

## A taxonomic review of the genus *Mustela* (Mammalia, Carnivora)

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The genus *Mustela* includes 17 species. Comparative analysis of skull structure, dentition, bacular structure and external characteristics make it possible to divide the genus into 9 subgenera: *Mustela*, *Gale*, *Putorius*, *Lutreola*, *Kolonokus*, *Pocoockictis*, *Grammogale*, *Cabreragale* and *Cryptomustela* subgen. n. The American mink is regarded as a representative of a separate genus *Neovison*.

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Species of the genus *Mustela* are widely distributed all over the world. It is one of the most speciose genera among the Mustelidae. The genus *Mustela* has been treated variously by different authors as consisting of 14 up to 17 species (Walker, 1964; Corbet, 1978; Corbet & Hill, 1980, 1992; Wozencraft, 1993; Pavlinov et al., 1995; Pavlinov & Rossolimo, 1998). I accept here 17 species in the genus *Mustela*: *erminea*, *frenata*, *nivalis*, *subpalmata*, *altaica*, *kathiah*, *lutreola*, *putorius*, *eversmanni*, *nigripes*, *sibirica*, *itsi*, *lutreolina*, *africana*, *felipei*, *nudipes*, *strigidorsa*. I regard the American mink as a species of the distinct genus *Neovison* (see below).

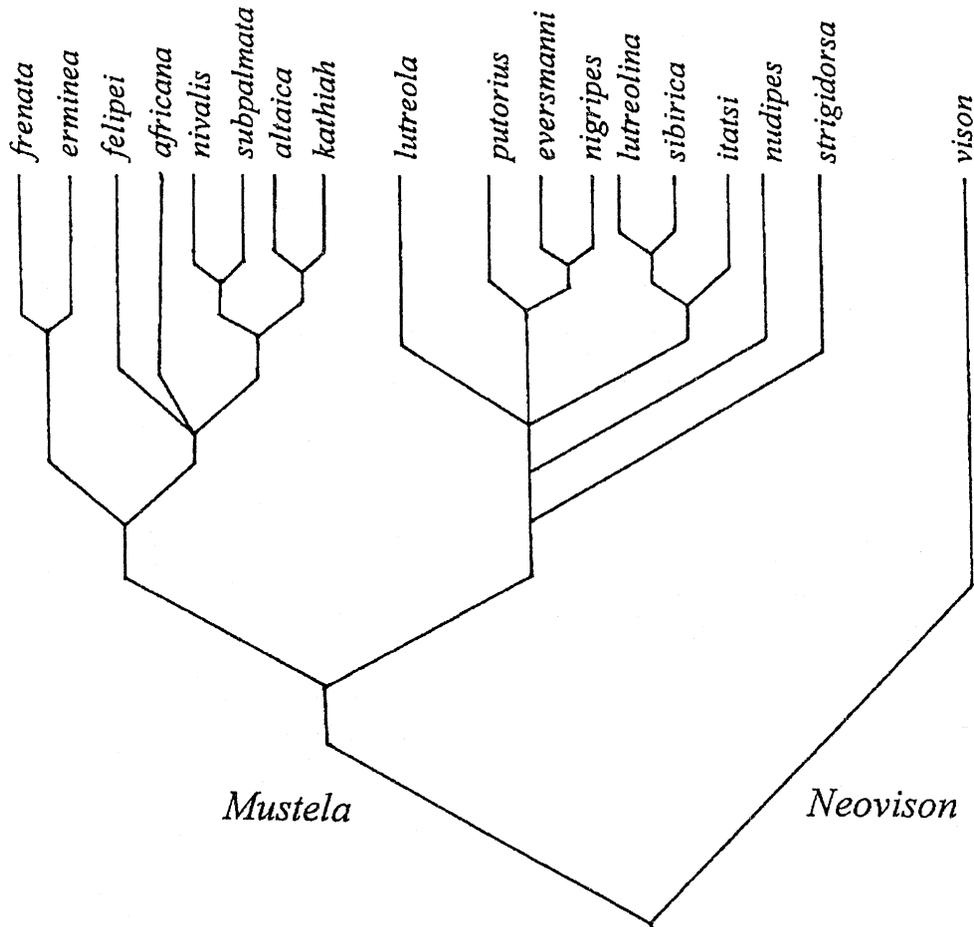
Many recent authors consider Egyptian weasel (*M. subpalmata*) as a subspecies of *M. nivalis*. However, *M. subpalmata* differs both morphometrically and with respect to sexual dimorphism of size from all the other taxa of *M. nivalis*. I regard the Egyptian weasel, following Zyll de Jong (1992), as a separate species.

