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On the nomenclature of the American clade of weasels (Carnivora: Mustelidae)

Bruce D. Patterson[1]*, Héctor E. Ramírez Chaves[2], Júlio F. Vilela[3], André E. R. Soares[4] and Felix Grewe[1]

[1]*Negaunee Integrative Research Center, Field Museum of Natural History, Chicago IL 60605, USA*
[2]*Department of Biological Sciences, University of Caldas, Manizales, Caldas, Colombia*
[3]*Núcleo de História Natural da UFPI, Campus Amílcar Ferreira Sobral, Universidade Federal do Piauí – UFPI BR343, Km 3,5 - Bairro Meladão, 64808-605, Floriano, PI, Brazil*
[4]*Department of Organismal Biology, Human Evolution, Evolutionsbiologiskt Centrum EBC, Norbyvägen18 A, Uppsala Universitet, 752 36, Uppsala, Sweden*
[*]*Corresponding author* ✉: *bpatterson@fieldmuseum.org*

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Abstract

A brief review of the phylogeny and nomenclature of the weasels, genus *Mustela* Linnaeus, 1758 in the broad sense, indicates continuing confusion over the appropriate name for the well-supported American clade included within it. A case is made that the American mink (*Neovison vison*) and three allied species (*Mustela frenata*, *M. felipei*, and *M. africana*) should now be recognized in the genus *Neogale* Gray, 1865. The ages and morphological disparities of both *Neogale* and *Mustela* sensu stricto indicate that both are in need of comprehensive revisions.

Key words: Classification, Mammalia, phylogeny, synonymy, taxonomy

There is much confusion and little agreement over the proper name for the American mink and its immediate relatives. The American mink *Neovison vison* (Schreber, 1777) was long considered to be a member of the genus *Mustela* Linnaeus, 1758 (e.g., Palmer, 1904; Pocock, 1921; Hall, 1951; Jones et al., 1997). On the basis of its distinctive morphology, the American mink was removed from *Mustela* and placed in its own genus *Neovison* by Abramov (2000). Wozencraft (2005) followed Abramov's arrangement in *Mammal Species of the World*, and the IUCN Red List of Threatened Species continues to use *Neovison vison* for this species in 2021 (iucnredlist.org).

However, there are issues with the use of *Neovison*. On the basis on mitochondrial Cytochrome b sequences, Harding and Smith (2009) showed that the American mink, long-tailed weasel (*Mustela frenata* Lichtenstein, 1831), Colombian weasel (*Mustela felipei* Izor and de la Torre, 1978), and Amazon weasel (*Mustela africana* Desmarest, 1818) form a well-supported clade that is sister to the remaining species of *Mustela*. Harding and Smith (2009) concluded that this group, which is endemic to the Americas (Fig. 1), should be recognized as *Vison* Gray, 1843. Most recently, Hassanin et al. (2021) analyzed numerous carnivoran mitogenomes and confirmed the membership of *Neovison vison* and *Mustela frenata* in a clade outside the remaining species of *Mustela*, as Dragoo and Honeycutt (1997), Koepfli and Wayne (2003), Flynn et al. (2005), Koepfli et al. (2008), Harding and Smith (2009), and others had previously documented. Arguing that this group should be recognized as a distinct genus, Hassanin et al. (2021) contended that the correct group name should be *Grammogale* Cabrera, 1940. Further complicating matters of nomenclature, other scientists have continued to recognize the American mink as *Mustela vison* (Flynn et al., 2005; Law and Mehta, 2018; Law et al., 2018; 2019; Burgin et al., 2020).

