CHAPTER 3

Form and function of the musteloids

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Introduction

With a fossil history dating back 30–32 million years ago (late Eocene and early Oligocene), the Musteloidea are now the most successful superfamily of the Carnivora, as shown by an abundance of species with a global distribution (Agnarsson et al. 2010; Sato et al. 2012). Ranging in size from tiny weasels (*Mustela nivalis*, which may weigh 30 g or less) to huge specialized sea otters (*Enhydra lutris*, >30 kg), they may not have evolved to be as physically large as members of other carnivoran families, but the ratio of the smallest to largest is the greatest—a massive 1000:1 in body masses (Table 3.1). With around 90 species, the Musteloidea is the most speciose superfamily (*c*.30% of carnivorans) and the Mustelidae (>60 species; *c*.20% of carnivorans) the most speciose family of the Carnivora (Wilson and Mittermeier 2009; Hunter 2011; see Chapters 1 and 2, this volume).

The mustelids are mostly specialized predators that generally have a thin, elongated body plan with short legs. This common body plan is adapted to three main functional types: terrestrial/fossorial (e.g. weasels, stoats, ferrets; see Chapters 10 and 15, this volume), scansorial/arboreal (e.g. martens; see Chapter 12, this volume), and aquatic/semi-aquatic (e.g. mink and otters; see Chapters 16, 17, 22, and 23, this volume), although many species are not restricted to one of these functional types, for example, martens (*Martes* spp.) may be terrestrial. Exceptions to this rule, the bear-like wolverines (Gulo gulo, see Chapter 18, this volume) and badgers (see Chapters 13, 19, and 21, this volume), have shorter, robust bodies and relatively longer legs compared with those of other mustelids. However, mustelids are not equally successful globally. Although about 43% of smaller carnivoran species in the Americas and the Oriental region are mustelids, they comprise a mere 12% of smaller carnivoran species in Africa (Figure 3.1). Despite colonizing Africa from the Miocene alongside viverrids and herpestids (Hunt 1996), the only mustelids, apart from otters, south of the Sahara all have black-and-white

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aposematic coloration (e.g. honey badger [*Mellivora capensis*], African striped polecats [*Ictonyx* spp.], and African striped weasels [*Poecilogale albinucha*]), backed up by anal sacs producing noxious secretions—perhaps the mustelids arrived a little later and only those mustelids packed with chemical weapons could muscle their way in. In contrast, in the Palaearctic all small carnivorans are mustelids with the possible exceptions of one or two marginal herpestids and viverrids, which may result from human introductions. Otters are almost unique among carnivorans (the only exceptions being otter civets [*Cynogale bennetti*], and aquatic genets [*Genetta piscivora*], among viverrids) in being adapted to aquatic environments; there are usually three to four species, differentiated by size and diet (usually fish versus crustaceans), per biogeographical region (see Chapter 1, this volume).

The other musteloid families, skunks (Mephitidae; see Chapters 24 and 25, this volume), raccoons, coatis, kinkajou (Procyonidae; see Chapters 26, 27 and 28, this volume), and red pandas (Ailuridae; see Chapter 29, this volume), are rather more eclectic and comprise fewer species, although procyonids show greater diversity of form than mustelids, if they do indeed form a monophyletic family (Koepfli et al. 2007; Koepfli et al., Chapter 2, this volume). In contrast to the other families, red pandas (*Ailurus fulgens*) have evolved as largely specialized vegetarians that show many evolutionary

Table 3.1 Body size of smallest and largest members of each musteloid family.

	Family			
	Mustelidae	**Mephitidae**	**Procyonidae**	**Ailuridae**
Number of species	**>60**	**11**	**14**	**1**
Largest species	***Enhydra lutris***	***Conepatus leuconotus***	***Procyon lotor***	***Ailurus (f.) styani***
Body mass (g)	45,000	4500	28,000	7500
HB (mm)	1200	510	620	730
Smallest species	***Mustela nivalis***	***Spilogale pygmaea***	***Bassariscus astutus***	***Ailurus (f.) fulgens***
Body mass (g)	25	130	800	4500
HB (mm)	114	190	305	510
Ratio body masses	**1800**	**34.6**	**35**	**1.7**
Ratio HBs	**10.5**	**2.7**	**2**	**1.4**

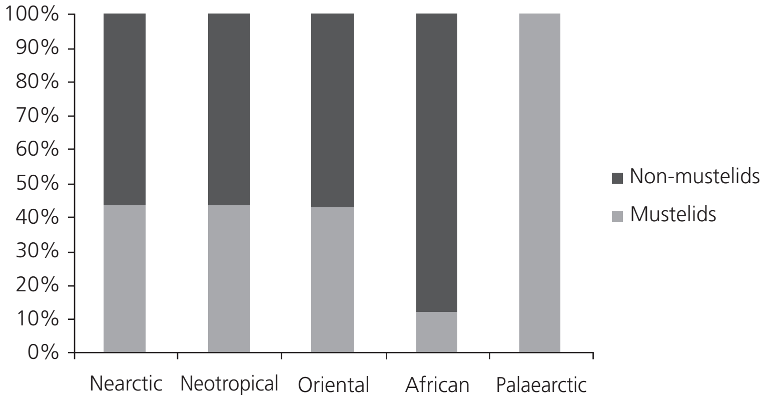


Figure 3.1 Proportion of small carnivorans that are mustelids in different biogeographical regions.

parallels to the unrelated giant panda (*Ailuropoda melanoleuca*). Procyonids and mephitids dominate the Americas, but tend to be less carnivorous and more omnivorous than sympatric mustelids.

In this chapter we review the form and function of the musteloid carnivorans to discover the key adaptations that have helped the musteloids in general and the mustelids in particular achieve global success in terms of numbers of species and geographical spread (see Macdonald et al., Chapter 1, this volume). We begin with a discussion of primarily terrestrial and arboreal species, followed by specific adaptations for those species that live partially or fully in aquatic environments.

Sexual dimorphism

It is very apparent from external appearances that there is a wide degree of sexual dimorphism in musteloids. Although much has been written about the causes of sexual dimorphism in musteloids (especially mustelids), there has been little investigation as to the degree of sexual dimorphism in different musteloid groups.

Therefore, based on data in the literature, we estimated sexual dimorphism in mean condylobasal skull lengths and mean body weights of the Melinae (badgers), Mustelinae (polecats, weasels, and martens), Lutrinae (otters), Mephitidae (skunks) and Procyonidae (raccoons and coatis) (Figure 3.2). The degree of sexual dimorphism in condylobasal skull length (CBL) is less than that in body weight. This is not surprising since the former is a linear measure whereas the latter is a cubic measure. However, even so the pattern is consistent with both measures. The Mustelinae show a much higher mean sexual dimorphism (1.71 body weight, 1.10 CBL) than other musteloid groups, which tend to display similar degrees of sexual dimorphism (1.3–1.38 body weight; 1.06–1.07 CBL) with the melines showing the least sexual dimorphism (1.22 body weight, 1.05 CBL). What is striking from this preliminary analysis is that the most carnivorous terrestrial musteloids, the mustelines, show the highest degree of sexual dimorphism.

Causes of sexual dimorphism among carnivorans are often discussed and centre around the following themes, which may not be mutually exclusive (Isaac 2005; Lindenfors et al. 2007). Sexual size dimorphism may be a consequence of sexual selection in polygynous species for larger males that compete for access to oestrous females. Females may also be smaller than males so that their total energy requirements are less than for males and so they can invest more energy in the development of young. Sexual dimorphism may also allow for a degree of niche separation between the sexes so that each sex can prey on animals of different sizes, thereby minimizing competition. Clearly there is interplay between these factors and considerations of population density, social behaviour, home-range size, length of oestrus and energy use (Ferguson and Larivière 2004). There is not space here to discuss further the causes and consequences of differential sexual dimorphism in musteloids but the theme is developed further in Macdonald et al., Chapter 6, this volume, and in Noonan et al. (2016).

Working from the outside in, let us take a closer look at the adaptations of musteloids.

Hiding in plain sight—pelage coloration and markings

Pelage has two main functions. First, pelage coloration and markings enable many musteloids to remain hidden from predators and prey. For example, weasels and stoats (*Mustela* spp.) at high latitudes moult into white winter fur to match the snow in contrast to the brown summer pelage. However, some markings may function in communication within and between species (see Buesching and Stankowich, Chapter 5, this volume). Second, the pelage ensures that musteloids are insulated to avoid excessive heat loss to (or gain from) the surrounding environment. This is especially important for weasels and stoats in colder northern latitudes, and also otters living in the sea and exposed to cold water for prolonged periods, owing to the high surface area to volume ratios of their elongated bodies (Kruuk 2006; King and Powell 2007).

Most musteloids have a uniform coloration either all over or dorsally, with typically paler coloration ventrally, providing counter-shading to remain hidden in a wide variety of habitats. Although most are brownish and dark, some, for example, Siberian weasel (*Mustela sibirica*), Malay weasel

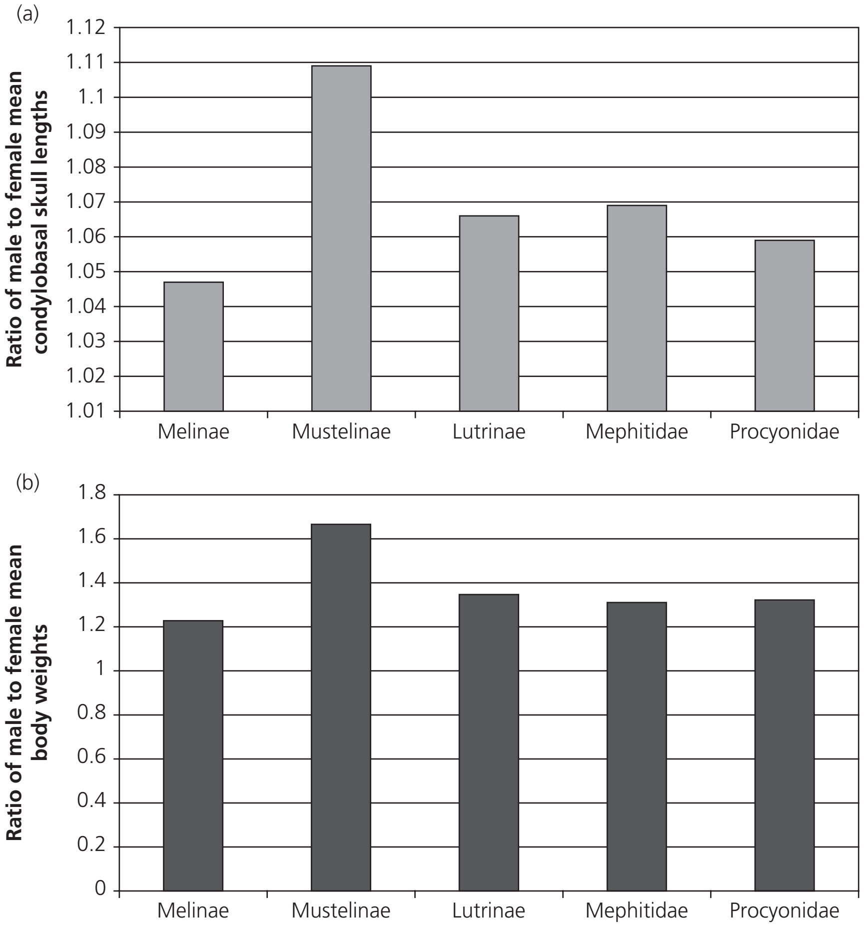


Figure 3.2 Sexual dimorphism in musteloids. a. Ratios of male:female body weights. b. Ratios of male: female condylobasal skull lengths. References: Abramov and Puzachenko 2005; Abramov and Tumanov 2003; Balharry et al. 2008; Begg et al. 2013; Birks and Kitchener 2008; d'Inzilla Carranza and Rowe-Rowe 2013; Copeland and Whitman 2003; Delahay et al. 2008; Dragoo and Sheffield 2009; Dunstone and Macdonald 2008; Elbroch 2006; Gittleman and Van Valkenburgh 1997; Gompper 1995; Gompper and Decker 1998; Heptner and Naumov 2002; Hwang and Larivière 2001, 2003, 2005; Jefferies and Woodroffe 2008; King and Powell 2007; Kinlaw 1995; Kitchener and Birks 2008; Larivière 1999c, 2001a, b, and c, 2002a and b, 2003a; Larivière and Walton 1998; Lindzey 2003; Lotze and Anderson 1979; Lynch and O'Sullivan 1993; McDonald 2013; McDonald and King 2008a and b; Meiri et al. 2005; Mendelssohn and Yom-Tov 1999; Monakhov 2011; Ohdachi et al. 2009; Pasitschniak-Arts and Larivière 1995; Redford and Eisenberg 1992; Reyes-Küppers 2007; Roberts and Gittleman 1984; Rosatte and Larivière 2003; Rozhnov and Abramov 2006; Somers and Nel 2013; Storz and Wozencraft 1999; Stuart and Stuart 2013; Van Gelder 1968; Vanderhaar and Hwang 2003; Verts et al. 2001; de Villa-Meza et al. 2011; Weckerley 1998; Wilson and Ruff 1999; Wisely et al. 2002; Youngman 1990.

(*Mustela nudipes*), Japanese marten (*Martes melampus*), Siberian or steppe polecat (*Mustela eversmanii*), and black-footed ferret (*Mustela nigripes*), are quite pale. Several have contrasting throat patches, including martens, some tayra (*Eira barbara*) individuals, and giant otters (*Pteronura brasiliensis*; see Groenendijk et al., Chapter 22, this volume). Others have striking pelage patterns. These include badgers (*Meles* spp., *Arctonyx* spp., *Melogale* spp., and *Taxidea taxus*), skunks (*Mephitis* spp., *Conepatus* spp., and *Spilogale* spp.), marbled polecats (*Vormela peregusna*), honey badgers, African striped polecats and African striped weasel, and grisons (*Galictis* spp.), which have mostly contrasting black-and-white pelages, comprised usually of white spots and stripes, with the dorsum often paler than the ventrum. Procyonids often have banded tails and dark facial masks surrounding the eyes, as do red pandas, and polecats and ferrets (*Mustela* spp.). This contrasting coloration is generally interpreted as aposematic (Newman et al. 2005; Caro 2009; Stankowich et al. 2011; Buesching and Stankowich, Chapter 5, this volume).

Aposematic or warning coloration, coupled with anal sacs that deliver a powerful, noxious olfactory deterrent, has evolved six times within the musteloids, demonstrating their value in effective deterrence of potential predators of these mostly small carnivorans. The highly contrasting black-and-white coloration of the skunks is well known, but is seen also in related stink badgers (*Mydaus* spp.), and among unrelated mustelids (e.g. Patagonian weasel [*Lyncodon patagonicus*], grisons, honey badgers, African striped polecats, polecats, ferrets, and marbled polecats, Caro 2009; Stankowich et al. 2011).

Although visual displays of contrasting pelage patterns mostly warn potential predators of chemical weapons, other mustelids, for example Old World badgers (*Meles* spp.), hog badgers (*Arctonyx* spp.), and American badgers (*Taxidea taxus*), have contrasting black-and-white head stripes that apparently warn of ferocious retaliatory behaviour, if attacked (Caro 2009). The mostly black-and-white honey badgers also combine ferocity with noxious anal gland secretions. Although wolverines are brown, they have contrasting pelage patterns and face masks that may signal that they are also fierce protagonists. Several skunk species are sympatric in parts of the Americas and it is likely that similar aposematic coloration coupled with anal sacs, producing noxious secretions, is an example of Müllerian mimicry (Caro 2009). A similar pattern is observed in Africa, where all known terrestrial mustelids south of the Sahara (African striped polecats, African striped weasel, and honey badgers) show aposematic warning coloration and chemical deterrents.

Dark facial masks are common among procyonids (raccoons [*Procyon* spp.], coatis [*Nasua* spp. and *Nasuella* spp.]), red pandas, some mustelids (e.g. polecats and ferrets), and skunks. Newman et al. (2005) reviewed the possible functions of facial masks in carnivorans, including as anti-glare devices, disruption of the face and hiding eyes from predators, or perhaps giving the impression of larger, more threatening eyes. However, they concluded that because facial masks are found mostly in mesopredators that risk predation from larger carnivorans, their facial masks probably have an aposematic role to deter predators, being particularly effective in low-light nocturnal conditions.

Contrasting facial stripes in badgers, dark facial masks in procyonids and ailurids, and throat patches in martens may have a primarily social function in species recognition and/or to warn predators or conspecifics of strong bites and sharp claws, but their specific functions for each species remain to be investigated. For example, the European badgers' facial stripes have also been interpreted as glare reducers, but other badger species (*Meles* spp.), may have less contrasting facial stripes or even lack them, so further investigation of why badgers have facial stripes is required. Banded tails in procyonids and ailurids probably function in signalling aggression and other social behaviours, depending on their positioning, but in ringtails and cacomistles (*Bassariscus* spp.), they have an apparently aposematic role, warning of noxious anal gland secretions (Caro 2009). Black tail tips in stoats (*Mustela erminea*), and long-tailed weasels (*Mustela frenata*), appear to divert the attention of attacking birds of prey, causing them to miss and result in lower predation risk (Powell 1982; see also Buesching and Stankowich, Chapter 5, this volume).