Some authors (Pocock, 1941; Ellerman & Morrison-Scott, 1951; Heptner et al., 1967; Lekagul & McNeely, 1988) consider *M. lutreolina* and *M. sibirica* to be conspecific. However most scientists believe that morphological differences (skull structure, coloration) and also geographic isolation are sufficient for considering *M. lutreolina* as a distinct species (Brongersma, 1940; Bree & Boeadi, 1978; Wozencraft, 1993). Very often *M. itsi* is also considered as conspecific with *M. sibirica* (Ellerman & Morrison-

Scott, 1951; Heptner et al., 1967; Pavlinov & Rossolimo, 1987, 1998; Corbet & Hill, 1992; Wozencraft, 1993; Pavlinov et al., 1995). However such a view contradicts many morphological and biochemical data (Stroganov, 1962; Ternovsky & Ternovskaya, 1994; Masuda & Yoshida, 1994). I also consider *M. itsi* as a separate species (Abramov, in press).

Some authors regarded *M. furo* as a distinct species. However cytogenetic and biochemical data confirm that *M. furo* and *M. putorius* are conspecific, the first is merely a colour variation of *M. putorius* (see also Ternovsky, 1977; Ternovsky & Ternovskaya, 1994).

Relationships between the species in the genus *Mustela* have not been fully examined. The groupings of species within the genus differ in the classifications of different authors. The majority of such classifications are based upon the analysis of a limited number of morphological characteristics (skull structure, exterior, etc.). Recently many studies have been performed in which relationships between the Palearctic species of *Mustela* were evaluated on the base of cytogenetic and biochemical characters (Graphodatsky et al., 1976; Belyaev et al., 1980; Lushnikova et al., 1989; Taranin et al., 1991; Masuda & Yoshida, 1994; etc.). In the current paper, I aimed to make the scheme of relationships of the *Mustela* species based on complex analyses of morphological and cytogenetic features (see Figure). I propose to divide the genus *Mustela* into 9 groups (subgenera).

Relationships of the species of *Mustela* and *Neovison*

Genus **Mustela** Linnaeus, 1758

Subgenus **Mustela** Linnaeus, 1758 – Ermine, Stoat

*Arctogale* Kaup, 1829: 30.

*Neogale* Gray, 1865: 114.

*Mustelina* Bogdanov, 1871: 167.

*Eumustela* Aclouque, 1899: 62.

Type species *M. erminea* L., 1758. The subgenus also includes *M. frenata* Lichtenstein, 1831.

*Distribution.* Eurasia (southwards to Chitral and Kashmir – *M. erminea*), North

America, also inhabits northern part of South America (*M. frenata*).

*Diagnosis.* Size small. Muzzle short, convex above; braincase long and narrow. Mastoids in full-age skulls sometimes prominent. Skull with a short, rather abruptly constricted postorbital area. Infraorbital foramen large. Auditory bullae large and inflated; their inner margins closely arranged and nearly parallel; anterior margins without prominent inner corners.  $Pm^2$  with two roots.

Dorsum brownish; throat and venter cream to white. Demarcation line between

these colours strongly marked. Distal third of tail black. Colour in winter typically all white with exception of the black tip of the tail. Plantar surfaces furred.

Bacula of the simplest structure in the genus *Mustela*: shaft gently curved downward, then upward to the tip, of S-shaped form. No typical hook at the distal end of the baculum.

In *M. erminea*, the diploid number of chromosomes  $2n = 44$ , in *M. frenata*  $2n = 42$ . The structure of karyotypes is similar.

There is a long-time delayed implantation; the gestation period is 270 to 340 days.

*Remarks.* Taxonomists very often include in the subgenus *Mustela* alongside with ermines other small-sized species of the genus (Walker, 1964; Youngman, 1982; Pavlinov et al., 1995). Sometimes all species of the genus, except polecats, are included in this subgenus (Ellerman & Morrison-Scott, 1951; Heptner et al., 1967). However, the ermines (*M. erminea*, *M. frenata*) essentially differ from other species of the genus in the cytogenetic and biochemical characters, biology (long delayed implantation), and structure of the baculum.