Nomenclature serves a crucial communication linkage between scientists. When based on phylogenetic

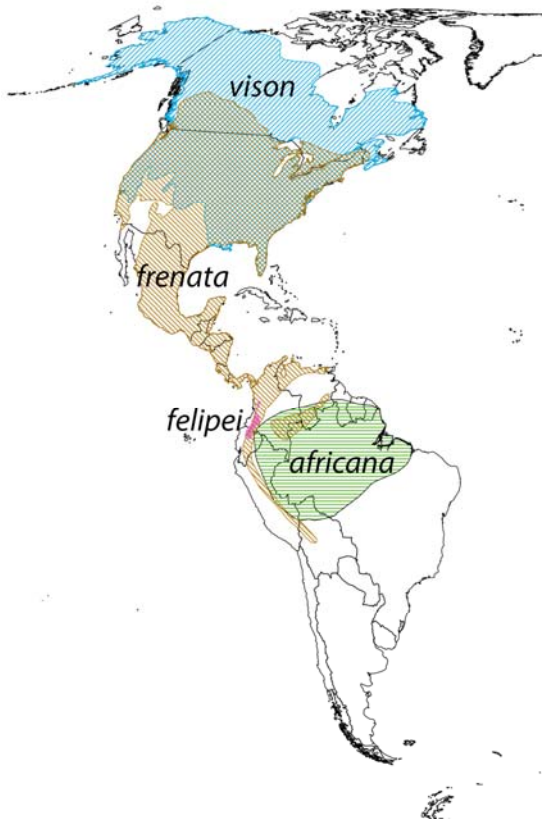

Figure 1: Distributions of the four mustelid species consistently recovered as a well-supported American clade in Mustelinae: *Neovison vison*, *Mustela frenata*, *Mustela felipei*, and *Mustela africana.* Distributions from IUCN (2019).

relationships, nomenclature allows both the storage and retrieval of biological information that is shared by evolutionary descent (Mayr, 1969; Benton, 2007). Inaccurate and unstable nomenclature serves to cloud this information and hinder communication across biological disciplines. Thus, the current nomenclatural status of the American mink and related species warrants scrutiny with respect to two determinations: what group-name applies to this clade, and what taxonomic rank should it be accorded?

What is the group name?

The generic name in current use for the American mink, *Neovison*, is not supported by any published phylogenetic analysis, and its use renders the genus *Mustela* paraphyletic. *Neovison* was proposed as a subgenus of *Mustela* on morphological grounds by Baryshnikov and Abramov (1997), without an accompanying phylogenetic analysis. These authors also proposed the new subgenus *Cabreragale* for *Mustela felipei*, recognized *Mustela africana* in the subgenus *Grammogale* Cabrera, 1940, and retained *Mustela frenata* in the nominate subgenus with *Mustela erminea* Linnaeus, 1758. Abramov (2000) subsequently elevated *Neovison* to generic rank and presented an unsupported tree of relationships that would justify his nomenclatural proposals: American mink appeared as sister to all species of *Mustela*, *M. frenata* and *M. erminea* were grouped as sisters, and *M. felipei* and *M. africana* were only distantly related. This topology for *Mustela* is contradicted by all subsequent phylogenetic analyses, including Koepfli and Wayne (2003), Flynn et al. (2005), Koepfli et al. (2008), Harding and Smith (2009), Sato et al. (2012), and Law et al. (2018; 2019). American mink are sister to all other *Mustela* only in analyses that lack its closer relatives *M. frenata*, *M. felipei*, and *M. africana.* In the only analyses to include all four species, Harding and Smith (2009) and Law et al. (2018) recovered the well-supported grouping *M. vison* (*M. frenata* (*M. africana*, *M. felipei*)) as sister to all other species of *Mustela*. This arrangement suggests the group's successive southward colonization of the Americas (see Fig. 1). What is the oldest available name for this group?

In his catalogue of the mammals in the British Museum, J. E. Gray (1843) proposed the name *Vison Lutreola* for "The Mink or Nurek Vison," specifying its basis on *Viverra Lutreola* Linnaeus, the European mink (Fig. 2). Nurek is a region in central Poland that is included within the range of *Mustela lutreola*. The other names listed in his account are attributed synonyms of *Vison lutreola*. Harding and Smith (2009) contended that, because Gray (1843) applied this name to 5 specimens in the British Museum collection, one collected in Siberia and the other four from North America, *Vison* constituted the oldest name for the American mink and its relatives and should therefore serve as their group-name. But Gray's use of this name for American mink simply reflected his mistaken judgement that the European and American minks were conspecific; it does not broaden the application of the group name. Gray (1843) clearly designated *Mustela lutreola* as the type species for *Vison*, as virtually all subsequent authors have recognized (Baryshnikov and Abramov, 1997; Wozencraft, 2005; Hassanin et al., 2021).