Keeping warm—pelage insulative properties

Although musteloids moult once or twice per year, depending on latitude (and the need for extra winter insulation), stoats, long-tailed weasels, and least weasels may also undergo dramatic changes in coloration from brown in summer to white in winter (King and Powell 2007). The mechanism for seasonal moulting in higher latitudes is similar whether the pelage changes coloration or not (Figure 3.3). Speed of pelage transition is affected by rate of day-length change, occurring in a few days in the Arctic and up to six weeks at lower latitudes. There are transition zones between animals that turn white in winter and those that do not, resulting in animals

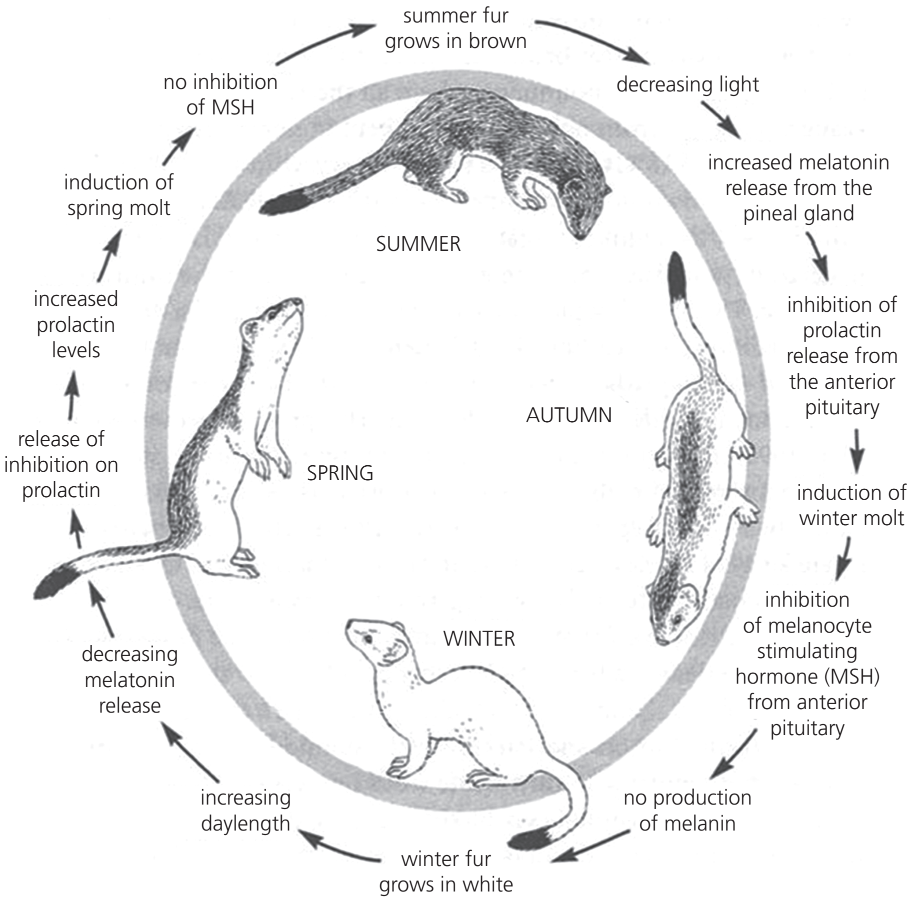


Figure 3.3 Seasonal moult cycle of stoats and weasels. Reproduced from King and Powell (2007).

of variable pelage coloration. In stoats this occurs between 52 and 56°N, in long-tailed weasels at 40°N in a 350 km-wide zone, and in least weasels at 59–60°N. King and Powell (2007) hypothesized that mustelines that partially change coloration in transition zones are effectively hybrids between northern populations with white winter pelage adapted to snowier, colder winters and southern populations with brown winter pelage adapted to milder, less snowy winters.

Owing to their small size and elongated bodies, most mustelids at colder, high latitudes require thick insulating pelages, and because of this high quality fur, have long been the target of the fur trade and fur farming (Harrington et al., Chapter 7, this volume). Otters, and especially sea otters, have exceptionally dense pelages (see Adaptations for aquatic living). Table 3.2 shows the seasonal differences in fur length and density for contour hairs, guard hairs, and underfur of mustelids and Figure 3.4 shows length of fur of various carnivorans. Autumn moult results in pelages with much higher densities of underfur, so that winter pelages may appear lighter than in summer, for example in polecats, but this is different to changes in fur coloration shown by stoats and weasels, which involves the replacement of the external guard hairs too. Wolverines' guard hairs resist hoar frost settling on them, so their fur does not become clogged with ice, while their underfur stays dry (Ewer 1973; Quick 1952). Chappell (1980) measured the insulation, radiation, and convection of small Arctic mammals using models covered in

Table 3.2 Pelage lengths, hair diameters, and hair densities of mustelids.

	Summer									Winter									
Species	Contour hair length (mm)	Contour hair diameter (μ)	Guard hair length (mm) (G)	Guard hair diameter (μ)	Underfur hair length (mm) (U)	Underfur hair diameter (μ)	Ratio G:U	Fur density (cm^{-2})	Locality	Contour hair length (mm)	Contour hair diameter (μ)	Guard hair length (mm) (G)	Guard hair diameter (μ)	Underfur hair length (mm) (U)	Underfur hair diameter (μ)	Ratio G:U	Fur density (cm^{-2})	Locality	Ref.
Martes zibellina	19.3	105	11.4–16.6	30–100	11.4	18			Moscow, Russia	42–56	85.1–114.7	29–50	25.9–114.7	25–38	11.1–22.2	1:55.6	19,988	Buryatia	2
Martes martes			23–27	100–150	11–12	15–16	1:4–5					36–38	75–90	22–22.5	14–15				2
Martes foina	25.1	112	13.2–19.9	48–154	9.7	22			Caucasus										2
Mustela nivalis	9.5	70	7.6–9	27–55	6	17			Pskov and Gellenor, Russia; Turkmenia	9.8	84	8.8–9.4	62–82	5.7	14	1:23	24,000	Vyborg, Russia	2
Mustela erminea	13.9	102	9.9–12.1	50–97	8.1	18	1:36.5	14,544	Moscow, Russia	15.75	96	11.5–13.7	55–98	9.1	14	1:27.1	19,232	Moscow, Russia	2
Mustela putorius			30–35							50	117	43	112	26	20	1:19–20	8500–9000		1,2
Mustela eversmanni	11.6	85	7.2–9.8	50–67	6.8	18			Askania Nova	16.8	110	11.6–14.1	82–111	8.8	13			Zaisan	2
Mustela lutreola	20.3	91	13.5	31	9.7	18	1:39.3	27,000	Tatar										2
Mustela sibirica	16.2	122	9.1–15.3	35–94	10.2	19	1:20.6	29,000	Shanganda River	35.0	106	25.2	86	18.0	14	1:14	8614	Sverdlovsk	2
Mustela sibirica			18–21				1:2–25.9	3476–4224	Sikhote-Alin, Russian Far East			27–31				1:3–34.7	9866–13,696	Sikhote-Alin, Russian Far East	2
Neovison vison							1:52.1	10,090		27	133	18.5–24.5	47–123	15.1	15	1:54.8	9266	Saltykovo	2

Neovison vison										27.9	100.9	21.9	47.4	13.3	15.3	1:63.6	14,712		2
Vormela peregusna	11.9	75	9.8–11.1	50–65	7.6	13	1:9.1	6660	Azerbaijan										2
Meles meles								550	Oxford										2
Lutra lutra							1:80	60,000–80,000		24.2		18.4		14.6		1:155	34,972		3
Lutra lutra	19.5	149	12.1–25	3.9–7.7	11.6	10	1:10.3	41,332		24.2		18.4		14.6			34,972		2
Lutra lutra										26.0	204	21.5	187	16.0	12			Urals	2
Lutra lutra										25.3	101			12.2	8			Sakhalin	2
Lutra lutra										24.4	170			15.8	11			W. Siberia	2
Lontra canadensis								58,000–70,000											3
Enhydra lutris			8.2–26.9	44–106	4.6–15.8	7.6–11.9	1:100+	26,413–164,662				27.7	123.9	22.5			16,325		3, 4

References: 1—Heptner and Naumov 2001; 2- Sokolov 1982; 3—Kuhn et al. 2010; 4—T.D. Williams et al. 1992

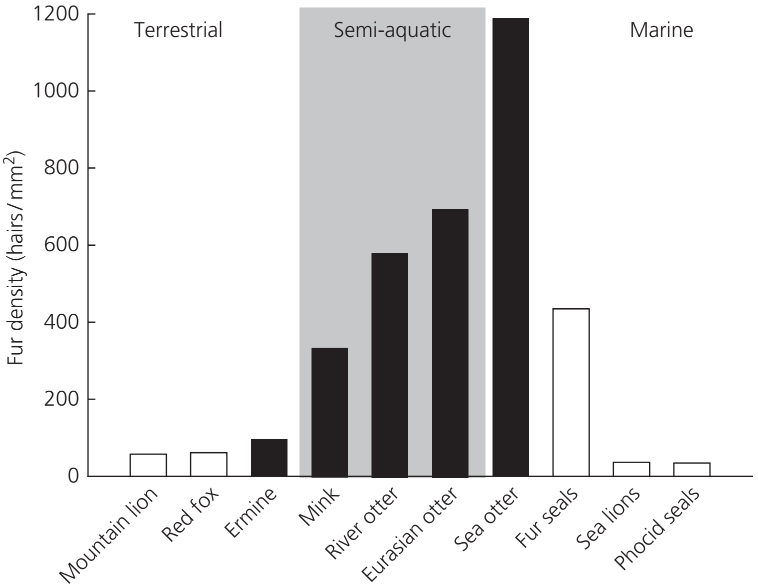


Figure 3.4 Fur density of mustelids and other carnivorans. From Liwanag et al. (2012).

fur. He found that insulation is correlated with fur thickness and density, so that weasels and stoats are actually relatively poorly insulated compared with lemmings (*Dicrostonyx torquatus* and *Lemmus sibiricus*, that have longer fur, 6.5–10.5 mm), and shrews (*Sorex* spp., that have short, but unusually dense fur). However, insulation loss was more rapid with increasing wind velocity in longer furred lemmings (35% loss from 1 to 6m per s) compared with shorter furred mustelids (25%), which may be partly due to fur layer compaction by wind pressure (Chappell 1980). Unlike other high-latitude mustelines, weasels and stoats cannot moult into long fur in the winter, because that would impede their locomotion in rodent burrows or under the snow, so their high surface area:volume ratio means that to maintain a body temperature of 39–40°C at rest in summer, a least weasel requires twice as much energy at three times the cost as a lemming of similar size, and that in winter in Alaska it may have to generate six times the resting basal metabolic rate to maintain body temperature (King and Powell 2007).

Russell and Tumlison (1997) compared the summer and winter guard hairs of Arctic mammals. They found that in stoats and weasels in the upper shaft of the guard hairs the medulla width and number of air cells within the medulla increased from summer to winter. This could have two effects; firstly, by allowing more scattering of light, the whiteness of the unpigmented hair may be enhanced, and secondly, by trapping more air, the insulative properties of the hairs may be increased. Interestingly, the lower shaft decreased in diameter in winter stoats, which Russell and Tumlison (1997) suggested could allow hairs to bend more easily in the wind to avoid disruption of the fur and also to allow a greater density of hairs for increased insulation.

Fur density is also correlated with buoyancy, because the pelage traps air when animals dive under water (Fish et al. 2002). For example, sea otters (Estes et al., Chapter 23, this volume) have the highest fur density of the aquatic/semi-aquatic musteloids (1,188.8 per mm^2), with a buoyancy force of 0.94 N compared with a fur density of 803.12 per mm^2 and a buoyancy of 0.82 N for the North American river otter, while the American mink's fur density of 338.45 per mm^2 generates a buoyancy force of 0.41 N (Fish et al. 2002).

Musteloid sense organs and senses

Eyes and vision

Mustelids have generally forward-facing eyes, but not to the same degree as in felids. For example, domestic ferrets (*Mustela furo*) have a binocular visual field of 80° and orbital convergence of 35.3° Compared with 120° and 65.4° For domestic cats (*Felis catus*) (Heesy 2004). Forward-facing eyes are advantageous for judging distances, which is essential for predators trying to catch prey or for arboreal species when leaping. Conversely, laterally-facing eyes are better at detecting potential predators, so that perhaps the smallest mustelids have an eye orientation and degree of binocular vision that balances the need to be effective predators as well as avoiding predation themselves.

Sunlight is 100 billion times brighter than overcast moonless nights (Kirk 2006), so eye structure and function varies considerably depending on preferred timing of daily activity. Nocturnal species, for example, badgers, raccoons, ringtails, and red pandas, have relatively larger and more curved eyeballs for collecting maximum light for the brightest retinal images, higher ratios of photoreceptors to ganglion cells (i.e. summation), and increased ratios of light-sensitive rods to cones than diurnal species. In contrast diurnal species, for example yellow-throated martens (*Martes flavigula*), have increased visual acuity to resolve fine spatial details through reduced retinal summation, reduced eyeball size and curvature for larger retinal images, and increased cone:rod ratios. Cathemeral species, for example weasels, marbled polecat, otters, and stink badgers, have intermediate eyeballs (Kirk 2006). European polecats and Asian small-clawed otters (*Aonyx cinereus*) have similar visual acuities to each other both in and out of water, but humans (out of water) have visual acuities ten times greater than those of otters (Ewer 1973).

Like many other carnivorans, musteloid eyes have a *tapetum lucidum*, a reflective layer of cells behind the retina, which reflects back any light that misses the photoreceptors onto the retina, thereby enhancing sensitivity of nocturnal vision. American minks' eyes have only a few layers of tapetal cells, which contain little, haphazardly arranged reflective material, suggesting a nonfunctional *tapetum lucidum* (Braekevelt 1989), but the domestic ferret does have a functional *tapetum lucidium* (Ollivier et al. 2004). Little has been recorded about pupil shape in musteloids, although weasels' and stoats' pupils close to horizontal slits (King 1989), which probably matches the horizontal visual streak of high densities of photoreceptors in their retinae and adjacent ganglion cells (King and Powell 2007; Heffner and Heffner 1992, below).

A major problem for aquatic and semi-aquatic species is how to adjust to seeing in air and under water, when the cornea cannot refract light entering the eyes. In otters and American mink (*Neovison vison*) the iris sphincter muscles are well developed to squeeze the anterior lens, which forms a protuberance, to increase its curvature and increase light refraction when submerged (Dunstone 1993; Figure 3.5).

As in many other carnivorans, mustelids have three visual pigments in the photoreceptor cells of their retinae. For domestic ferrets these include a rod opsin, with maximum absorbance (λ_{max}) of 505 nm, a short (S) wavelength cone opsin with λ_{max} of c.430 nm and a medium-long (M/L) wavelength cone opsin with λ_{max} of 558 nm (Calderone and Jacobs 2003). The ferret's retina contains about 1.3 million cones, but M/L cones outnumber S cones by 14:1. Sea otters have similar visual pigments, but with slightly different λ_{max}s: rod opsin 501 nm, S cone opsin 441 nm, and M/L cone 545 nm (Levenson et al. 2006). Even though they have cone opsins, musteloids are not trichromatic like humans and probably do not see colours as such, but rely on cones to see in daylight when rod visual pigments are bleached. Among procyonids, kinkajous (*Potos flavus*) and raccoons have monochromatic cone vision (long wavelength [L] cones

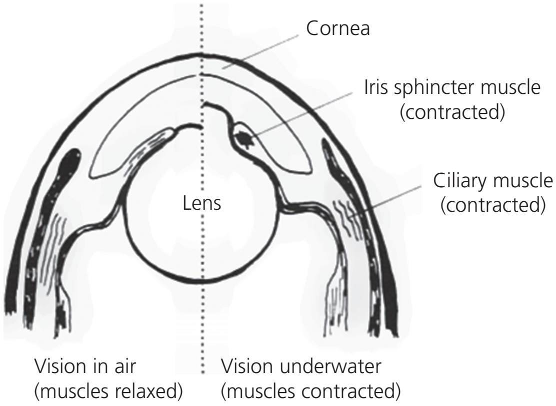


Figure 3.5 Cross-section through otter's eye showing mechanism for accommodation under water. From Dunstone 1993.

only) (Jacobs and Deegan 1992), consistent with their nocturnal lifestyles, but diurnal coatis have S and L cones.

Examining ganglion cell distributions in mammal retinae reveals how their eyes are adapted to being most sensitive to detecting predators or prey in diverse environments. Weasels have a horizontal visual streak with a maximum ganglion cell density of 17,895 cells per mm^2, which is more than three times greater than that of domestic ferrets (that have ganglion cell densities up to 5,200 cells per mm^2, Henderson 1985). Thus weasels' eyes have a low visual acuity (ability to resolve detail) of 2.2 cycles/degree and are most sensitive to detecting prey horizontally against the horizon (Heffner and Heffner 1992, Figure 3.6). Sea otters also have a naso-temporal (i.e. horizontal) visual streak with an area of high ganglion cell density of 4,000 cells per mm^2 corresponding to a much higher visual acuity, compared to that of weasels, of 50–60 cycles per degree (Mass and Supin 2007; Figure 3.6). Humans have a similar visual acuity of 67 cycles per degree (Heffner and Heffner, 1992).