The name *Eumustela* Acloque, 1899 was based on two species, *erminea* and *vulgaris* (junior synonym of *nivalis*). They belong to different subgenera. In the absence of a previous type designation, *M. erminea* Linnaeus, 1758 is designated here as the type species of *Eumustela*.

#### Subgenus *Gale* Wagner, 1841 – Weasel

*Ictis* Kaup, 1829: 35, not Schinz, 1824-1828.

*Type species* *M. nivalis* L., 1766. The subgenus also includes *M. subpalmata* Hemprich & Ehrenberg, 1833, *M. altaica* Pallas, 1811 and *M. kathiah* Hodgson, 1835.

*Distribution.* Eurasia, North America, North Africa.

*Diagnosis.* Size small. Muzzle short; braincase long and narrow. Skull without noticeable projecting mastoid processes. Postorbital constriction short. Auditory bullae large and inflated, bean-shaped; their inner margins nearly parallel; anterior margins with prominent inner corners. Foramen lacerum medium displaced to anterior part of bullae. Dentition weaker than in the subgenus *Mustela*.  $Pm^2$  with two roots.

Dorsum brown; throat and venter cream to white. Demarcation line between these

colours strongly marked. Distal third of tail not black. Colour in winter lighter, only *M. nivalis* has complete whitening. Plantar surfaces furred, except for *M. kathiah*.

Baculum with a hook on the distal end of the shaft.

*M. altaica* has the diploid number of chromosomes  $2n = 44$ . *M. nivalis* has a stable chromosome set  $2n = 42$  over the whole range, except the Japanese subspecies *M. n. namyei* which has  $2n = 38$ . *M. nivalis* is very close to *M. altaica* in the karyotype structure (Graphodatsky et al., 1976).

The gestation period is 34-42 days. *M. altaica* has a short period (12 days) of delayed implantation (see Ternovsky & Ternovskaya, 1994).

*Remarks.* Many authors unite *M. nivalis*, *M. altaica* and *M. kathiah* with *M. erminea* and *M. frenata* in one subgenus *Mustela* (Miller, 1912; Ellerman & Morrison-Scott, 1951; Stroganov, 1962; Walker, 1964; Heptner et al., 1967; Ternovsky, 1977; Youngman, 1982; Yudin, 1984; Ternovsky & Ternovskaya, 1994; Pavlinov et al., 1995; Pavlinov & Rossolimo, 1998). However these two groups (*Mustela* and *Gale*) show very significant differences in the baculum structure, time of gestation, karyotypes, and external features (coloration of the tail). These species have to be distinguished as separate subgenera, as has been already suggested by Poock (1921).

#### Subgenus *Putorius* G. Cuvier, 1817 – Polecat

*Foetorius* Keyserling & Blasius, 1840: 68.

*Cynomyonax* Coues, 1877: 99.

*Type species* *M. putorius* L., 1758. The subgenus also includes *M. eversmanni* Lesson, 1827 and *M. nigripes* (Audubon & Bachman, 1851).

*Distribution.* Eurasia, North America.

*Diagnosis.* Size large. Skull robust and strongly built, rather flat, relatively short and broad. Muzzle relatively long; braincase shorter than muzzle. Zygomatic arches widely arranged. Postorbital area prolonged; constriction strongly marked. Cranial crests well developed. Auditory bullae relatively very small, strongly flattened and distinctly triangular in outline; their inner margins not parallel and diverging posteriorly; anterior margins with prominent inner corners. Foramen lacerum medium distinctly displaced posteriad.  $Pm^2$  with one or two roots: *M. nigripes* and about half specimens of *M. eversmanni* have two-rooted premolar, some of the latter and *M. putorius* have a single root.

The polecats differ from all the other species of *Mustela* in the coloration: feet, tail and venter (partly) blackish, remainder of the body with long black hairs producing a clouded effect over whitish or yellowish under fur. There is a brown "mask" on the muzzle. Plantar surfaces furred.

Baculum with a hook on the distal end of the shaft.

Karyotypes in *M. nigripes* and *M. eversmanni* with  $2n = 38$ , in *M. putorius* with  $2n = 40$ .

There is a short period of delayed implantation; the gestation is 37-45 days.