In his subsequent revision of Mustelidae, Gray (1865) divided the species of *Mustela* in the broad sense into four genera: *Mustela*, *Putorius* Cuvier, 1817, *Vison*, and *Gymnopus* Gray, 1865. He further divided his restricted *Mustela* into three groups by proposing two new names as subgenera: (1) *Mustela* sensu stricto, containing *M. erminea*, the type species of the genus, including with it *Mustela agilis* Tschudi, 1844, which is now regarded as a subspecies of *M. frenata* (Wozencraft, 2005); (2) *Gale* containing *Mustela nivalis* Linnaeus, 1766 as well as *M. altaica* Pallas, 1811, *M. subpalmata* Hemprich and Ehrenberg, 1833, and *M. albinucha* Gray, 1864; and (3) *Neogale* containing various forms of *M. frenata*. Interestingly, Gray gave "American" in the group diagnosis of *Neogale*, recognizing that its distribution in North and South

The Vormela, or Peregusna. Putorius Sarmaticus, *Gray*. Mustela Sarmatica, *Pallas, Spic. Zool.* xiv. t. 41. M. Peregusna, *Guld.* M. præcincta, *Ranz.*

a. Ears large, much fringed, spots and bands large. Siberia.

b. Larger; ears not fringed, spots and bands small. Siberia.—From M. Brandt's Collection.

The Mink, or Nurek Vison. Vison Lutreola. Viverra Lutreola, *Linn.* Mustela Vison, *Brisson.* M. lutreocephala, *Harl.* Lutra minor, *Erxl.* *Pallas, Spic.*

t. 3. f. 1. *Buffon*, xiii. t. 43. Otay, *Sagard.* Fontereau, *La Hontan.* Jackash, *Hearne.* Mink or Minx, *Fur Traders.* ?Marsh Otter, *Langsdorff.*

a. Pale brown, chin and upper part of throat white. N. America.

b. Paler brown. N. America.

c. Dark brown, chin white. N. America.—Presented by Capt. Sir G. Back, R.N.

d. Male. Dark brown, head black, chin and upper lip white. Siberia.

e. Dark brown, chin white. Delaware.—Presented by Edward Doubleday, Esq.

f. Small; rather dark, chin white. N. W. Coast of America.—Presented by Capt. Sir E. Belcher, R.N., C.B.

The Weasel. Mustela vulgaris, *Brisson, Linn.* Mustela nivalis, *Schreb.* from *Buffon, H. N.* vii. t. 29. f. 1. *Females*, Mousehunter, *Cambridgeshire, Bell, B. Q.*

Figure 2: J. E. Gray's 1843 description of the genus *Vison*, pages 64 and 65 in the 1843 *List of the Specimens of Mammalia in the Collection of the British Museum*.

America differed from his Holarctic subgenera *Mustela* and *Gale*. Gray's genus *Vison* included as separate species both the European and American mink, as well as *M. sibirica* Pallas, 1773.

Gray (1865) also proposed the new genus *Gymnopus* for the weasels with unusually naked feet: *M. nudipes*, *M. kathiah*, *M. strigidorsa*, and *M. africana*. Cabrera (1940) understood the type species of *Gymnopus* to be *M. nudipes*, for the virtual tautonomy (in Latin and Greek) represented by their names; *M. nudipes* was also the first species he listed under the new genus. By recognizing the Amazon weasel in *Gymnopus*, Gray placed the three known species of the American clade in three separate genera.

The only remaining genus-group name for these weasels was proposed 75 years later by Angel Cabrera (1940). Cabrera recognized that the unique external (ventral stripe) and dental (loss/reduction of anterior premolar) characters of *M. africana* clearly separated it from *M. nudipes*, the type species of *Gymnopus*, and other Old World weasels. He proposed the name *Grammogale* for *M. africana*,

considering the genus monotypic. The other weasel species endemic to South America, *M. felipei*, was not discovered and named until 1978 (Izor and De La Torre, 1978). Sharing naked foot soles, extensive interdigital webbing, a trifid tip to the baculum, and reduced anterior premolars with the Amazon weasel, the Colombian weasel was described in the subgenus *Grammogale*. The two South American species appear as sisters in the published phylogenies (Harding and Smith, 2009; Law et al., 2018), joined successively by pan-american *M. frenata* and the Nearctic American mink (Fig. 1).