Ears and hearing

Ear flap structure in mustelids appears correlated with preferred habitat and behaviour. Ear flaps are larger in the arboreal martens, smaller in terrestrial species, including mustelines, wolverines, ferret badgers (*Melogale* spp.), tayra, grisons, African striped polecats, and smallest in fossorial and/or social forms, for example badgers, where large ear flaps would be susceptible to injury underground or in intraspecific agonistic encounters, and aquatic forms, for example otters, Lutrinae (Pocock 1920a, b, 1921b, c, 1926), where they could affect swimming and diving efficiency. Sea otters' ears open as slits, presumably lacking flaps that would affect streamlining and may risk thermal injury and excessive heat loss in cold high-latitude seas. Honey badgers and stink badgers have ear flaps reduced to thickened ridges of skin (Pocock 1920a), presumably to protect them against insect stings and/or injury when digging. Fossorial species can close up their ears to prevent soil ingress while digging, and otters' ears have valves to prevent water ingress while swimming and diving.

There have been few investigations detailing the upper limits to hearing frequencies in musteloids (Table 3.3). The upper range for humans (*c.*20 kHz) is much lower than those recorded for musteloids. As suggested for other predatory carnivorans (Ewer 1973), the ability to hear high-frequency sounds allows musteloids to hear the high-pitched communication of rodents and other small mammals, and thus detect their presence. For example, American mink respond to ultrasound up to 40 kHz, which is within rodents' vocal range of frequencies (Powell and Zielinski 1989). However, weasels can hear at even greater frequencies, presumably reflecting the

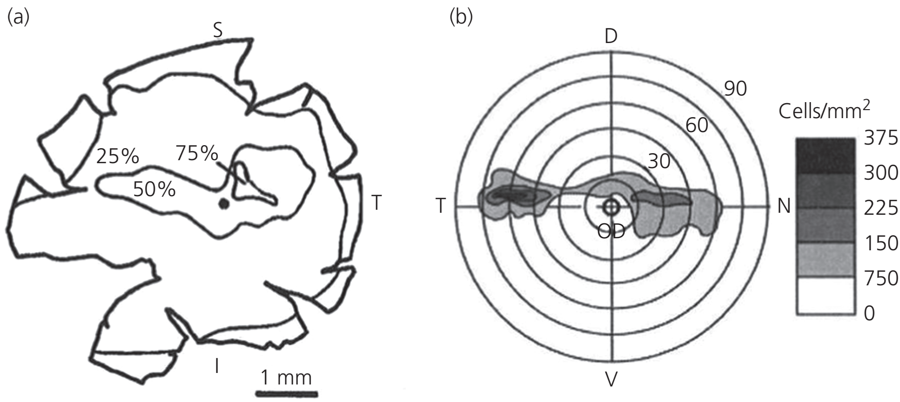


Figure 3.6 Visual streaks of a. weasel and b. sea otter, showing horizontal area of high density of ganglion cells. Reproduced from Mass and Supin (2007) and Heffner and Heffner (1992).

Table 3.3 Upper limits of hearing (kHz) in musteloids and humans. Sources: Gunn 1988; Kelly et al. 1986; Heffner and Heffner 1985; Ghoul and Reichmuth 2014; Voigt et al. 2013; Wollack 1965.

Species	Upper limit	Maximum sensitivity	Octaves
(kHz)	**(kHz)**		
Raccoon	38	1–16	7.1
Weasel	60.5	2 (range 1–16)	
Ferret	44	8–12	5.3
Eurasian otter	30	4	
River otter	35	16	
Sea otter[1]	38	2–26	3.7
Sea otter[2]	38	1.2–27	4.5
Human	20	1–4	8.5

[1]underwater, [2]aerial

higher-pitched vocalizations of their even smaller prey (Table 3.3).

Lower limits to hearing range from 200–300 Hz, which is ten times higher than that of humans (*c*.0.2 kHz). Overall hearing ranges are not vastly different from those of humans, but are shifted higher in musteloids. For example, human hearing ranges over *c*.8.5 octaves compared with seven octaves or less in musteloids (Table 3.3), which is less than for some felids and viverrids and more than in canids and ursids.

Smell and taste—detecting chemicals

Musteloids have a good sense of smell for detecting prey and communicating using scent marks. Musteloids typically use the olfactory epithelium on the turbinate bones of their noses, but some species, for example domestic ferrets and European badgers, also have a vomeronasal organ (VNO), with an opening into the roof of the mouth (Kelliher et al. 2001; Buesching and Stankowich, Chapter 5, this volume). This is a paired olfactory organ, positioned in a cartilaginous capsule at the base of the nasal septum, whose occurrence has been little investigated in musteloids. For example, tayras exhibit flehmen (a characteristic open-mouthed response to intraspecific scent secretions, Ewer 1973), which usually involves the VNO in other carnivorans, but this is so far unknown in tayras. The surface area of the VNO's olfactory epithelium is very small (*c*.1.6 cm^2), but impulses from the VNO's olfactory receptors are processed in a small discrete accessory olfactory bulb (0.15% of olfactory bulb volume), which is caudal and on the medial surface of the main olfactory bulbs of the anterior brain. The function of the ferret's and badger's VNOs is unknown, but in other carnivorans it usually detects the reproductive status of individuals from scent secretions by detection of non-volatile ingredients in scent (either very long-chained fatty acids or proteins, i.e. MUPs).

Van Valkenburgh et al. (2011) used CT scanning to look at volumes and surface areas of turbinate bones in carnivorans. The maxilloturbinates within noses warm and moisten inhaled air, while the ethmoturbinates bear most of the olfactory receptors. Terrestrial musteloids have greater ratios of ethmoturbinate to maxilloturbinate surface areas (*c*.2–3), with wolverines having the largest ratio (4–5), probably owing to their scavenging behaviour and need to detect carcasses. Interestingly, aquatic and semi-aquatic musteloids evolved independently much lower respiratory to olfactory turbinate surface area ratios (*c*.0.5–0.8), suggesting less reliance on olfaction, but this may also reflect the need for relatively larger maxilloturbinates to prevent thermal loss from exhaled air by acting as counter-current heat exchangers. In water, aquatic mustelids lose body heat rapidly so preventing heat loss in this way may be an important adaptation (we discuss adaptations to an aquatic lifestyle further towards the end of this chapter).

The mammalian sense of taste is through G protein-coupled receptors (GPCRs) (Jiang et al. 2012). Sweet foods are detected by heteromers (combinations of two different receptor subunits) of two type 1 GPCR taste receptors, i.e. Tas1r2/Tas1r3, and umami (savoury) flavours are mediated through Tas1r1/Tas1r3. Bitter tastes are detected by type 2 GPCR receptors, Tas2rs (Jiang et al. 2012). Cats cannot taste sweetness, because of pseudogenized (hence non-functional) Tas1r2 genes that affect the Tas1r2 taste receptors' ability to respond to sweet foods. Among mustelids functional Tas1r2 genes occur in domestic ferrets and North American river otters, but non-functional genes occur in Asian small-clawed otters

(Jiang et al. 2012). Raccoons and red pandas also have intact and active Tas1r2 genes, presumably related to their omnivorous diets, but it is unclear why carnivorous ferrets and North American river otters (*Lontra canadensis*) can taste sweetness.

Touch

The most important tactile sensory organs in musteloids are their well-developed vibrissae (whiskers). Musteloids mostly have the typical carnivoran arrangement of vibrissae, with subtle variations related to ecological niches (Figure 3.7; Pocock 1920a, b, 1921a–c, 1926, 1928). Snouts are usually well endowed with mystacial (muzzle) and submental (under the chin) whiskers, which are important in foraging, especially when catching prey. Superciliaries (above the eyes), lower and upper genals (on the cheeks), and unpaired interramals (on the throat) are important in preventing accidental injury, especially to eyes, and allowing unimpaired locomotion at night or in burrows. For example, the mainly terrestrial coatis have stouter vibrissae than arboreal kinkajous, which have only a single genal tuft (Pocock 1921a). Vibrissae are longer and more abundant in predators, for example martens, mustelines, and striped polecats, compared with those of fossorial Old World badgers, honey badgers, and striped skunks (*Mephitis mephitis*), which may damage vibrissae while digging (Pocock 1920a, b, 1921c). Ferret badgers have many long whiskers, with the submentals being unusually well developed, perhaps for terrestrial foraging (Pocock 1921c). Vibrissae are very well developed, abundant, and stiff in otters (Lutrinae, Pocock 1921b), for detecting prey movements under water, but Congo clawless otters

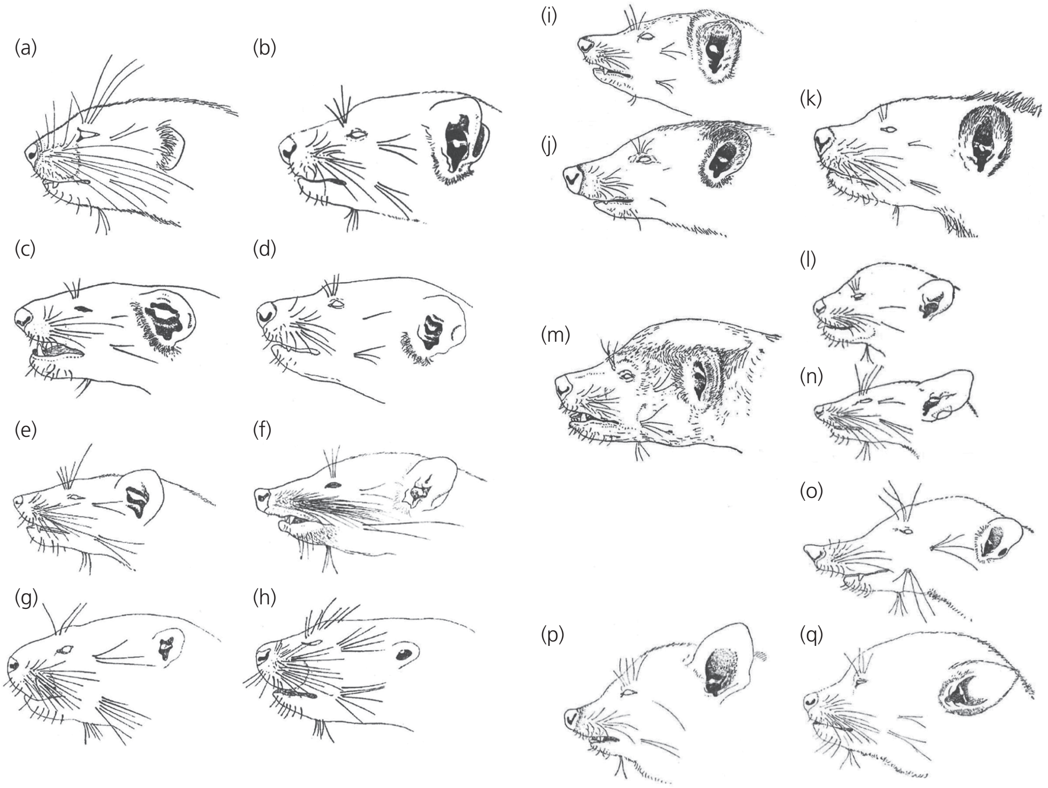


Figure 3.7 Vibrissae of musteloids. a. *Lyncodon patagonicus*, b. *Martes flavigula*, c. *Grison furax*, d. *Eira barbara*, e. *Ictonyx striatus*, f. *Melogale personata*, g. *Amblonyx cinerea*, h. *Hydrictis maculicollis*, i. *Taxidea taxus*, j. *Meles meles*, k. *Gulo gulo*, l. *Potos flavus*, m. *Mellivora capensis*, n. *Bassariscus astutus*, o. *Nasua nasua*, p. *Procyon lotor*, q. *Ailurus fulgens.* From Pocock, 1920a, b, 1921a, b, c, 1926, 1928.

(*Aonyx congicus*) apparently lack superciliary and upper genal tufts, presumably because their diet is richer in invertebrates (Harris 1968). European badgers may lack upper genal tufts, although why tayras lack interramal whiskers is unclear.

Many musteloids have laterally projecting carpal (wrist) vibrissae that appear to be important in prey capture (Figure 3.8). They are recorded in coatis, kinkajous, ringtails, olingos (*Bassaricyon* spp.), raccoons (poorly developed), red pandas (poorly developed), ferret badgers, European badgers, Patagonian weasels, African striped polecats, mustelines, grisons, martens, and tayras (Pocock 1921a–c, 1926, Figure 3.8). Carpal vibrissae are well developed in predators, but (similar to facial vibrissae) much less so in fossorial forms, which instead have a swelling where the vibrissal nerve ends, for example, honey badgers and American badgers, because carpal vibrissae would be broken off while digging underground.

The skin of mammals is usually well-endowed with touch receptors for sensing their environments, but these have been hardly investigated in musteloids. Raccoons are renowned for apparently 'washing' their food or foraging in shallow water. Their forefeet are quite dexterous (see Paws and claws) and well-endowed with touch receptors compared with those of coatis (Welker et al. 1964, Figure 3.9). Raccoons and humans have very similar abilities to discriminate (by touch) between spheres differing in diameter by only 0.53% (Welker et al. 1964).

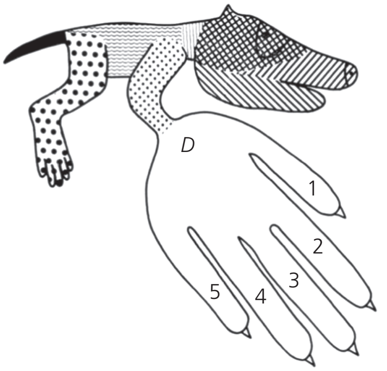


Figure 3.9 Relative degree of enlargement of body subdivisions in the ventro-basal nuclear complex (Vb) of the dorsal thalamus of the brain of the raccoon, showing the importance of the manual tactile sense, which accounts for almost 50% of the Vb volume. From Welker and Johnson 1965.

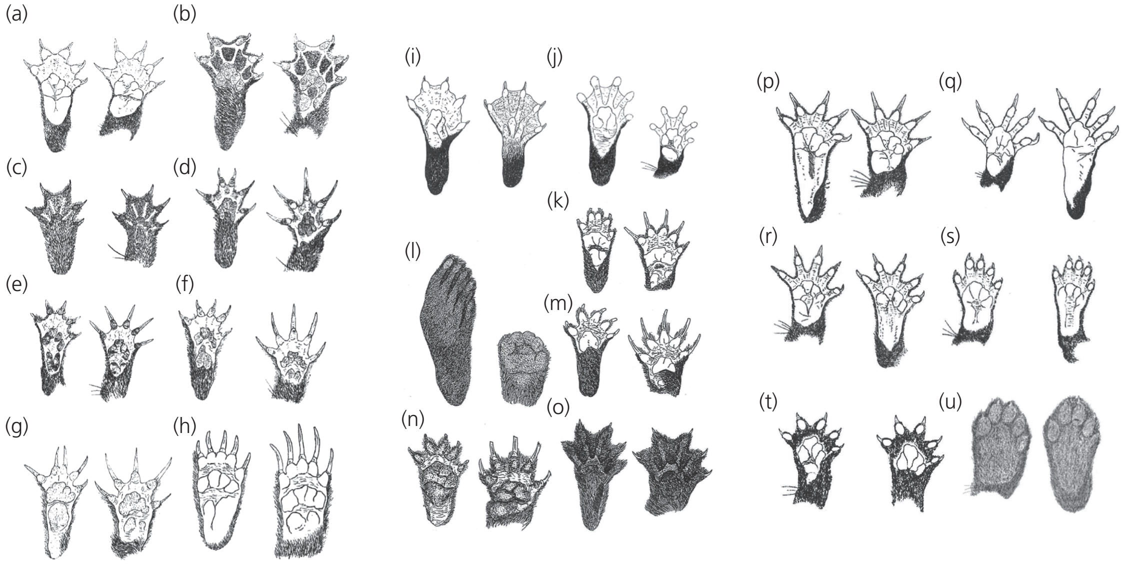


Figure 3.8 The undersides of hind (left) and front (right) paws of musteloids. a. *Eira barbara*, b. *Martes flavigula*, c. *Mustela putorius*, d. *Ictonyx striatus*, e. *Lyncodon patagonicus*, f. *Spilogale putorius*, g. *Mephitis mephitis*, h. *Mydaus javanensis*, i. *Hydrictis maculicollis*, j. *Aonyx capensis*, k. *Enhydra lutris*, l. *Meles meles*, m. *Taxidea taxus*, n. *Mellivora capensis*, o. *Gulo gulo*, p. *Nasua nasua*, q. *Procyon lotor*, r. *Potos flavus*, s. *Bassaricyon* sp., t. *Bassariscus astutus*, u. *Ailurus fulgens* From Pocock 1920a, b, 1921a, b, c, 1926, 1928.

Communication—scent glands

Musteloids communicate using visual displays (see Pelage coloration and markings) and vocalizations, but the most important channel of communication is through scent marks from specialized cutaneous glands, although they frequently make use of urine and faeces that are free as waste products (see also Buesching and Stankowich, Chapter 5, this volume). Musteloids have a variety of scent glands that produce secretions for marking home ranges and territories, but also for communicating other information, for example, individual, age, sex, aggression/territoriality, and reproductive state (Macdonald 1985). The principal scent glands of musteloids are anal sacs (often called anal glands), foot glands on foot pads and in interdigital cavities, ventral glands which open onto the abdomen in front of or behind the genitals, and subcaudal glands that open ventrally at the root of the tail.

