* sensu Link and *Myodes* sensu Pallas correspond to 5 and 6 modern genera, respectively (Table 1); thus, their specific contents as originally denoted by those authors are not taxonomically congruent as revealed by systematic research conducted since 1896. Investigator disagreement in adjudging taxonomic equivalence inherent in this approach to resolving generic synonymy, coupled with its restrictive temporal window, offers another example of the arbitrariness that influenced our nomenclatural codes to gravitate to the Principle of Typification (ICZN 1999: Article 61). As applied to the taxa of interest here, the type species of *Lemmus*, *Mus lemmus* Linnaeus as originally fixed by absolute tautonomy, and that of *Myodes*, *Mus rutilus* Pallas as subsequently designated by Lataste (1883d), provide a decisive and objective standard for definition of those genus-group taxa and for circumscription of their specific contents according to hypothesized relationships, evaluated using whichever information sources, with respect to their type species. For Miller and his contemporaries, the "method of types," particularly as applied to the genus-group ranks (e.g., Cook 1898), was an inchoate nomenclatural principle in the 1890s and a secondary or irrelevant consideration for him when deciding entangled issues of generic synonymy.

Hypudaeus Illiger, 1811, figured prominently in the classification of red-backed voles over the middle 19th century. The taxon is illustrative of the nomenclatural irregularities that plagued early zoological study and moved Coues (1877:131) to complain, "The name '*Hypudaeus*' appears to have been loosely, if not indiscriminately, used by authors." Why Keyserling and Blasius (1840), and others (Baird 1857; Blasius 1857; Fatio 1869), ever associated the name with red-backed voles is incongruous by today's nomenclatural standards because Illiger (1811:88) included none among the 3 arvicoline species he recognized within *Hypudaeus* (Table 1). Nonetheless, the grafting of one name onto a wholly different taxonomic construct sometimes occurred in the early 1800s. Coues's (1874, 1877) timely description of *Evotomys*, with explicit designation of its type species *Mus rutilus*, established a sound nomenclatural framework to address the taxonomy of red-backed voles going forward.

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The subsequent appearance of *Hypudaeus* in genus-group synonymies and designation of type species therewith are confusing, in some cases incorrect. Within the synonymy of *Evotomys*, Coues (1877:131) cited *Hypudaeus*, as recognized by Keyserling and Blasius (1840), as a junior synonym and identified its type species as *Arvicola glareola* (= *Mus glareolus* Schreber). We presume that Coues so listed the type because Keyserling and Blasius (1840:34) included only a single species of red-backed vole, *Arvicola* (*Hypudaeus*) *glareola*, in their coverage of European vertebrates; that is, Coues was following a type-by-monotypy rationale for the initial application of the name in a novel taxonomic context. The treatment of *Hypudaeus* by Miller (1896) is internally contradictory. In his introductory review of older generic names, Miller (1896:14–15) commented about *Hypudaeus* Illiger, 1811, "As no type was designated, and as both *Lemmus* and *Microtus* were included in the then undivided genus *Lemmus* Link, the name *Hypudaeus* must lapse into synonymy." His statement implicates its equivalence to *Lemmus*, but, inexplicably, Miller (1896:36) didn't list *Hypudaeus* within the generic synonymy of *Lemmus* (or of *Microtus*—1896:62). Within the synonymy of *Evotomys*, however, Miller (1896:42) did acknowledge *Hypudaeus* sensu Keyserling and Blasius (1840), with the type as *Mus glareolus* Schreber; this association and type indication plausibly observed the judgment of Coues (1877), an interpretation repeated by Miller (1912:623) and Hinton (1926:210). With advent of the seminal classifications of Rodentia and Mammalia in the 1940s, Ellerman (1941:561) would indicate *Hypudaeus* as a full synonym of *Lemmus*, whereas Simpson (1945:87) associated *Hypudaeus* under *Clethrionomys*.

As reasoned by Coues (1874, 1877), initial application of the genus-group taxon *Hypudaeus* to red-backed voles was wrongly considered by Keyserling and Blasius (1840) because Illiger's (1811) original definition included no species of red-backed voles. Pertinent in this regard, current nomenclatural tenets (ICZN 1999: Articles 62.7.2.1, 67.3.2, 69.1) disqualify *Mus glareolus* as a subsequently designated type of *Hypudaeus*, as indicated by Coues (1877), Miller (1896), and others, because it was never included among the original nominal species that Illiger (1811) had assigned to his new genus when it was described (Table 1). Kretzoi and Kretzoi (2000:176) ultimately settled the issue of *Hypudaeus* as a synonym of *Lemmus* instead of *Myodes* by indicating *Mus lemmus* Linnaeus, 1758, as the type species of *Hypudaeus* Illiger, 1811. Their action makes *Hypudaeus* Illiger, 1811, an objective junior synonym of *Lemmus* Link, 1795, and disentangles the name from the taxonomy of red-backed voles (sensu lato).

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