††† *Back streaked.*

7. MUSTELA ALBINUCHA.

Black; forehead, crown, and nape white; four stripes on the back, converging in front and behind, pale-brownish white; tail white, tapering.

Zorilla albinucha, Gray, Proc. Zool. Soc. 1864, p. 69, pl. x.
Hab. Africa, Angola.
This is a *Mustela* having the coloration of a *Zorilla*.

** *Face with pale spot in front of ears; back uniform; tail-end black.* American. Neogale.

8. MUSTELA BRASILIENSIS. Black-faced Weasel. B.M.

Brown; head and tip of tail blackish; spot before ears, another on centre of forehead, chin, and throat white; chest and belly yellow.

Mustela brasiliensis, Sewast. Mém. Acad. Pétersb. iv. 356, t. 4 (good), 1813.
M. (*Putorius*) *brasiliensis*, D'Orb. Voy. Amér. Mérid. t. 13. f. 3 (skull).
M. frenata, Licht. Darstell. Säugeth. t. 42; Gray, Voy. Sulph. t. f. 2; Cat. M. B. M. 65; Gerrard, Cat. Bones B. M. 94.
Putorius frenatus, Bachm. N. A. Quadr. ii. 71, t. 60; Mamm. N. A. 173, t. 77. f. 1, 2 (skull); Mexico, 19.

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Mustela javanica, &c., Seba, Thesaur. 177, t. 48. f. 4.
M. erminea, var., Pallas, Zoogr. Ross.-Asiat. 92 (from Seba).
Mustela gale leucogenis, Schinz, Syn. Mamm. i. 344 (from Seba).

Var. 1. Spot before ears and that on forehead confluent. B.M.

Var. 2. With a small white spot under the eyes. B.M.
In some specimens the feet are white or brown, with white toes; and in others the feet are brown-yellow.
Hab. Mexico, Matamoras (*Baird*); California.

Var. *brasiliana*. Feet white; underside bright yellow. B.M.
Hab. Brazil.
Dr. Spencer Baird refers *M. brasiliensis*, Sewastonoff, to this species with great doubt, though it is a very good description, and moderate but characteristic figure.

9. MUSTELA AUREOVENTRIS. B.M.

Dark brown; head and tip of tail blacker; chin and sides of the throat white; a spot in front of ears, throat, chest, insides of fore

Figure 3: J. E. Gray's 1865 description of the subgenus *Neogale*, pages 114–115 in the *Proceedings of the Zoological Society of London* for 1865.

Thus, each of the four species in the American clade of weasels is the type species for a genus-group name: *vison* for *Neovison* Baryshnikov and Abramov, 1997, *frenata* for *Neogale* Gray, 1865, a*fricana* for *Grammogale* Cabrera, 1940, and *felipei* for *Cabreragale* Baryshnikov and Abramov, 1997. Clearly, the senior name for this group is *Neogale*, and *Grammogale*, *Cabreragale*, and *Neovison* should all be considered its subjective synonyms. As earlier noted, the synonymy of *Vison* Gray, 1843 follows the generic allocation of its type species, *M. lutreola*; it is currently in the synonymy of *Mustela,* listed there as an objective synonym of *Lutreola* Wagner, 1841.

At what rank should it be recognized?

The advent of molecular genetics has given systematists access to an abundance of characters, and quantitative phylogenetic methods enable identifying even very fine degrees of relationship. This raises the questions: which of those degrees warrant recognition as groups and at what rank should they be recognized? Because Linnaean binomials are used throughout the biological sciences, nomenclatural changes involving genus and species are especially disruptive, altering usage and impeding communication.