Musteloids, especially mustelids and mephitids (but with some exceptions), have well-developed anal sacs, which are paired glands that open via ducts into the rectum either side of the anal orifice (Macdonald 1985; Pocock 1920a, b, 1921a–c, 1926, Figure 3.10). Anal sacs are not enlarged in martens, wolverines, tayras, otters, badgers, and stoats and weasels (except polecats and ferrets), and, not surprisingly, are completely absent in the aquatic sea otters. Old World badgers also have typical (non-enlarged) anal sacs, but American badgers' anal sacs open into a protuberant anus and produce a sweet-smelling secretion. Anal sacs are enlarged in honey badgers, grisons, African striped polecats, polecats, ferrets, Patagonian striped weasels, skunks, and stink badgers, and produce foul-smelling secretions, which are squirted at potential attackers to deter them. Heidt and Morgans (1982) examined anal sac histology in five species of skunks, including *Mephitis mephitis, M. macroura, Conepatus mesoleucus, Spilogale putorius*, and *S. pygmaea*, and concluded that they are highly enlarged and modified apocrine sweat glands. The walls of the anal sacs are made up of a keratinized mucosal epithelium and layers of striated muscles, which are encapsulated by a thick fibrous layer of connective tissue. The papilla connecting the sac to the anus has a similar histology and its lumen closes up into a u-shape, presumably to prevent inadvertent leakage of secretions. The mucosal layer of the anal sac and papilla are heavily keratinized to withstand high pressures produced when anal sac secretions are forced out. Within anal sacs, glandular tissue occurs in two to three lobes, sometimes subdivided into lobules (in some species) on one side. The noxious anal sac secretion is squirted vigorously via papillae at great pressure, either as a highly atomized mist, or mostly like rain drops, and spread through an arc of 30–45°.

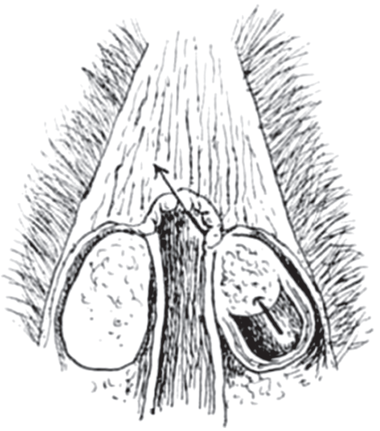


Figure 3.10 The anal sacs of the Patagonian striped weasel. From Pocock 1926.

Anal sac secretion is apocrine (secretions released in membrane-bound vesicles from the surface of secretory cells) and sebaceous (secretion (sebum) produced by the rupture of secretory cells) in origin in most musteloids (Macdonald 1985). The sac comprises an inner sebaceous layer that produces waxy monoesters and an inner apocrine layer that produces an immiscible aqueous solution—both secretions are rich in sulphur-containing hydrocarbons, for example thietanes and dithiolanes (dithiacyclopentanes) in stoats, weasels, polecats, and American mink (although derived from a different biochemical pathway in mink). Different compounds are produced by the anal sacs of Eurasian otters (*Lutra lutra*), badgers, and martens. The apocrine secretion is modified by anaerobic bacteria in the anal sac prior to use. For example, 2-piperidone is produced by anaerobic bacteria in the American mink, which also produces two sulphur-rich compounds that are common to eight other mustelid species (Sokolov et al. 1980).

Some musteloids have unusual glands. Badgers (*Meles* spp.) and hog badgers (*Arctonyx* spp.) have subcaudal glands inside subcaudal pouches (Macdonald 1985; Buesching et al. 2002). Honey badgers have a muscular and eversible anal pouch, and when everted it dribbles a suffocating anal sac secretion (Pocock 1908, 1920a; Kingdon 1977). Macdonald (1985) noted a bristle in the ratel's anal sac from Pocock (1920a), but this was added by the author to indicate a connection between sac and rectum and is not an anatomical feature of this species. American badgers have an abdominal or ventral gland, as do wolverines and martens, for marking branches and other objects. Tayras may possess a gland in a depression above the anus (Macdonald 1985). Some mustelines probably have chin or facial glands, which they rub on objects or each other, for example sable (*Martes zibellina*), fishers (*Pekania pennanti*, after eating, drinking, or playing), American martens, long-tailed weasels, stoats, and ferrets (Macdonald 1985). Fishers and other martens have plantar glands within whorls of hair on their hindfeet (Buskirk et al. 1986).

Procyonids also have anal sacs and ventral glands (Macdonald 1985). Anal sacs are small in raccoons and cacomistles (*Bassariscus sumichrasti*), but they are similar to those of dogs, whereas coatis have anal sacs that open as a series of four to five parallel slits formed by folds of the anal epithelium (Pocock 1921a). Otherwise scent glands are poorly known among procyonids. Kaufmann (1962) noted penile dragging in *Nasua narica* and A.C.K. has seen this behaviour in *N. nasua*. This appears to be a form of scent marking, which uses the males' preputial glands (Shannon et al. 1995). Kinkajous lack anal sacs, but have abdominal, sternal, and mandibular glands on the lower lips and jaws, which they use for scent marking in trees (Pocock 1921a; Macdonald, 1985; see Brooks and Kays, Chapter 26, this volume). The red panda has typical anal sacs, but the anal skin is also glandular and indented, similar to the anal pouches of mongooses (Pocock 1921a).

Skulls, jaws and teeth—processing food

Skull architecture in musteloids varies in relation to diet and body size, although members of the same clade tend to share similar cranial morphology (Figure 3.11). Herbivory and piscivory impose the most extreme morphological constraints on musteloid skulls, while carnivory and omnivory favour some morphological overlap between some members of different families (e.g. small predatory mustelines and mephitids).

Mustelids have the most distinctive and peculiar skull shapes of any carnivoran group (Ewer 1973; Radinsky 1981), which include generally a short rostrum, elongated braincase with sagittal crest, short lateral profile with small orbits, and enlarged carnassials (P4/m1). Mephitids have similar skulls, although modified to their generally insectivorous diet (enlarged M1, well-developed crushing molars), while most procyonids have a longer rostrum, no sagittal crest, and a higher lateral skull profile. Major skull modifications between and within these clades are closely linked to arrangements of masticatory muscles and diet. The temporalis, masseter, and pterygoideus muscles represent the main masticatory complex for closing the jaws, while the digastric muscle is involved in jaw opening (Turnbull 1970). Where the temporalis and masseter muscles are similar in size, this generally reflects a predatory lifestyle (i.e. small mustelines); otters have an enlarged digastric.

Predatory musteloids generally have a relatively powerful bite force and there is an evolutionary tendency for higher bite forces among mustelids; high bite force quotients (BFQs) characterize species that kill prey larger than themselves (Christiansen and Wroe 2007). Mephitids have the lowest BFQs, owing to insectivorous diets, while omnivorous procyonids have BFQs similar to those of mustelids. So, how are powerful bite forces achieved by musteloids? Their skull architecture and dentition are very different to those of more specialized killers, the felids (Ewer 1973). The very thin zygomatic arches of the most predatory—and smallest—mustelines (stoat and weasels) indicate very small attachment areas for the masseter muscle complex, but this is counterbalanced by an elongated braincase, providing attachment for anterior and well-developed posterior temporalis muscles. The posterior temporalis muscle fibres produce maximum forces horizontally, when jaws are nearly closed. This system, with long, straight upper canines, is very efficient for crushing the necks and skulls of small rodents (Ewer 1973).

The upper and lower canines of stoats and weasels are frequently fractured, owing to high

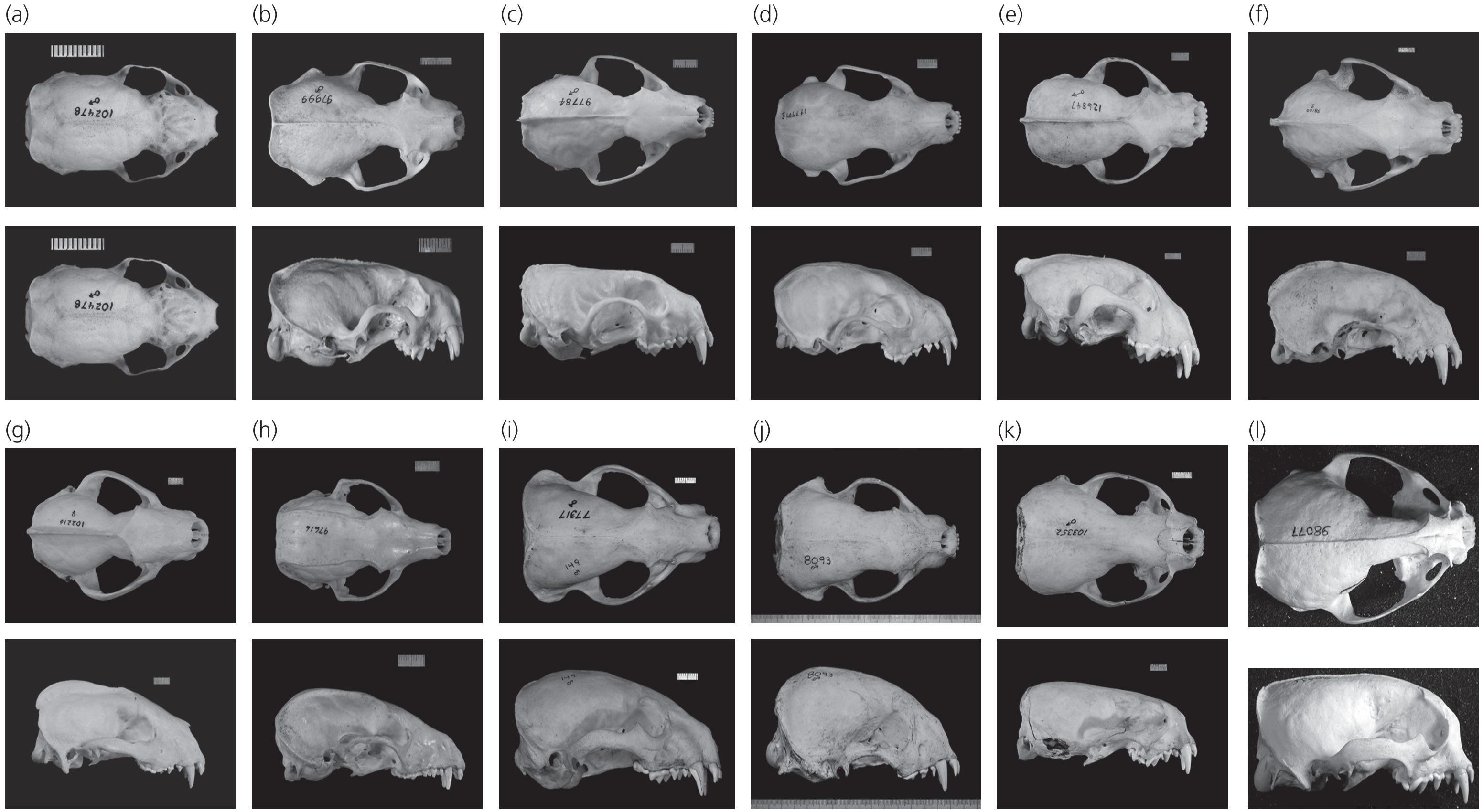


Figure 3.11 Dorsal and lateral views of musteloid skulls. a. *Mustela erminea*, b. *Neovison vison*, c. *Martes americana*, d. *Pekania penannti*, e. *Eira barbara*, f. *Gulo gulo*, g. *Meles meles*, h. *Melogale moschata*, i. *Taxidea taxus*, j. *Mellivora capensis*, k. *Lontra canadensis*, l. *Pteronura brasiliensis*, m. *Enhydra lutris*, n. *Galitcitis vittata*, o. *Ailurus fulgens*, p. *Procyon cancrivorus*, q. *Nasua narica*, r. *Bassaricyon gabbii*, s. *Bassariscus sumichrasti*, t. *Potos flavus*, u. *Mephitis macroura*, v. *Spilogale putorius*, w. *Conepatus chinga.*

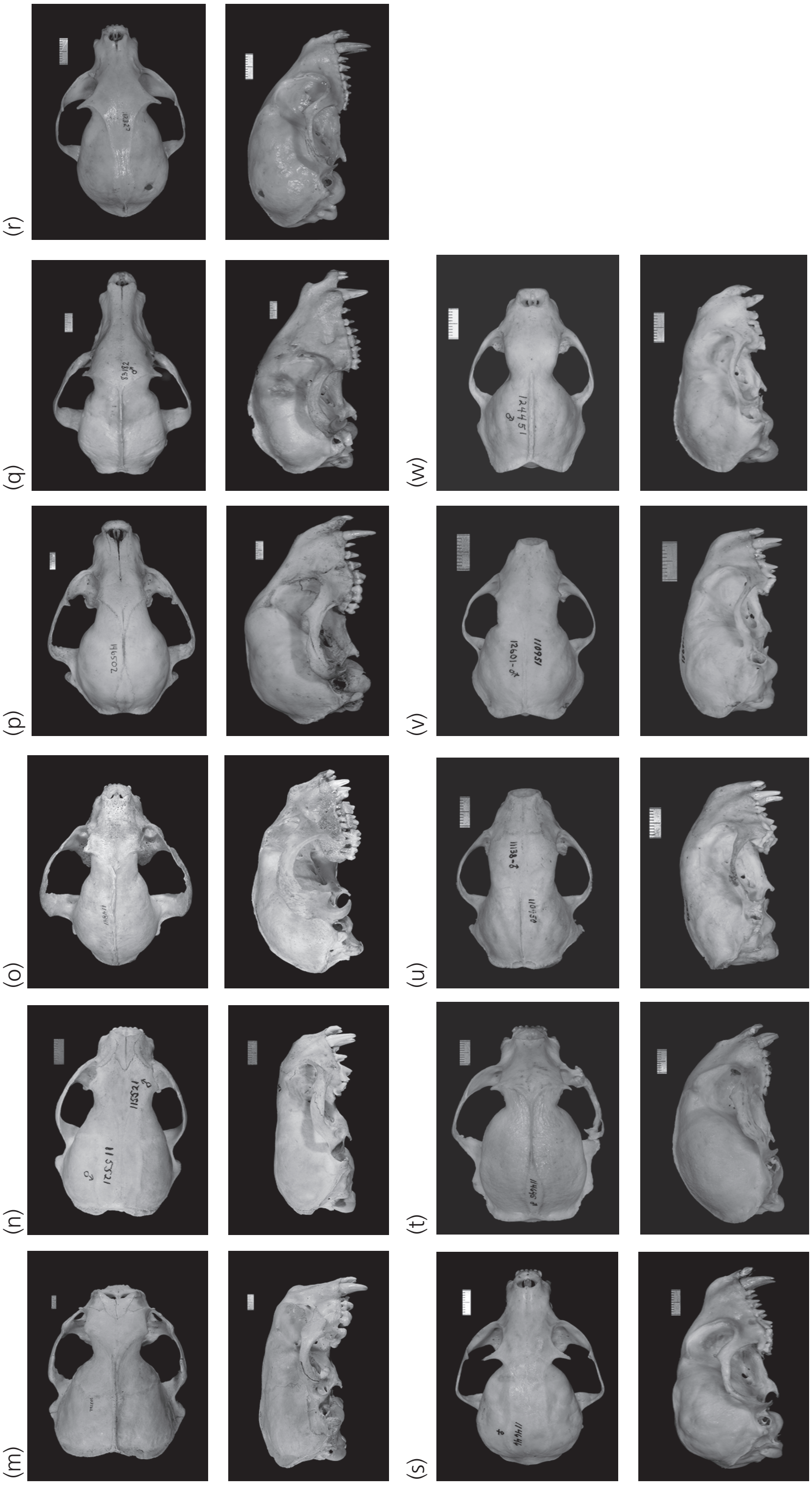


Figure 3.11 *Continued*

mechanical stresses in their canines (Van Valkenburgh 2009; Meloro 2012). Robust glenoid fossae (articulations on the skull for the lower jaw) prevent lateral mandibular (jaw) movements and may be so tight that mandibles cannot disarticulate, as in, for example, European badgers. The mustelid jaw mechanism dissipates high stresses at the craniomandibular articulation due to torque exerted by masticatory muscles. The low, narrow skull profile of small predatory mustelids is difficult to interpret, although Ewer (1973) suggested this is an adaptation for hunting small prey in burrows. If so, the transition to a semi-aquatic lifestyle required relatively simple skull changes. Otter skulls are similar in shape to those of weasels, with a long braincase and narrow, low lateral skull profile, although otters have a more expanded basi-occipital area for attachment of powerful neck muscles (Lee and Mill 2004). Otters also have relatively weak zygomata, indicating the greater importance of the temporalis muscle (for closing and pulling back the mandible), although its relative weight is less in otters specializing on crustaceans or molluscs, where the masseter muscle is more important for crushing shelled prey (e.g. *Aonyx, Enhydra*) (Ewer 1973; Riley 1985). Among procyonids, raccoons have a temporalis with a higher weight relative to the masseter (60% vs. 15%, Gorniack 1986). The arrangement of the lines of action of jaw muscles suggests very similar jaw movements of musteloids to those of typical carnivorans, with large vertical components and limited lateral movements (Turnbull 1970). Coatis and kinkajous have unusual skull architectures among carnivorans; coatis have the longest rostrum (snout) relative to braincase length among musteloids, which is related to their omnivorous lifestyle and elongated rhinarium (hairless surface around the nostrils), which they use to search for food on the ground. In comparison, kinkajous are specialist herbivores that are peculiar outliers within the Carnivora and Procyonidae, owing to their very tall, globular skulls, with large orbits and high, straight nasals. Some of these features occur also in red pandas, but are less well developed (see Box 3.1).