*Remarks.* Polecats always were included in the separate taxon (subgenus or genus) *Putorius*. There are no convincing evidence for generic rank. There are some similarities between *Putorius*, *Lutreola* and *Kolonokus* in biochemical and cytogenetic data (Graphodatsky et al., 1976; Lushnikova et al., 1989). The hybrids between *M. putorius* and *M. lutreola* are known in nature and laboratory conditions. The hybrids between *M. eversmanni* and *M. sibirica*, *M. putorius* and *M. sibirica* (Novikov, 1956; Ognev, 1931; Heptner et al., 1967; Ternovsky, 1977; Ternovsky & Ternovskaya, 1994) also are known. *Putorius* is a specialized and distinct group related to *Lutreola* and *Kolonokus*. Coues (1877) placed *M. nigripes* in the separate subgenus *Cynomyonax* and regarded it as intermediate between *Putorius* (*M. putorius*) and *Lutreola* (*M. vison*).

Subgenus **Lutreola** Wagner, 1841 – European mink

*Hydromustela* Bogdanov, 1871: 167.

*Vison* Gray, 1843: 64.

Type species *M. lutreola* (L., 1761).

*Distribution.* Europe.

*Diagnosis.* Medium-sized. Skull pronouncedly flattened. Auditory bullae small, inflated, relatively short and narrow; their inner margins closely arranged, not parallel-sided and diverging posteriorly. Shape of bullae different from that in other *Mustela*. The lateral part of bullae is separated from mastoids by a deep groove, and mastoids do not form the lateral wall of the bullae, while in the other *Mustela* the bullae are connected to mastoids. Anterior margin of bullae convex; inner corner very prominent and hangs over neighbouring bones. Foramen lacerum medium situated at the middle part of the bullae. Posterior part of bullae with addi-

tional large foramen near to the foramen lacerum posterius.  $Pm^2$  with one root.

Dorsum and venter dark brown. Lower lip and chin white. Plantar surfaces not furred.

Baculum with a hook on the distal end of the shaft. The karyotype is  $2n = 38$ .

There is a short period of delayed implantation; the gestation is 40-43 days.

*Remarks.* Various authors have different opinions on the systematic position of *M. lutreola*. Some of them consider European mink to be close to the American mink and place it into one subgenus (genus) *Lutreola* (Ognev, 1931; Novikov, 1956; Stroganov, 1962; Walker, 1964; Yudin, 1984; Ternovsky & Ternovskaya, 1994). This is incorrect. There are very significant differences between these two species. According to another point of view, European mink is close to *M. sibirica*, *M. nudipes*, *M. lutreolina* and *M. strigidorsa* (Youngman, 1982; Pavlinov et al., 1995; Pavlinov & Rossolimo, 1987, 1998). *M. lutreola* differs from these species in the unique shape of auditory bullae, coloration, some details of the structure of the baculum. Both cytogenetic data and hybridization experiments show that *M. lutreola* is equally close to (or distant from) *Putorius* and *Kolonokus*.

Subgenus **Kolonokus** Satunin, 1911  
Kolonok

*Kolonokus* Satunin, 1914: 124.

Type species *M. sibirica* Pallas, 1773. The subgenus includes also *M. lutreolina* Robinson & Thomas, 1917 and *M. itatsi* Temminck, 1844.

*Distribution.* Asia from the Urals and South Siberia up to Java and Sumatra.

*Diagnosis.* Medium-sized. Skull elongate and narrow. Postorbital region long and parallel-sided; constriction weakly marked. Auditory bullae inflated, but not so strongly as in *Mustela* or *Gale*, elongate, bean-shaped; their inner margins semi-parallel and slightly diverging posteriorly; anterior margins with prominent inner corners. Foramen lacerum medium situated near one-third of bullae length from anterior margin. *M. itatsi* usually with single-rooted  $Pm^2$ , but *M. sibirica* and *M. lutreolina* with two-rooted one.

Colour of entire body brown: from reddish to black-brown with no sharp contrast between upper and lower sides. Muzzle (upper and lower lips and chin) white. Plantar surfaces furred, but in *M. itatsi* naked.

Baculum with a hook on the distal end of the shaft.

Karyotypes of *M. sibirica* and *M. itatsi* are similar,  $2n = 38$ , but *itatsi* has a greater amount of additional heterochromatin.