Although the rank of all higher taxa is subjective, categories are most informative when closely related organisms are ranked by the same age or divergence criteria. This comparability heightens the information storage-retrieval capacity of nomenclature. Time of divergence is an important criterion, signaling the time of evolutionary independence between lineages and their opportunities for the acquisition of novel traits. A number of studies, including Koepfli et al. (2008), Sato et al. (2012), Law et al. (2018), and Hassanin et al. (2021), have published estimates of divergence times for the genera and species of Mustelidae (Table 1). Having different taxon sampling schemes, fossil calibrations, and inference methodologies, some were based on both nuclear and mitochondrial loci (Koepfli et al., 2008; Sato et al., 2012; Law et al., 2018), whereas that of Hassanin et al. (2021) was based solely on mitochondrial sequences. The absolute dates of these estimates vary, with those based on mitogenomes typically far older than those based on also nuclear loci, which are *inter se* largely concordant. And of course, stem age estimates are older than crown age estimates, as they include time since divergence from a sister. Nevertheless, comparisons of divergence estimates by each of these studies document the relative antiquity of the split between *Mustela* and *Neogale.* In all of these chronograms, the divergence of *Mustela* and *Neogale* preceded the appearance of any genus of otters (Lutrinae) save *Pteronura* Gray, 1837, or the genera *Ictonyx* Kaup, 1835, *Poecilogale* Thomas, 1883, *Vormela* Blasius, 1884, *Melogale* Geoffroy, 1831, or *Martes* Frisch, 1775. In the Guloninae, only *Pekania* Gray, 1865 and *Eira* Smith, 1842 are older. Few mustelid genera are as old as *Neogale*.

Neogale and *Mustela* are certainly old enough to be recognized as genera, as Hassanin et al. (2021) also recognized, albeit with the name *Grammogale*. How does the content of these genera, meaning their internal heterogeneity, compare to that of other mustelids? Species of *Mustela* sensu stricto began diversifying soon after the divergence of *Neogale* (Table 1). The only sampled mustelid genus with a comparably old crown radiation of species is *Martes*. Crown ages of other sampled mustelid genera are roughly half as old (e.g., dates for *Lutra*, *Lontra*, *Meles,* and *Melogale*). The divergence of extant *Neogale* species (initiated by the split between *vison* and *frenata*) also preceded splits in most of these polytypic genera (Table 1). *Neogale* is old enough to warrant recognition as a valid genus; in fact, few mustelid genera are as old. And the speciation events that gave rise to its four extant species are old enough to rank *Neogale* among the more encompassing and potentially diversified genera.

Both the age of *Neogale* and the age of its component species relative to other mustelid groups argue against recognizing *Neogale* as a subgenus of *Mustela.* Like genera, subgenera are governed by the rules of the International Commission on Zoological Nomenclature (iczn.org), so that their usage is constrained, and their stability promoted, by typification and priority (cf. Voss et al., 2014; Teta, 2018). Use of the subgenus category permits authors to identify clades within genera in a manner that does not disrupt the customary use of binomial nomenclature. Recognizing *Neogale* as a subgenus of *Mustela* (i.e., *Mustela* (*Neogale*) *vison*, *M.* (*N.*) *frenata, M.* (*N.*) *felipei*, and *M.* (*N.*) *africana*) would conserve traditional usage of their binomials. But this group is older and encompasses more genetic diversity than all but a few other mustelid genera. Even its most recently diverged species, *Neogale felipei* and *N. africana,* differ substantially from each other and from *N. frenata* in color pattern, bacular shape, and even dental formulae (Izor and de la Torre, 1978). The group's morphological disparity is so great that molecular phylogenies were needed to identify American mink as a member of this group. With the phylogenetic relationships of *Neogale* now well established (e.g., Law et al., 2018), the time is ripe to identify its morphological synapomorphies and provide a robust group diagnosis.

The American distribution of *Neogale* (Fig. 1) also deserves mention, as both Gray (1865) and Harding and Smith (2009) clearly recognized. In their analysis of mustelid biogeography, Koepfli et al. (2008; see their Figure 3) noted a repeated pattern of basal splits between New World and Old World clades in four subfamilies: Lutrinae, Mustelinae, Ictonychinae, and Guloninae. In each subfamily, except for the Mustelinae, taxonomists had recognized that split by

assigning members in each hemisphere to different genera. Recognizing *Neogale* as a valid genus that is sister to the largely Old World *Mustela* brings equivalent rank and taxonomic conformity to the pattern of late Miocene divergences that Koepfli et al. (2008) identified.