Box 3.1 Red panda

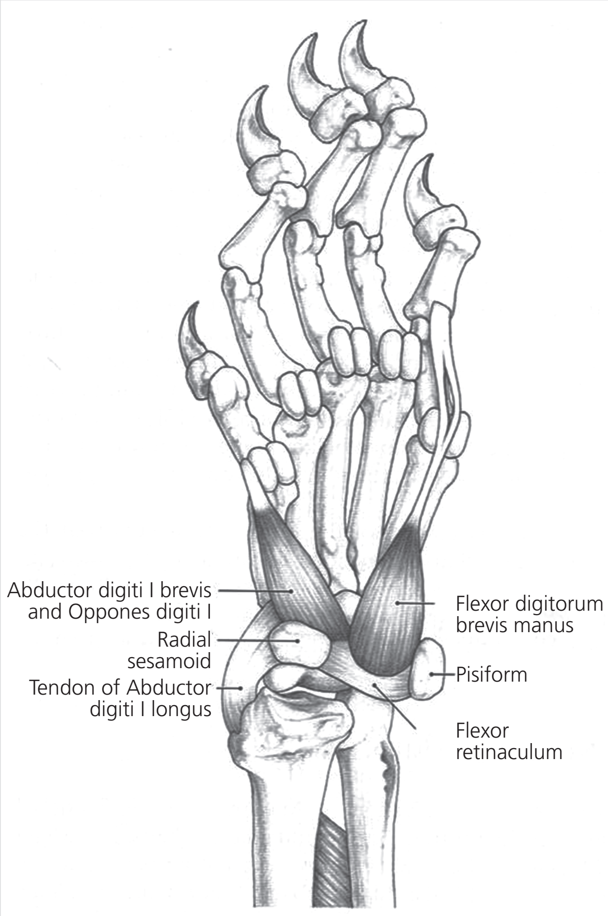
Red pandas (Hu et al., Chapter 29, this volume) show remarkable convergent evolution with giant pandas. This has led to consistent confusion as to which family the red pandas should be placed in. They have been variously treated as procyonids or in a separate family with the giant panda or in their own family, the Ailuridae (Pocock 1939; Kundrát 2011). Molecular phylogenies have established that red pandas are in their own family, but they are a sister family to either procyonids, mephitids, or a clade composed of mustelids and procyonids (Kundrát 2011; see also Koepfli et al., Chapter 2, this volume).

Morphological convergence with giant pandas is related to their diets. Red pandas are unique among the musteloids, because they are highly adapted to feeding on bamboo, although their overall diet is omnivorous (Fisher 2011). Like giant pandas, *Ailuropoda melanoleuca*, red pandas have well-developed premolar and molar teeth with accessory cusps that create elaborate crowns for crushing bamboo shoots and leaves (Fig. 3.11), and a high arched skull for the attachment of well-developed temporalis muscles for a powerful grinding action (Fisher 2011; Figueirido et al. 2012). The zygomatic arches are well developed and widely flared to accommodate the temporalis muscles and provide origins for the masseter muscles for chewing a tough diet. The mandibles are also robust with large condyles, tall rami, and robust coronoid processes, reflecting the highly developed jaw musculature (Fisher 2011).

Red pandas also posses a well-developed radial sesamoid (often known as the ‘panda’s thumb’), which articulates with the scapholunar bone of the wrist and has four muscles attached to it (see figure). The radial sesamoid assists with holding bamboo stems while feeding. Although superficially similar to the even larger radial sesamoid of giant pandas, its structure and ontogeny are quite different (Antón et al. 2006; Endo et al. 2001). There are different interpretations of its anatomy; Endo et al. (2001) suggest that it acts as a supporting ridge to help grasp bamboo stems, while Antón et al. (2006) claim that the radial sesamoid and its associated musculature affect the supination of the forearm (outward rotation) and adduction of the palm (moving towards the body), which is probably linked to efficient locomotion along thin branches. It is this exaptation that allows today’s red pandas to grasp slender bamboo stems for feeding (Antón et al. 2006).

continued

Box 3.1 *Continued*



Box, Figure 3.1 The radial sesamoid complex of the red panda. From Fisher 2011.

The numbers and form of musteloid teeth vary considerably between clades and reflect feeding adaptations. Dental formulae are given in Table 3.4 and examples of dentitions are in Figure 3.12. Typically, procyonids retain the complete upper dentition of the Caniformia (I3, C1, P4, M2), but the lower jaw lacks the third molar. Carnassials have evolved according to diet, so that predatory forms, for example *Mustela* spp., spotted skunks (*Spilogale* spp.), and wolverines, have sharp, elongated teeth. Omnivorous badgers have a well-developed M1, owing to a very elongated crushing area, but P4 is much shorter than M1, which is extremely long and thick. The first upper molar (M1) varies considerably between clades, so that in mustelids and mephitids it is generally rectangular (more developed and larger in insectivorous skunks and badgers), while in procyonids it is triangular and resembles that of canids. Owing to this broad variation in tooth form and function, musteloids (and mustelids in particular) are the most ‘polymorphic’ group among carnivorans (Crusafont Pairó and Truyols-Santonja 1957). Just as omnivory and carnivory are generally reflected in the relative proportions

AQ1

Table 3.4 Dental formulae of musteloids, adapted from **Ewer (1973)**.

Taxon	Incisors	Canines	Premolars	Molars	Total teeth
Mustelidae					
Mustela	I3/3	C1/1	P3/2–3	M1/2	32–34
Poecilictis	same	same	same	same	same
Ictonyx	same	same	same	same	same
Taxidea	same	same	same	same	same
Martes	I3/3	C1/1	P4/4	M1/2	38
Gulo	same	same	same	same	same
Meles	same	same	same	same	same
Arctonyx	same	same	same	same	same
Lyncodon	I3/3	C1/1	P2/2	M1/1	28
Poecilogale	same	same	same	same	same
Mellivora	I3/3	C1/1	P3/3	M1/1	32
Lutrinae	I3/3	C1/1	P3–4/3	M1/2	34–36
Enhydra	I3/2	C1/1	P3/3	M1/2	32
Galictis	same	same	same	same	same
Eira	same	same	same	same	same
Mephitidae					
Conepatus	I3/3	C1/1	P2/3	M1/2	32
Mephitis	I3/3	C1/1	P3/3	M1/2	34
Spilogale	same	same	same	same	same
Mydaus	I3/3	C1/1	P3/4	M1/1	34
Procyonidae	same	same	same	same	same
Procyon	I3/3	C1/1	P4/4	M2/2	40
Nasua	same	same	same	same	same
Nasuella	same	same	same	same	same
Bassaricyon	same	same	same	same	same
Bassariscus	same	same	same	same	same
Potos	I3/3	C1/1	P3/3	M2/2	36
Ailuridae					
Ailurus	I3/3	C1/1	P3/4	M2/2	38

of crushing versus slicing areas of the teeth of terrestrial musteloids, semi-aquatic otters have modified dentitions in relation to aquatic diets. Sea otters (and also clawless otters, *Aonyx* spp., to some extent) have highly-developed molar crushing areas in both upper and lower premolars and molars. These bunodont molar teeth and highly-molarized premolars evolved to crush tough exoskeletons of molluscs and crustaceans (see Estes et al., Chapter 23, this volume).

Musteloid dental forms are broadly correlated with jaw functionality and mandibular shape (Crusafont Pairó and Truyols-Santonja 1957; Meloro et al. 2011). Small predatory mustelines have thin,

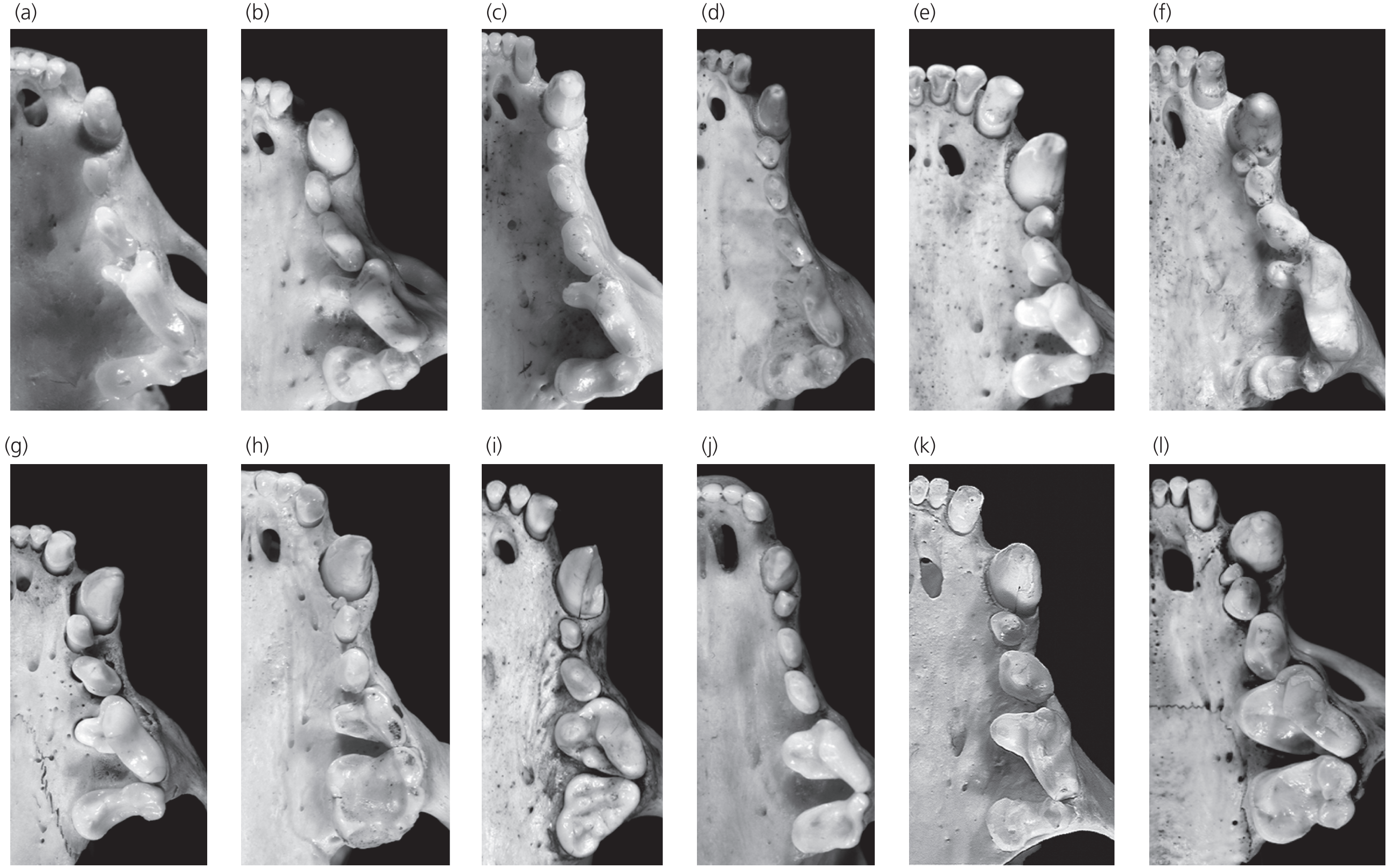


Figure 3.12 Upper left dentition of musteloids. a. *Mustela erminea*, b. *Neovison vison*, c. *Martes americana*, d. *Pekania penannti*, e. *Eira barbara*, f. *Gulo gulo*, g. *Galitcitis vittata, h. Meles meles*, i. *Taxidea taxus*, j. *Melogale moschata*, k. *Mellivora capensis*, l. *Lontra canadensis*, m. *Pteronura brasiliensis*, n. *Enhydra lutris*, o. *Mephitis macroura*, p. *Spilogale putorius*, q. *Conepatus chinga*, r. *Procyon cancrivorus*, s. *Nasua narica*, t. *Bassariscus sumichrasti*, u. *Bassaricyon gabbii*, v. *Potos flavus*, w. *Ailurus fulgens*.

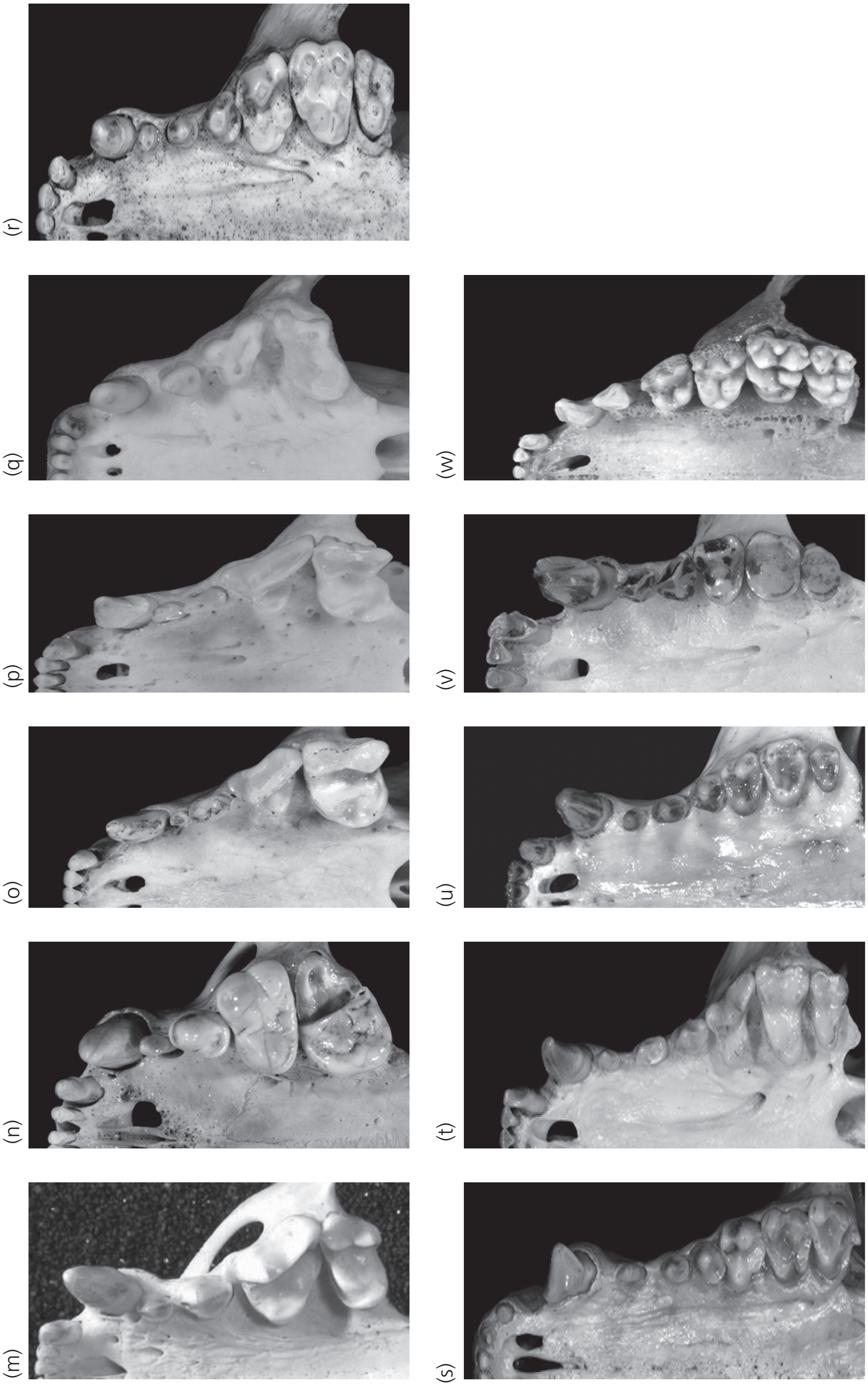


Figure 3.12 *Continued*

curved mandibles with well-developed lower carnassials, and relatively high, straight ramus (posterior jaw that articulates with the cranium) for the attachment of the temporalis; omnivores have a thicker corpus (body of the jaw which bears the teeth) and long crushing molar areas, so that corpus thickness is even more pronounced posteriorly, providing a larger area for masseter attachment, while piscivores have short, anteriorly projected rami to optimize hydrodynamic skull shape (Bininda-Emonds and Gittleman 2000; Meloro and O'Higgins 2011). The mandibles of red pandas and kinkajous show adaptations for herbivory, including high condylar and coronoid processes, and well-developed angular processes, which provide greater attachment surface areas for both temporalis and masseter muscles (Figueirido et al. 2010, 2012; Meloro 2011).

Locomotion

Paws and claws

Mustelоids have pentadactyl (five-digit) limbs and show none of the specializations evident in other carnivorans, which have resulted in reductions of numbers of phalanges. All musteloids possess plantigrade feet (Andersson 2004), although certain groups tend to exhibit a semi-digitigrade stance when moving (e.g. weasels, otter, badgers; Polly and MacLeod 2008, Table 3.5). In plantigrady, locomotory forces transmit through the tarsals and carpals, metapodials (metatarsals and metacarpals—the long bones that connect the digits to the tarsals/carpals), and phalanges (digital bones), rather than just the phalanges as in digitigrady. For this reason musteloids tend to show relatively longer propodial elements (bones forming the upper segment of the limb) compared to metapodial elements (Taylor, 1989; Van Valkenburgh, 1987).