There is no delayed implantation; the gestation period is 33-35 days.

*Remarks.* Some authors believe *M. sibirica* to be close to *M. altaica* and unite them into the subgenus (or genus) *Kolonokus* (Satunin, 1911, 1915; Ognev, 1931; Novikov, 1956; Yudin, 1984). There are many differences in the structure of the skull, exterior and karyotypes between these species. Now these species are placed in different subgenera (Ternovsky & Ternovskaya, 1994; Pavlinov et al., 1995; Baryshnikov & Abramov, 1997; Pavlinov & Rossolimo, 1987, 1998).

Subgenus **Pocockictis** Kretzoi, 1947 – Malaysian weasel

*Gymnopus* Gray, 1865: 118, non Brooks, 1828.

*Plestiogale* Pocock, 1921: 805, non Pomel, 1853.

Type species *M. nudipes* Desmarest, 1822.

*Distribution.* Thailand, Malaysia, Indonesia.

*Diagnosis.* Medium-sized. Auditory bullae narrow and relatively elongated; their inner margins not parallel-sided and diverging posteriorly; anterior margins with very prominent inner corners sometimes extended as processus. Anterior and lateral parts of bullae more flattened and inner part more inflated compared to *Kolonokus*. Foramen lacerum medium distinctly displaced anteriorly and situated near foramen rotundum. Lateral wall of bullae, posterior to meatus, with two small foramina absent in all other *Mustela*.  $Pm^2$  with one root. Entire body and tail uniformly reddish brown.

Easily distinguished from all other *Mustela* by the white on the head which extends back up to the nape. Plantar surfaces not furred.

Baculum different from that of any other *Mustela*: distal end of the shaft curved upwards without hook; tip divided into broad oval plate formed by left wall of urethral groove and cylindrical processus on right wall of the groove.

*Remarks.* Some authors place this species, together with *M. lutreola* and *M. sibirica*, in the subgenus *Lutreola* (Brongersma & Junge, 1942; Youngman, 1982; Pavlinov et al., 1995). The unique coloration, the differences in bacula structure, shape and structure of auditory bullae do not support this point of view.

Subgenus **Grammogale** Cabrera, 1940 – Amazon weasel

Type species *M. africana* Desmarest, 1818.

*Distribution.* Amazon Basin in Brazil, Ecuador and Peru.

*Diagnosis.* Size small. Auditory bullae widely spaced, narrow and very elongate. In difference from other small species of the genus, inner margins of the latter not parallel and diverging posteriorly. Foramen lacerum medium noticeably displaced anteriorly.  $Pm^2$  usually absent or with one root.

Dorsum brown; venter white or yellow-cream with a median brown stripe. Plantar surfaces not furred.

Baculum peculiar: distal end of the shaft curved upwards without hook; tip divided into left broad plate and right thin round processus; bacular shaft distally becomes very broad and shallow, with widely flaring margins at the level of the dorsal bend.

*Remarks.* Based on the loss of the upper premolars, Cabrera & Yepes (1960) considered *Grammogale* (*africana*, *felipei*) as a separate genus. However such character as reduction of premolars varies in the genus *Mustela* (see also Hall, 1939, 1951; Izor & de la Torre, 1978).

Subgenus **Cabreragale** Baryshnikov & Abramov, 1997 – Colombian weasel

Type species *M. felipei* Izor & de la Torre, 1978.

*Distribution.* Not more than five specimens of this extremely rare species are known from only two localities in the Cordillera Central of Colombia, South America.

*Diagnosis.* Size small. Skull reminds that in the subgenus *Mustela* or *Gale*. Muzzle short; braincase inflated. Palatine short and broad. Auditory bullae oval, very small and strongly flattened, twice smaller than those of *M. nivalis* or *M. erminea* having a similar size of the skull. Inner margins of bullae nearly parallel; anterior margins with prominent inner corners. Foramen lacerum medium displaced to the anterior part of the bullae.  $Pm^2$  with one root.

Snout, dorsum and tail dark brown; venter pale yellow from chin to the groin. Plantar surfaces not furred.

Baculum different from that of any other *Mustela*: shaft strongly curved upward; distal end terminating in three equal processes (as fingers).

*Remarks.* Some authors unite this species and *M. africana* in the subgenus *Gram-*

*mogale* (Izor & de la Torre, 1978; Youngman, 1982; Izor & Peterson, 1985), but *M. felipei* has a differing structure of the skull (especially auditory bullae) and unique structure of the tip of the baculum.