Table 1: Age of Mustelidae genera as estimated from molecular phylogenies, in millions of years. The studies differed in taxonomic sampling, genetic sampling, fossil calibrations, and prior distributions. Crown ages for genera are reported where two or more congeners were sampled; crown plus stem ages are indicated by asterisk (*). Subfamily classification follows Nascimento (2014) and Koepfli et al. (2017).

Taxa		Koepfli et al. (2008)[1]	Sato et al. (2012)[2]	Law et al. (2018)[3]	Hassanin et al. (2021)[4]
Mustelinae	*Neogale*	3.3–3.2	6.56*	4.11	7.4–6.5
Mustelinae	*Mustela*	5.3–5.0	6.3	7.35	11.8–10.3
Mustelinae	*Mustela-Neogale*	6.2–6.0*	7.13*	8.69*	13.4–11.8
Lutrinae	*Lutra*	1.8	4	1.67	3.8–3.4
Lutrinae	*Lutrogale*	1.4–1.3*		1.59*	3.9–3.4*
Lutrinae	*Aonyx*	2.7–2.4	4*	3.11	3.9–3.4*
Lutrinae	*Enhyra*	5.0–4.8*	5.76*	6.19*	12.8–11.2
Lutrinae	*Lontra*	3.4–2.8	2.25	3.37	15.4–13.5*
Lutrinae	*Pteronura*	7.7–7.4*		9.96*	
Ictonychinae	*Poecilogale*	2.7–2.2*	4.27*	3.87*	8.1–7.1
Ictonychinae	*Ictonyx*	2.7–2.2*	4.85*	5.12*	8.1–7.1
Ictonychinae	*Vormela*	4.6–4.0*	6.48*	7.12*	
Ictonychinae	*Galictis*	3–2.8	2.03	2.96	15.9–13.9*
Helictinae	*Melogale*	2.5–2.2	12.5*	3.96	1.9–1.7
Guloninae	*Martes*	5.1–4.7	6.56	5.79	10.8–9.4
Guloninae	*Gulo*	6.2–5.6*	7.3*	6.5*	12.1–10.6*
Guloninae	*Pekania*	7.2–6.4*	7.9*	6.03*	14.2–12.4*
Guloninae	*Eira*	7.7–6.7*		6.03*	
Melinae	*Arctonyx*	4.4–3.6*	3.28*	4.54*	8–7*
Melinae	*Meles*	4.4–3.6*	1.94	2.5	4.9–4.3
Mellivorinae	*Mellivora*	12.6–12.4*	12.55*	15.49*	22.5–19.6*

[1] Range of five estimates; data from their Table 2.
[2] Posterior mean from BEAST analysis; their Figure 3.
[3] Posterior mean of FBD model; data from their Supplementary Table S7.
[4] Range includes uniform and log-normal priors from their Figure 3.

Even after the removal of *Neogale*, *Mustela* sensu stricto remains an old and diverse genus. Long ago, Izor and de la Torre (1978) observed "*Mustela* is in many respects a primitive mustelid, retaining most of the family's basic characters. For this reason, care must be exercised so that it does not become a catchall genus, collecting diverse, structurally generalized species without true phylogenetic affinities." Molecular phylogenies have confirmed their suspicions that this is an old and disparate group, one characterized mainly by plesiomorphies. A grouping that Gray (1865) recognized as *Gymnopus* (*M. nudipes* + *M. strigidorsa*) is consistently recovered as the oldest split within *Mustela* (Koepfli et al., 2008; Sato et al., 2012; Law et al., 2018), perhaps warranting recognition as a valid genus.

However, the antiquity of the weasel radiation, its highly variable morphologies, and its still-incomplete phylogeny warrant a truly comprehensive revision, which has not been attempted since molecular phylogenies have resolved natural groupings. Analyses of morphology, genetics and other biological traits resulting in new diagnoses should be possible through an integrative taxonomic revision.

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Conflict of interest

All the authors declare that there are no conflicting issues related to this Review article.

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