Table 3.5 Digitigrady and plantigrady in musteloids (Carrano 1997).

Plantigrade	Semi-plantigrade	Digitigrade
Eira	*Gulo*	*Mustela*
Galictis	*Martes*	*Vormela*
Mellivora		*Lyncodon*
Meles		*Poecilogale*
Arctonyx		*Poecilictis*
Melogale		*Ictonyx*
Mephitis		
Mydaus		
Taxidea		
Lutrinae		
Procyon		
Nasua		
Bassariscus		
Bassaricyon		
Potos		

The morphology of paws and claws is broadly similar among musteloids. Many have enlarged strong claws on their forepaws for digging, for example, honey badgers (32–46 mm long, cf. 10–18 mm on hind paws), European badgers (30–35 mm along the curve), and also ferret badgers, hog badgers, American badgers, skunks, and stink badgers (Pocock 1920b, 1921c, Figure 3.8). Terrestrial forms, for example, coatis, skunks (but less so in *Spilogale* spp.), grisons, African striped polecats, and Patagonian striped weasels, have long, powerful, slightly-curved blunt claws on their forepaws, with webbing up to the proximal ends of the digital pads (Pocock 1921c, 1927) as adaptations for digging for food. Kinkajous, olingos (*Bassaricyon* spp.), ringtails (*Bassariscus astutus*), and martens have similar paws, but their claws are shorter, more curved and sharper for climbing (Pocock 1921a, Figure 3.8). Mustelines have shorter more curved claws for gripping, even though they are mostly terrestrial (Pocock 1921c). The claws of martens, wolverines, fishers, and ringtails are semi-retractile, presumably to prevent them becoming blunt when not used for climbing (Harris and Ogan 1997; Poglayen-Neuwall and Toweill 1988). High-latitude species have heavily furred pads, so that effective foot size is increased for walking on snow without sinking. Wolverines are renowned for these snowshoes, which are able to bear a load of 27–35 $g.cm^{-2}$, so that they can move on crusty snow and easily kill much larger reindeer (*Rangifer tarandus*) or caribou (*R. t. caribou*), which sink into the snow (Pasitschniak-Arts and Larivière 1995). However, sable also have furred foot pads, and stoats develop these in winter. Red pandas have fully furred pads, which are thought to allow better grip on wet branches (Pocock 1921a).

Most mustelids have some webbing between the toes, but semi-aquatic European mink (*Mustela lutreola*) and otters have well-developed interdigital webbing, reaching near the distal end of the distal phalanges (Pocock 1921b, c, Figure 3.8). Interestingly, the American mink has no more interdigital webbing than other terrestrial mustelids, but typically swims and dives (Dunstone 1993; Harrington et al. 2012b; Bagniewska et al. 2015). Otters' toes are also relatively longer to increase the area of webbing for propulsion when swimming (Pocock 1921b). Sea otters are most highly adapted to an aquatic lifestyle. Digits of the hind feet are united into a flipper-like arrangement and fused to the distal-most phalanges, so that the digits do not appear segmented externally (Pocock 1928). Furthermore, the length of the phalanges of the sea otters' hind feet are reversed in order relative to most other mustelids with the longest digit in the outer fifth position. In Asian small-clawed otters webbing extends only to the proximal ends of the digital phalanges and African clawless otters have similar hindfeet. For many of these otters, webbing is reduced only until the distal first phalanges on the forefeet, freeing the shorter digits to allow manipulation of mollusc and crustacean prey. As their names suggest clawless otters lack claws on their forefeet, and have only small flattish nails on the third and fourth digits of their hindfeet (Pocock 1921b).

Martens, procyonids, and red pandas use their foot pads and sharp, curved claws for climbing. Red pandas have an enlarged radial sesamoid to aid their grip in climbing and for holding bamboo stems (see Box 3.1).

Raccoons forage in shallow water and appear to 'wash' their food. Their forepaws are adapted for high manual dexterity with long claws and naked pads that lack interdigital webbing (Pocock 1921a), which leave the digits unencumbered when manipulating prey. Iwaniuk and Whishaw (1999) studied northern (or common) raccoons' (*Procyon lotor*) ability to manipulate food and found they were not especially dextrous, compared with kinkajous, olingos, and non-piscivorous otters (see following paragraph), but were more dextrous than ringtails and coatis (Ewer 1973; McClearn 1992). Raccoons cannot grasp objects like primates, but grip food between two forepaws, as a scissor grip between digits of the same hand, and between apical digits and carpal pad (Iwaniuk and Whishaw 1999), while sitting or standing bipedally. Kinkajous and olingos grip using a single-handed converging grip (Rensch and Ducker 1969; McClearn 1992). Coatis are good at digging and shredding, and hence have little need of manual dexterity, whereas arboreal kinkajous do, when foraging.

Some non-piscivorous otters (*Aonyx* spp., *Lutrogale perspicillata*, and *Enhydra lutris*) detect and catch most of their food using forepaws. Like raccoons, these otters can roll food or other objects between two paws, exercising fine motor control of their digits for manipulating difficult food items such as molluscs and crustaceans (Radinsky 1968). Sea otters are renowned for using stones against which they crack open hard-shelled prey.

Skeletons and locomotion

Musteloids have the widest repertoire of locomotory adaptations within the Carnivora, including digging, climbing, swimming, and walking, which are represented across a broad range of taxa. Therefore, skeletal form and function vary considerably within and between musteloid clades. However, a significant phylogenetic signal occurs in the long bone proportions of carnivorans (Samuels et al. 2013), so that musteloid skeletons are adapted for particular locomotory behaviours, but within constraints of shared ancestry. Bertram and Biewener (1990) identified isometric patterns of limb length in mustelids and procyonids. With their relatively small body size and elongated body shape, this isometry was interpreted as size-dependent change in limb posture. For these animals, bone length and depth increase with body mass to maintain similar peak stresses in limb skeletons. Similarly, Heinrich and Biknevicius (1998) identified strong positive allometry in bone robusticity of different mustelids, ranging from *Mustela* to *Gulo*. This trend was stronger in humeri than in femora, because of higher mechanical stresses in the anterior body related to a scansorial (climbing) mode of locomotion. However, skunks (*Mephitis mephitis* and *Spilogale putorius*) exhibit similar scaling patterns in fore- and hindlimbs due to their generalized modes of locomotion (mostly slow walk and gallop). More recently, Fabre et al. (2013a, b) showed that body mass has a significant effect on forelimb bone shape in musteloids. Humerus and radius shapes appear to be better adapted for load bearing than the hindlimb bones, although other factors, such as locomotory behaviour (including grasping ability) strongly interact with size and shape evolution (Andersson 2004).

Van Valkenburgh (1987) noted that arboreal carnivorans have significantly smaller body masses than all other species, hence many musteloids would be expected to climb trees. However, the smallest musteloids, weasels and stoats, are generally terrestrial (although stoats are agile climbers, see King et al., Chapter 10, this volume). Many musteloids have scansorial adaptations (e.g. martens, raccoons, and coatis), but the most specialized climbers are red pandas, ringtails, and kinkajous. The most distinctive skeletal adaptations occur in aquatic otters that are considerably different from all the other carnivorans in the proportions of their hindlimbs, which are adapted for different modes of swimming propulsion (e.g. paddling or rowing, Samuels et al. 2013). Digging musteloids have adaptations that characterize the closely related, but distinct, tribes of badgers (Melinae, Taxidiinae, and Mellivorinae) and the distantly related skunks, like *Conepatus* (Dragoo and Sheffield 2009).

Previous interpretations of skeletal variation in mustelids supported a continuum in locomotory modes and hence morphological adaptations (Holmes 1980). Musteloids appear to have evolved skeletal morphology in a mosaic fashion. Looking at the first piece of mosaic in terrestrial musteloids, weasels move using the sinuous half-bound (Taylor 1989). This is a form of gallop, where one forefoot touches the ground, closely followed by the other one, and the hindfeet touch the ground together (Taylor 1989). Such a pattern is typical of carnivorans with elongated, thin bodies and short fore- and hindlimbs (Ewer 1973; Williams 1983b). Many mustelids with long, arching backs and short legs go from walking to bounding without trotting. Musteloids that bound or half-bound extend and flex their vertebral columns to increase stride length, so vertebral columns are more flexible and lack the heavy dorsal spines of gallopers. Consequently, the back and abdominal-wall muscles are well-developed in bounders, forcefully extending and flexing the back while running. Schutz and Guralnick (2007) noted that weasel femora have an expanded gluteal tuberosity (a ridge posterior to the femoral head that tracks the attachment of the gluteus maximus muscle) and a relatively enlarged, rounded femoral head. These features are associated with well-developed hindlimb muscles that allow strong propulsion in half-bounding. As the spine flexes and extends, mechanical stresses on fore- and hindlimbs alternate. The gluteus muscle complex is strongly involved in the propulsive phase, as seen also in the greater grison (*Galictis cuja*, Ercoli et al. 2012). Weasels and grisons have an expanded lumbar region and strong development of muscles responsible for tarsal joint movements as adaptations for chasing prey in burrows, using powerful hindlimb movements. In the forelimb, the humerus and radius–ulna complex are relatively thin and gracile (Fabre et al. 2013a) and limited in their movements along a vertical plane as expected for generally cursorial (running) carnivorans (Taylor 1989). Large mustelids with rigid backbones, for example badgers, trot or gallop and do not bound. The larger scansorial martens share weasels' morphological modifications in the lumbar region, where strong interspinous muscles attach for efficient bounding or half-bounding (Salesa et al. 2008). Tree climbing requires very stable elbow joints, so that humeri appear elongated with a reduced lateral epicondyle at the distal epiphysis. The ulna is also characterized by a short olecranon with a large attachment area for the triceps brachii, a muscle that extends the forearm for propulsion up trees (Schutz and Guralnick 2007). Enlargement of the lesser trochanter of the femur allows efficient rotation of the hip. Raccoons and coatis can climb and their skeletons share with martens modifications of the forearm apparatus (especially the trochlear rim morphology; part of the elbow joint articulation) but not the hindlimb (Heinrich and Rose 1997).

Most musteloids walk with symmetrical ambulatory gaits, where each foot is on the ground for more than half the duration of a stride (Taylor 1989). Some musteloids such as the omnivorous raccoons and striped skunks only walk, and do not use additional gaits. Consequently, their skeletal morphology is generalized, allowing a broad range of lateral movements in both fore- and hindlimbs. Raccoons abduct their limbs more than those of cats and dogs, and their limbs do not move in the parasagittal plane. Raccoons' scapulae are inclined on the thorax at an angle of *c*.20° and supported by the clavicles, in contrast with cursorial species, such as cheetahs, whose scapulae are perpendicular to the ground and lack clavicles (Taylor 1989). Clavicles act as struts in raccoons to prevent shoulders compressing the thorax, especially when climbing. However, thorax shape and humerus orientation determine shoulder movements as much as the presence/absence of clavicles. In raccoons the thorax widens sharply to splay the scapulae. Sea otters lack a clavicle, which increases flexibility around the shoulder for grooming and swimming (Taylor 1989).

A broad range of movements also influences the hips and hindlimbs, so that femora appear to articulate with a long, inclined fovea capitis (attachment of the ligament on the femoral head). Femora project laterally and the articular cartilage in the acetabulum (hip joint articulation) of the pelvis is medial, allowing much greater limb adduction when climbing or moving over uneven ground, whereas in cats and dogs the femoral articulation is centred on the acetabular fossa (depression in acetabulum where the ligament from the femoral head attaches to the pelvis) (Taylor 1989). In skunks, van de Graaff et al. (1982) noted how the femoral long axis intersects with the parasagittal plane at a relatively large angle (25–40°), thus allowing a wide stance and femoral abduction. Schutz and Guralnick (2007) found no particular modifications in the shape of the epiphyses of the humerus, ulna, femur, and tibia of ambulatory skunks, and concluded that their morphology is generalized and overlaps with that of other locomotory categories. Ankle movements are greater in skunks compared with cats, and the primary ankle extensors produce greater forces through a wider range of angles than in cursorial carnivorans. This suggests the skunks' adaptations for ambulatory locomotion are ancestral, as noted also in the study of their relative long bone proportions (Samuels et al. 2013).

Fossorial musteloids are scratch diggers (Taylor 1989) and include true burrowers (the honey badgers, Old World badgers, American badgers, and hog badgers) and burrow modifiers (the stink badgers and ferret badgers). American badgers cut through soil with the claw tips of their forefeet, which they use alternately. They may even rest their head against the opposite side of the burrow to gain extra purchase while digging, and use their less specialized hindfeet to shift loose soil backwards (Taylor 1989). Not surprisingly, the forelimb skeleton and muscles are well developed in fossorial mustelids, which tend to have relatively large body masses. Van Valkenburgh (1987) and Samuels et al. (2013) noted that the midshaft of the long bones of both fore- and hindlimbs of diggers are highly robust. This robusticity is related to bulky muscles needed to generate high forces, especially at the shoulders (Taylor 1989). Consequently, badgers' scapulae appear thick, with enlarged posterior flanges for the attachment of the teres major (a muscle that abducts and stabilizes the humero-scapula complex). Badger humeri are massive, with large heads, short shafts and heavy flanges for insertion of several muscles, for example the pectoralis, deltoid, latissimus dorsi, and teres major. Distal epiphyses and medial epicyondyles are enlarged, increasing areas of origin for manual and digital flexors, while lateral epicondyles are reduced. Such modifications are accompanied by long olecranon processes that support triceps muscles for generating powerful digging forces at the distal ends of forearms (Van Valkenburgh 1987; Taylor 1989). Humeri are supported internally by well-developed trabeculae to resist forces while digging. The deep trochlea adds stability and prevents lateral displacement of forelimbs while digging. Forces produced by the triceps are related to olecranon length on the ulna, which is longer in diggers, giving a greater lever arm. For example the in-lever:out-lever ratio in non-diggers is 1:6 in mustelids, but in diggers it is 1:3.5. American badgers' ulnae have a cross-sectional shape similar to that of an I-beam, but the direction of forces is restricted to the plane of the deepest part of the ulna, providing maximum structural stiffness and strength. Radii are short and robust, with wide distal ends to articulate with scapho-lunars. European badgers' forefeet are digitigrade and carpi can hyperextend by only 10°, but American badgers, which are more plantigrade, can hyperextend their carpi by 50° (Taylor 1989). Hindlimbs are used in digging to push back loose soil. Hence, fossorial musteloids' femora have short necks and large attachments for the gluteus maximus and iliopsoas, while tibiae are curved at the shaft to provide a larger surface for hindfoot muscle attachment.

Some musteloids are arboreal to different degrees. Taylor (1989) described three principal arboreal locomotory modes, including horizontal walking (e.g. red pandas), vertical looping (e.g. ringtails), and jumping (e.g. martens and ringtails). In horizontal walking, pads, claws, and a high supinatory stance (limbs rotated outwards laterally) allow better grip and sufficient friction between feet and tree branches. Vertical looping requires coordinated actions of hind- and forelimbs for up-and-down vertical progression, while jumping is much commoner among musteloids. Long jumps of up to 10 metres are recorded for martens (Taylor 1989). Increased friction through paw pads is needed for vertical climbing, but as increasing body size overcomes friction, tree-climbers just have to hang on. Red pandas use sharp recurved claws, but larger animals supinate (turn or rotate outwards) their fore and hind limbs. When climbing horizontally, the whole body is kept close to the branch, but in vertical climbing the upper body is closer. Ringtails may climb using vertical looping or shinning, where fore- and hindlegs are moved separately from each other, but in unison, so that the back is stretched and flexed, allowing ringtails to creep along tree trunks and branches. Therefore, even though being terrestrial imposes constraints on musteloid skeletal functional morphology, arboreality requires an even narrower set of adaptations of whole body form and function. Arboreal musteloids, such as martens, ringtails, and red pandas, have long tails that generally act as balancing organs, or possibly even as parachutes, when leaping. Kinkajous and binturongs, (*Arctictis binturong*, a viverrid), the only carnivorans with a prehensile tail, have relatively long proximal caudal regions, both in overall length and number of caudal vertebrae, and more robust distal caudal vertebrae with expanded transverse processes, compared with those of other arboreal carnivorans (Youlatos 2003). These adaptations are associated with enhanced flexion–extension of the proximal tail and increased strength and flexing ability of the distal tail, and are similar to those found in woolly (*Lagothrix* spp.), spider (*Ateles* spp.), and howler monkeys (*Alouatta* spp.). Van Valkenburgh (1987) also listed other typical modifications for arboreality, such as elongated phalanges relative to carpals. Forelimbs appear to sustain higher biomechanical stresses in arboreal compared with terrestrial locomotion, although this may depend on the kind of locomotion. Owing to the high importance of supination (outward rotation of the forelimb), arboreal musteloids' scapulae and humeri are modified. For an effective and enlarged attachment of the teres major and subscapularis minor muscles, red pandas, but also raccoons and coatis to a lesser extent, have a postscapular fossa on the scapula; the subscapularis muscle inserts on the head of the humerus, where it prevents the humerus pulling away from its articulaton when climbing (Davis 1949, Figure 3.13). The postscapular fossa is poorly developed in ringtails, which leap and jump around between branches, but it is very well developed in very heavy bears, where the loads on the humerus are much higher. This adaptation is also well developed in arboreal kinkajous where the postscapular fossa is large and its triangular surface extends caudally. Also in kinkajous, the distal humeral epiphysis has a thin, long trochlea with a well-developed lateral condyle for attaching the manus flexor muscles thus allowing better grasping ability (cf. diggers, Taylor 1989; Fabre et al. 2013b). The ulna has a short olecranon, ensuring limited lateral movements and greater supinatory stability. Pronation-supination (rotation about the long axis) is also favoured by the radial epiphysis, which shows strong torsion (twisting) compared with the distal one, a highly derived character only shared by kinkajous and coatis (Salesa et al. 2008). The feet of jumping and leaping musteloids are not as modified as scansorial species', where the feet do the gripping (Taylor 1989). Wrist movement is considerable in scansorial species, which have large radial sesamoids and pisiforms associated with large radial and ulnar deviations. The metacarpals are short, but the proximal phalanges are long. The first metacarpal has a distinct waist and the proximal articular surface allows a high degree of adduction to grip branches more effectively. Hindlimbs are also adapted for arboreality, because they must hold on, if the forelimbs lose their grip. There must be sufficient joint mobility to allow supination for different branch diameters. Ringtails and kinkajous have ankle joints that are fully flexible at the talo-crural joint, so they can be

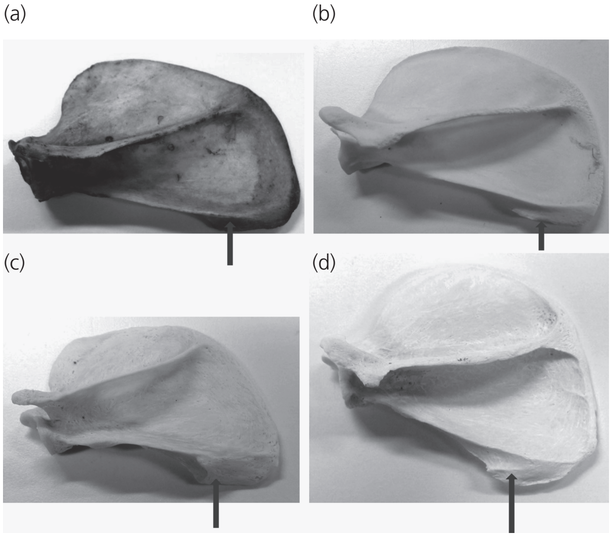


Figure 3.13 Postscapular flanges on the scapulae of arboreal musteloids. a. raccoon, b. coati, c. kinkajou. © National Museums Scotland.

reversed though 180°; these species can climb head first down trees, holding on with their hind feet (Taylor 1989, Figure 3.14). Coatis and raccoons are able to partly reverse their hindfeet for head-first locomotion down trees (McClearn 1992).