Subgenus **Cryptomustela** subgen. n. – Back-striped weasel

Type species *M. strigidorsa* Gray, 1853.

*Distribution.* Not more than 10-15 specimens of this rare weasel are known from Sikkim, Nepal, Laos, Vietnam, Burma, Tenasserim and Nan Province in Thailand.

*Diagnosis.* Medium-sized. Auditory bullae relatively short and broad, strongly flattened; their inner margins not parallel-sided and diverging posteriorly; anterior margins straight, without prominent inner corners. Foramen lacerum medium markedly displaced anteriorly and situated near anterior apex of the bullae. This species has the normal three lower premolars as in all *Mustela*, not four as reported by Lekagul & McNeely (1988).

*M. strigidorsa* can be distinguished from all the other species of *Mustela* by the presence of a narrow silvery dorsal streak extending from the back of the head almost to the root of the tail. Colour generally dark brown on the back, tail and legs. Upper lip, cheeks, chin and throat pale yellowish, such light coloration spread as ventral streak. Tail rather bushy and relatively long. Plantar surfaces not furred.

Baculum strongly curved upward and backward in its distal third, resembling in this respect that of *Charronia flavigula*; tip divided into two processes (one on each side of urethral groove), of which the left is large, sublaminar and hooked forwards at the tip and the right is small, slender, cylindrical and slightly bent inwards.

*Remarks.* Sometimes *M. strigidorsa* was included in the subgenus *Lutreola* together with *M. lutreola* and *M. sibirica* (Brongersma & Junge, 1942; Youngman, 1982; Pavlinov et al., 1995). Other authors united *M. strigidorsa* and *M. nudipes* in the subgenus *Pocockictis* (Gray, 1865; Pocock, 1921, 1941). *M. strigidorsa* differs from other *Mustela* in the unique coloration of the body, skull structure and the baculum. I consider these differences to be enough for referring this species to a new subgenus.

Genus **Neovison** Baryshnikov & Abramov, 1997 – American mink

Type species *Neovison vison* (Schreber, 1777). This genus includes also *N. macrodon* (Prentis, 1903), an insufficiently known species from North America which became extinct in the last century (last specimen was collected in 1894).

*Distribution.* North America. Was introduced in Europe and Northern Asia, including Japan.

*Diagnosis.* Medium-sized. Skull flattened. Braincase shorter and broader than in *Kolonokus* or *Lutreola*, but not so strong built as that of *Putorius*. Muzzle relatively long (as in *Kolonokus*). Postorbital region elongated; constriction well marked. Crests well developed. Auditory bullae small and flattened, their length equals to about 25% of condylobasal length of the skull (28-32% in species of the genus *Mustela*). Anterior part of bullae flat, margin almost straight. Auditory meatus narrow. Lateral part of bullae near the meatus forms a structure resembling the meatal tube. Foramen lacerum medium displaced anteriorly. Teeth larger and stronger than those of larger *Putorius*. Lower carnassial with small metaconid, as that of *Martes* (all *Mustela* have lower carnassial without metaconid).  $Pm^2$  with two roots.

Venter and dorsum dark brown. Lower lip white. Plantar surfaces furred.

Baculum with a hook on the distal end of the shaft; the base of the shaft with distinct "collar" and reminding the handle of a rapier, partly similar to that of *Gulo gulo* and *Vormela peregusna*.

Karyotype with  $2n = 30$ , strongly different from the karyotypes of all *Mustela*.

There is delayed implantation; the gestation period about 44-60 days.

*Remarks.* There are significant differences between the American mink and other Mustelidae in cytogenetic and biochemical data, the level of these differences is higher than differences between *Mustela* species (Graphodatsky et al., 1976; Belyaev et al., 1980; Lushnikova et al., 1989; Taranin et al., 1991; Masuda & Yoshida, 1994). In some characters (immunologic affinities, karyotype, structure of auditory bullae, dentition), the American mink is close to the genus *Martes* (particularly to *Martes zibellina*). According to the level of cytogenetic differences between the American mink and species of *Mustela*, and the American mink and other Mustelidae, I regard *Neovison* as a separate genus, as was suggested by Petrov (1956) and Yermolaev & Savina (1995).

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