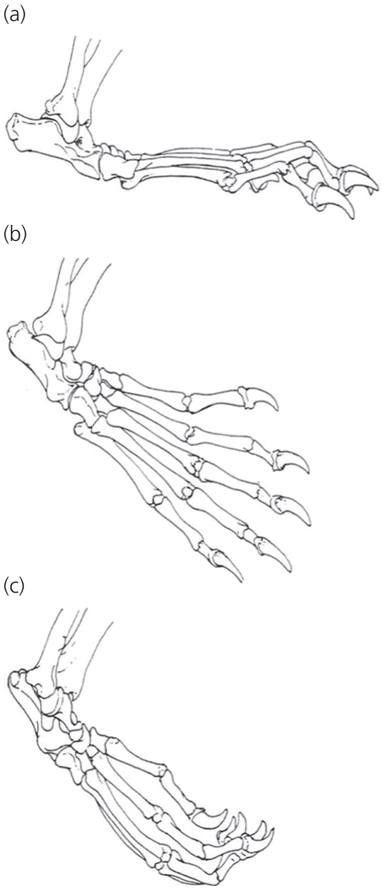
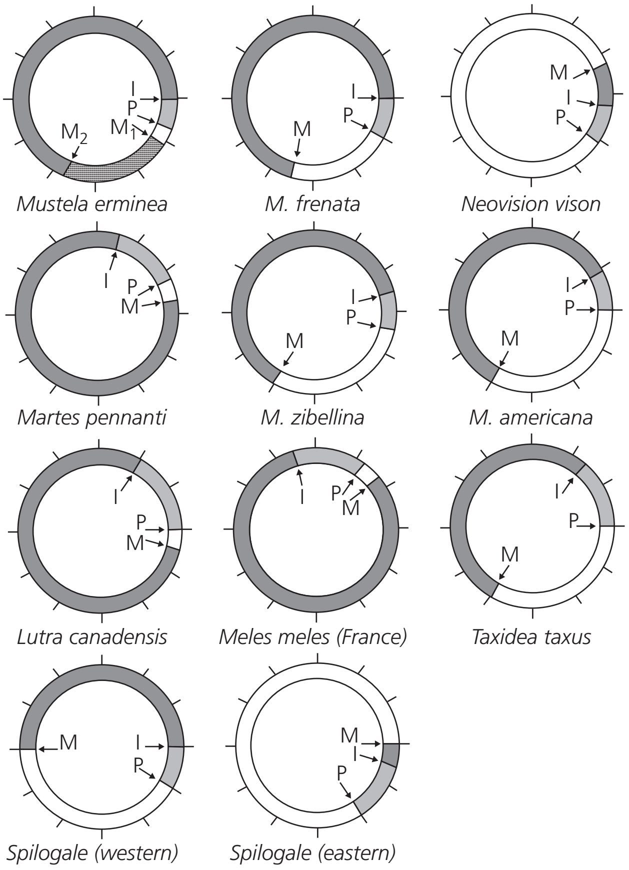


Figure 3.14 The flexible talo-crural joint of the kinkajou. From Taylor 1989.

Reproductive physiology: delayed implantation and superovulation

Delayed implantation, where the blastocyst embryo does not implant into the uterine wall for several weeks up to several months (Figure 3.15), is characteristic of the reproductive cycles of many musteloids, especially the mustelids (Table 3.6). Coupled with superovulation, where individual females may ovulate and fertilize eggs serially over periods of several weeks or even months (Yamaguchi et al. 2006), these two reproductive strategies may explain part of the mustelids' global success. Delayed implantation appears to be ancestral among mustelids (Lindenfors et al. 2003; Thom et al. 2004b), but is not retained by all species today, although it is especially common in mustelids. Of the 53 mammal species that display delayed implantation, 40% are mustelids and 49% are musteloids (Lindenfors et al. 2003; Thom et al. 2004b). Several theories attempt to explain why mustelids use delayed implantation, for example, as allowing mating when parents are in prime condition and births when resources are optimal, effects of winter on sperm



Mustela erminea *M. frenata* *Neovision vison*

Martes pennanti *M. zibellina* *M. americana*

Lutra canadensis *Meles meles (France)* *Taxidea taxus*

Spilogale (western) *Spilogale (eastern)*

Figure 3.15 Delayed implantation in musteloids. From Ewer 1973.

Table 3.6 Musteloids with delayed implantation (Lindenfors et al. 2003; Thom et al. 2004b).

Mustelidae	Mephitidae	Ailuridae
Mustela erminea	*Conepatus mesoleucos*	*Ailurus (fulgens) fulgens*
Mustela frenata	*Mephitis mephitis*	
Neovison vison	*Spilogale gracilis*	*Ailurus (fulgens) styani*
Martes americana		
Martes zibellina		
Martes martes		
Martes foina		
Martes flavigula		
Martes gwatkinsii		
Pekania pennanti		
Gulo gulo		
Vormela peregusna		
Mellivora capensis		
Arctonyx collaris[1]		
Meles meles[2]		
Taxidea taxus		
Lontra longicaudis		
Lontra canadensis		
Enhydra lutris		

[1] probably also in *Arctonyx hoeveni*, and *A. albogularis*

[2] probably also in *Meles anakuma, M. amurensis, M. canescens*, and *M. leucurus*

production and encounter rates for mating, limiting population size by restricting breeding to one litter annually, or even no adaptive value at all (Lindenfors et al. 2003). It is problematic to attempt to find a one-size-fits-all explanation for delayed implantation that may have evolved in different families, including pinnipeds and bears, for different reasons compared with mustelids. However, in general, carnivorans with delayed implantation tend to live at much higher latitudes, live longer, and have lower maternal investment (gestation plus lactation) in their young, but no factors appear to explain the variable length of diapause (Thom et al. 2004b).

Taking a closer look at mustelids, they are mostly smaller than other carnivorans, they live at low population densities, and rely mostly on scent marking to communicate. Females in oestrus may have difficulty in finding territory-holding males in short time periods to allow for successful mating. Induced ovulation gets over the problem of wasted egg production without mating. However if females mate with suboptimal males, which may be at risk from losing their home range, the females may risk losing their young through infanticide by incoming males, thereby wasting reproductive effort. By extending the period in which females can mate by superovulation (Macdonald et al. 2015a), females can choose when, who, and how many males to mate with, and presumably how many young to produce, thereby maximizing or optimizing their reproductive success to prevailing ecological conditions.

Interestingly, carnivoran baculum length is not linked to induced ovulation, but it is greater at higher latitudes in areas with greater accumulations of snow, where population densities are low and multi-male mating systems occur, such as in many mustelids (Ferguson and Larivière 2004). Females may assess male quality through baculum size (and musteloids in general have large bacula, Figure 3.16) by mating with multiple males, which, linked with superovulation and delayed implantation, could explain part of the success of mustelids, particularly at higher latitudes. Baryshnikov et al. (2003) examined variability and scaling of bacula in mustelids and other carnivorans. In general mustelines and procyonids have longer bacula relative to skull size than other carnivorans, whereas otters and mephitids have shorter bacula. Otters, including the sea otter, have bacula that are believed to facilitate mating in water, even though they may mate on land.

The daylight-mediated hormonal pathway that elicits pelage moult in mustelids (see Pelage insulative properties), also stimulates production of progesterone, causing blastocysts to implant and restart their development (King and Powell 2007). Therefore, increasing day length synchronizes blastocyst development, which may result from matings with different males at different times. If the reproductive cycle depends on spring ovulation, involving oestrogen, this may be interrupted by hormonal changes associated with pelage moult and progesterone production. Either ovulation would be delayed until after moult, providing sufficient time in the rest of the year for litters to grow and become independent, or moult would be delayed, which may compromise thermoregulation and, in some species, cryptic coloration, leading to higher probability of predation.

Winter torpor

Some musteloids have evolved physiological adaptations for surviving winter, when food may be unavailable or limited. Northern raccoons build up large fat deposits, on which they depend in higher latitudes by sitting out the coldest winter periods, but body temperatures and metabolic rates are not reduced, and heart rates are higher than in summer (Lotze and Anderson 1979). Striped skunks, American badgers, European badgers,

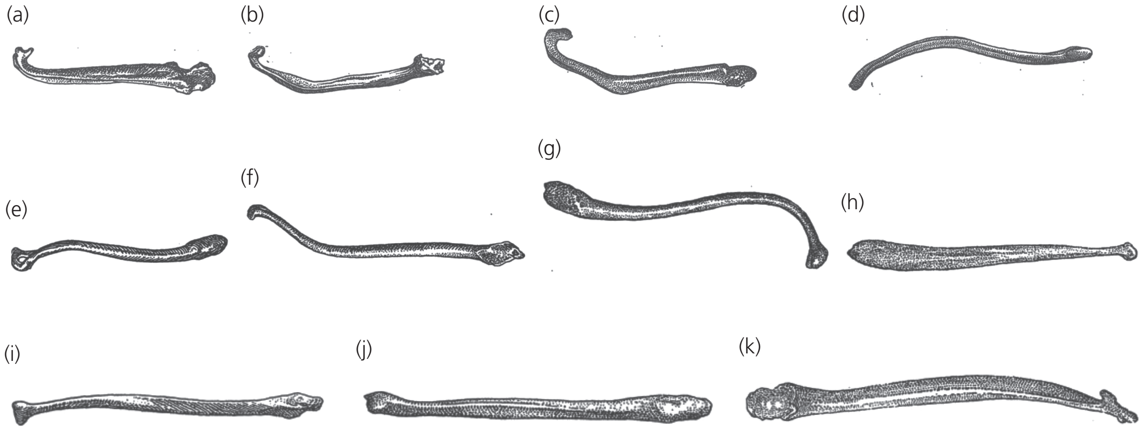


Figure 3.16 Bacula of musteloids. a. *Mustela putorius*, b. *Mustela luteola*, c. *Mustela nivalis*, d. *Mustela erminea*, e. *Martes martes*, f. *Martes foina*, g. *Procyon lotor*, h. *Procyon cancrivorus*, i. *Nasua nasua*, j. *Nasua narica*, k. *Potos flavus*. From Didier 1947, 1950.

and Japanese badgers (*Meles anakuma*) all undergo forms of torpor or hibernation to survive winters. To undergo torpor, these musteloids deposit large amounts of fat, providing an energy store during the winter when food consumption is severely limited. For example, American badgers reach their maximum fat deposits (*c*.31% of body weight) in November and these reduce by 37% during the winter, when they spend up to 93% (70 days) of their time in burrows where ambient temperatures are higher and more stable (0–4°C) (Harlow 1981, see Weir et al., Chapter 19, this volume). During this time they enter torpor up to 30 times, when heart rate is reduced by 50% (from 55 down to 25 beats per minute) and body temperature is reduced by 9°C (to 29°C), giving mean torpor cycle periods of 29 hours. The torpor cycle comprises 15 hours entering into torpor, 8 hours in torpor and 6 hours in arousal. The energetic benefit is profound, with torpor reducing energy expenditure by 27% or 81 kcal per cycle (Harlow 1981).

During winter in southeast Saskatchewan, Canada, solitary striped skunks enter daily torpor spontaneously, reaching body temperatures as low as 26.0°C for 50 out of 120 days (Hwang et al. 2007). Only some that lived in communal dens went into daily torpor, but then it was shallow and occurred infrequently. On average solitary skunks entered torpor for 7.8 hours and reached body temperatures of 26.8°C when active compared with 5.4 hours and 30.9°C for communal skunks, but only when they were resting diurnally (Hwang et al. 2007). Not surprisingly, solitary skunks emerged from winter with lower fat deposits (mean 9.3% body mass) compared with communal skunks (mean 25.5% body mass) (Hwang et al. 2007). Clearly, communal denning has energetic advantages for surviving winter.

European badgers were also recorded entering torpor or winter lethargy during winters in Scotland, but this differs from the periodic bouts of torpor of American badgers (Fowler and Racey, 1988). Body temperatures reduced by up to 8.9°C to 28–34°C between October and March, and activity levels decreased outside setts by up to 90%, indicating that badgers took advantage of higher ambient temperatures within setts compared with outside. Overall, winter lethargy reduced energetic demands on adipose tissue and was most closely linked to photoperiod, but ambient external temperatures and precipitation were also influential.

Japanese badgers have also been recorded entering into winter torpor for 42–80 days (Tanaka 2006). From December to March the mean body temperature of a male cub varied between 32°C and 35°C and it lost 32.1% of its body weight. Although modest compared with body temperature decreases (from a mean of 37°C) in European badgers, this reduction in body temperature would reduce the loss of adipose tissue for metabolism.

Adaptations for an aquatic lifestyle

Musteloids are unique among carnivorans in that they include semi-aquatic and aquatic species. The resulting diversity in form and function among mustelids required to meet the demands of these disparate lifestyles is remarkable, especially when compared to specialist terrestrial carnivoran lineages, such as the Felidae and Canidae (Van Valkenburgh 1999). Malleability of three morphophysiological characters were key to the successful occupation of water by mustelids: 1) hair and pelage modification for thermoregulation while immersed; 2) limb and paw anatomy for locomotor efficiency in water; and 3) specific adaptations for diving.

Thermoregulation

The thermal challenges for aquatic mammals are well documented (Irving 1973; Whittow 1987; Williams 1998; Yeates et al. 2007; Thometz et al. 2014), and demonstrate the difficulty of sustaining the semi-aquatic habits of many mustelid species. Disparate thermal properties for air and water, for example in heat capacity and conductivity, result in a 25-fold increase in heat transfer from the body when animals are immersed compared to when exposed to air of similar temperature (Schmidt-Nielsen 1997). Comparatively small size, elongated body shapes, and resultant high surface-area-to-volume ratios of mustelids promote heat transfer, exacerbating problems of maintaining thermal stability for aquatic foragers, such as mink and otters. Therefore, mustelid bodies can cool rapidly during underwater hunting, especially in smaller species. For example, the core body temperature of a 1 kg mink begins to decline within 2 to 4 minutes of immersion, with the rate of cooling dependent on activity level and seasonal insulation provided by the pelage (Williams 1986). For female mink, resting for 12 minutes in water at 24.6°C, core body temperature declined by 3.3°C compared to no change for the same animals resting in air at approximately the same temperature. Interestingly the rate of cooling for swimming mink was greatest at intermediate swimming speeds when convective heat losses associated with limb movements exceeded the level of heat produced by exercise (Williams 1986). Such high activity levels and associated heat production, as may occur with clustering dives into bouts, may explain in part the ability of free-ranging mink to offset excessive heat loss and forage for periods longer than expected by simple heat loss models based on individual dives (Bagniewska et al. 2015).

Likewise, the rate of body cooling in 7 kg Eurasian otters, foraging in 2–16°C freshwater lochs in Scotland, averages 2.3°C per hour during short feeding bouts (Kruuk 1995), which is 12 times the average level measured in 27 kg sea otters feeding in 10–19°C coastal waters. Despite being the largest mustelids, even sea otters experience sequential variations of >1.5°C in core body temperature throughout the day, with increases and declines matched to activity level and the digestion of food (Yeates 2006; see also Estes et al., Chapter 23, this volume). Overall, aquatic mustelids are often only marginally successful at maintaining stable core body temperatures when immersed, with the timing and duration of aquatic forays by mink (Williams 1986; Dunstone 1993; Bagniewska et al. 2015), Eurasian otters (Kruuk 1995), and sea otters (Yeates 2006) dictated by the balance between activity-induced heat production and the threat of hypothermia. This physiological challenge, along with breath-holding capabilities (Stephenson et al. 1988), undoubtedly influences foraging and requires further investigation, particularly in small mustelids.

Lacking a significant blubber layer, as found in cetaceans, sirenians, and pinnipeds (Williams and Worthy 2002), the pelage is the primary insulating barrier for aquatic mustelids. A suite of unique morphological adaptations enable the pelage of aquatic mustelids to trap an insulating layer of air next to the skin. By physically preventing infiltration of water, heat loss is diminished. Among semi-aquatic and marine otters, pelage density, hair length and shape, as well as surface architecture of individual hairs, are correlated with degree of aquatic specialization (Fish et al. 2002; Kuhn and Meyer 2010b). Liwanag et al. (2012) documented a continuum in gross morphology (hair cuticle shape, circularity, length, and density) of individual hairs as well as thermal conductivity of pelage as mammals move from terrestrial to semi-aquatic to fully aquatic lifestyles. In general, aquatic mustelids have significantly flatter, shorter hairs and increased overall pelage density compared to those of terrestrial forms (Figure 3.17). Interestingly, mustelid exploitation of aquatic habitats has coincided with some of the highest fur densities measured for carnivorans, giving an unprecedented range of values within a family. Thus, the fur density of stoats (97 hairs per mm^2) is similar to that of other terrestrial carnivorans, while that for sea otters (>1200 hairs per mm^2) is 12 times higher and is the densest pelage for any mammal (Liwanag et al. 2012; see also Table 3.2). Semi-aquatic North American mink, North American beaver (*Castor canadensis*), and muskrat (*Ondatra zibethicus*), have fur densities between these extremes, averaging *c.*350 hairs per mm^2, which indicate the importance of an aquatic lifestyle rather than being a mustelid in determining this trait (Fish et al. 2002; see also Table 3.2).

Elongated cuticular scales on both guard hairs and underfur are also evident with increased aquatic specialization by mustelids (Figure 3.17). Such geometric scale patterning promotes interlocking or 'felting' of fine underhairs (Weisel et al. 2005; Kuhn et al. 2010; Kuhn and Meyer 2010a). Together, these characteristics assist in establishing and maintaining the insulating air layer, especially as the pelage flattens with compression during immersion.

Grooming the fur to ensure the integrity of such specialized, waterproof pelage is both time consuming and metabolically expensive for aquatic mustelids. In general, the degree of water salinity appears to dictate investment in grooming and successful colonization of different waterways by mustelids (Kruuk and Balharry 1990; Kruuk 1995). River otters may spend 6% of their day grooming, depending on exposure to fresh or salt water

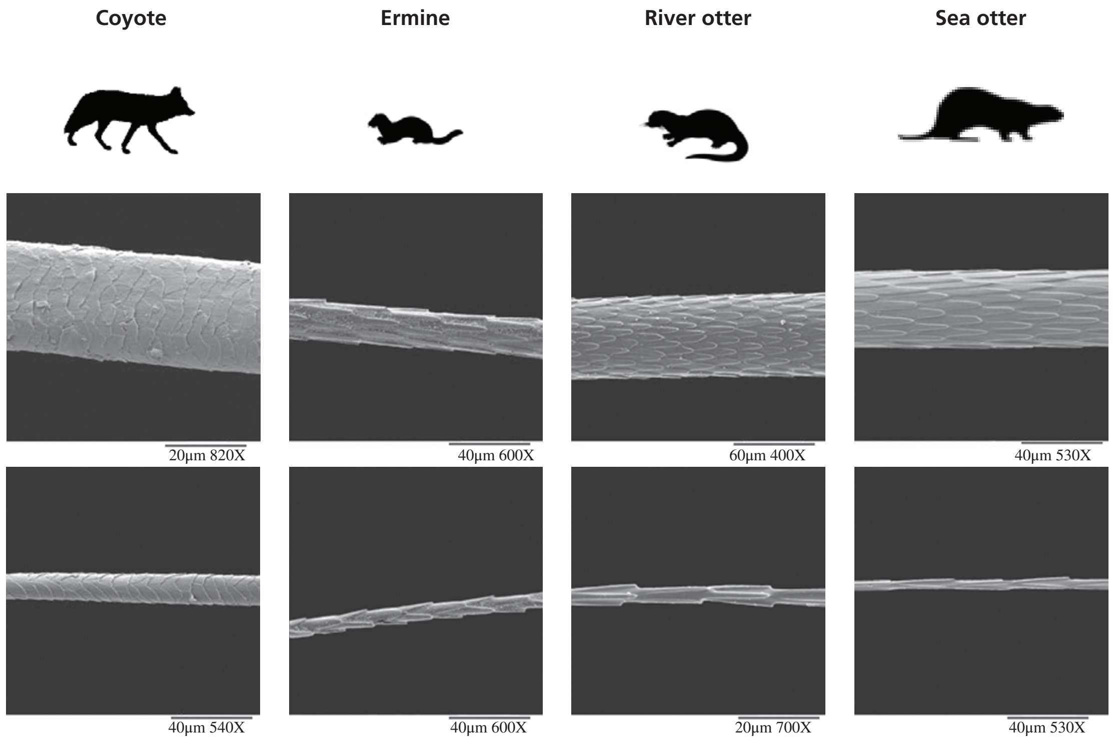


Figure 3.17 Scanning electron micrographs of guard hairs (upper pictures) and underhairs (lower pictures) for terrestrial (ermine), semi-aquatic (river otter), and fully marine (sea otter) mustelids. A non-mustelid, terrestrial carnivore (coyote) is shown for comparison. Magnifications are noted on the scale bars. Micrographs provided by H. Liwanag, Adelphi University, NY.

(Nolet and Kruuk 1989). This increases to 8% of the day for marine otters (*Lontra felina*, Medina-Vogel et al. 2006), and sea otters (Yeates 2006). Often grooming involves high-intensity rolling, rubbing, and fur pleating that can be energetically costly. Somersaulting, vigorous kneading, and fur blowing by grooming sea otters raised metabolic rates to 22 mlO_2 per kg per minute, a 64% increase over resting values that even exceeded the cost of submerged swimming (Williams 1989).

Metabolic responses that enhance heat production, including shivering and non-shivering thermogenesis, increased skeletal muscle activity, and the processing of food, are important for defraying excessive heat loss in aquatic mustelids. American mink (Williams 1986; Bagniewska et al. 2015), Eurasian otters (Kruuk 1995), and sea otters (Costa and Kooyman 1984; Yeates 2006) delay or mitigate cooling through increased heat generated by being active. These activities may occur in water (American mink, sea otter) or on land prior to a dive (Eurasian otter). An additional metabolic mechanism, the specific dynamic action from digestion of prey, provides endogenous heat for sea otters that can last 4 to 5 hours. This allows post-prandial sea otters to slow body cooling while resting in water (Yeates 2006), and probably contributed to their ability to develop a fully aquatic lifestyle.

Locomotor efficiency on land and in water

Elongate body shapes and aquatic or semi-aquatic habits present unique challenges to locomotion for mustelids foraging in water and on land. Body streamlining, short legs, and enlarged plantar surface areas that enhance propulsive efficiency during swimming (Fish 1993) can result in both energetic and biomechanical disadvantages during running. Yet, these species may travel long distances and move across extensive home ranges both on land and in water. Home-range length varies from 1 to 5 km along edges of waterways for American mink (Gerell 1970; Dunstone 1993; Macdonald et al. 2015a) and is similar to the daily running distances of much smaller weasels (Chappell et al. 2013). Otter movements are even greater. Home ranges can exceed 40 km for transient Eurasian otters in Shetland (Kruuk 1995), and may cover hundreds of kilometres for sea otters on the Californian coast (Kage 2004). Therefore, this is a highly mobile group that takes advantage of a wide variety of resources across different habitats regardless of apparent locomotory disadvantages.

Among aquatic mustelids, morphological adaptations for swimming have required compromises in biomechanics, locomotor speed, and energetic efficiency on land. In comparing the running biomechanics of American mink, North American river otters, and sea otters, Scaramozzino (2000) found that degree of aquatic specialization correlated with progressive decreases in predicted stride frequency, stride length, and speed at the walk/bound gait transition. While all three species use walking gaits at low speeds and change to bounding or half-bounding at high speeds (Tarasoff et al. 1972; Williams 1983b), distinguishing between these gaits, particularly at intermediate speeds, becomes complicated with increased hindfoot plantar area (Figure 3.18). Therefore, gait transitions in aquatic mustelids occur at slower speeds in aquatic mustelids than predicted for other mammals (Heglund et al. 1974), with the greatest discrepancies between measured and predicted transition speeds, coinciding with the degree of aquatic specialization of the limbs. Thus, the observed gait transition speed for running sea otters (0.83 m per s) is less than one quarter of the predicted transition speed (3.4 m per s) for terrestrial long-legged quadrupeds.

Despite marked differences in body mass, maximum voluntary running speeds for sea otter, North American mink, and river otter averaged 2.0 m per s (Scaramozzino 2000). These speeds are not remarkable, considering the 0.8–1.4 m per s maximum speed range of diminutive terrestrial weasels (Chappell et al. 2013) and the 2.8–3.3 m per s running speed range of 3 to 4 kg fishers (Powell 1979b). This occurs even though aquatic mustelids partially overcome mechanical limitations of their limb morphology by employing spinal flexion to lengthen their stride to achieve greater maximum speeds, a strategy especially notable for the sea otter (Figure 3.18).

Like running, swimming by aquatic mustelids shows a biomechanical progression in moving from

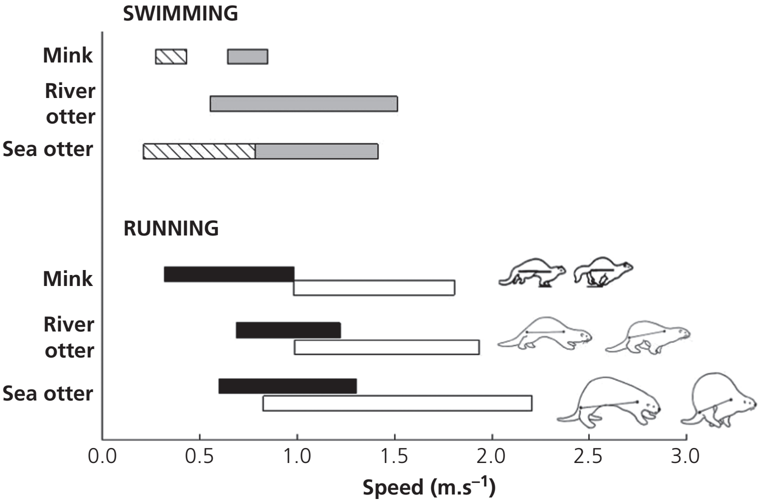


Figure 3.18 Running and swimming speeds of aquatic mustelids. Swimming includes surface (hatched bar) and submerged (grey bars) routine activities. Running is divided into walking (black bar) and bounding/half-bounding (white bars) gaits. Spinal flexion and footfall patterns during maximum extension and flexion for bounding North American mink, river otter, and sea otter are shown in the illustrations. Length of the lines denotes the relative length between the shoulder and tail. Redrawn from Williams 1983b and Scaramozzino 2000. Additional data are from Dunstone 1993, Williams 1989, and Nolet et al. 1993.

terrestrial to semi-aquatic and fully aquatic lifestyles. Mustelids that swim at the surface demonstrate inefficient swimming styles in terms of thrust production. This includes thrust-recovery paddling by semi-aquatic American mink (Figure 3.19, Williams 1983a) and river otters (Fish 1994), in which all four limbs or alternate limbs move posteriorly to move them forward in the same manner as swimming by terrestrial mustelids, including stoats (King et al. 2013) and ferrets (Fish and Baudinette 2008). For these species the body is held horizontally at the water surface, with limbs remaining submerged throughout the stroke cycle. Swimming speeds for thrust-recovery paddling are comparatively slow. For example, the range of surface speeds for American mink in a water flume is 0.13–0.70 m per s (Figure 3.19). In comparison to semi-aquatic mustelids, sea otters show considerable variation in swimming styles when at the water surface, alternating between ventral-down and ventral-up positions, depending on swimming speed and associated behaviours (i.e. eating, resting, patrolling). Rowing and sculling by surface-swimming sea otters, in which hind flippers moved alternately or simultaneously to provide propulsion, are used primarily for slow transects at <0.8 m per s (Williams 1989). Also, as witnessed by any casual observer of wild otters and mink, swimming sprints of short duration, especially when chasing fish or cohorts, may be even faster.

Higher speeds and greater efficiency are achieved under water (Fish 1993). In addition to reducing

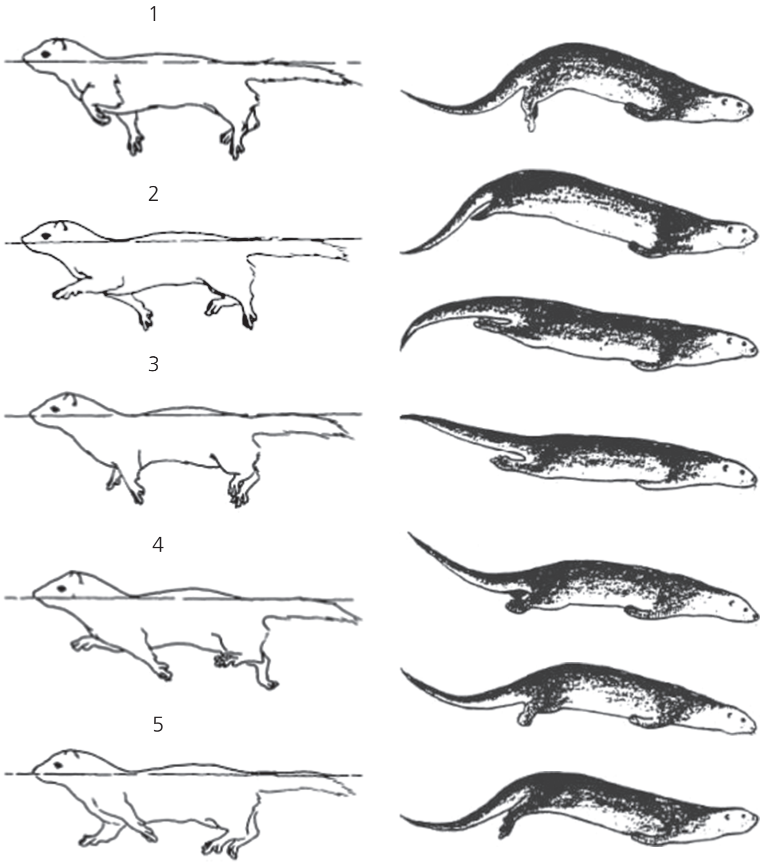


Figure 3.19 Swimming mechanics for one stroke cycle for the North American mink (left) and North American river otter (right). Note that all four limbs are used for propulsion with diagonal limbs moving in synchrony for the mink. Reprinted from Williams 1983a. In contrast, body undulation provides the major propulsive force for the submerged river otter. Reprinted from Fish 1994.

overall drag, submergence allows otters to employ body undulation when swimming (Figure 3.19). When submerged, the body and tail are moved dorso-ventrally to provide thrust. Otters generally have long dorso-ventrally flattened tails that are thick at the base for this form of locomotion, and sea otters' tails are especially thick and muscular.

For both river otters and sea otters dorso-ventral undulation of the body replaces simple limb movements as the major propulsive mechanism (Tarasoff et al. 1972; Williams 1989; Fish 1994). This mode of swimming achieves higher transit speeds when submerged (Figure 3.19). The average underwater swimming speed for North American river otters in pools is approximately 1.4 m per s (Fish 1994). This compares with estimated swimming speeds of 0.26 m per s for wild Eurasian otters, when slowly searching for fish along the water bottom, and 1.52 m per s during routine rectilinear movements (Nolet et al. 1993). By changing from surface to submerged swimming modes, sea otters nearly double their travelling speed to 1.4 m per s (Williams 1989), but they can swim much faster for short periods.

The energetic consequence of a semi-aquatic lifestyle by mustelids is increased costs of locomotion for both running and swimming when compared with transport costs of terrestrial and marine mammal specialists. The cost of transport, defined as the amount of energy it takes to transport one unit of body weight over a unit distance (Schmidt-Nielsen 1972), shows consistent but modest elevations for running in both terrestrial and semi-aquatic mustelids. Depending on species, these elevated running costs occur because of: 1) inherent high resting metabolic rates of mustelids (Iverson 1972; Yeates et al. 2007; Thometz et al. 2014); 2) unique biomechanical costs in musteloids (Williams 1983b), and 3) postural costs from supporting long, slender bodies on short legs (Williams et al. 2002; Chappell et al. 2013). By subtracting resting metabolism from total energetic costs during locomotion, the confounding effects of elevated resting metabolic rates of some mustelid species can be accounted for. The resulting net cost of transport for running fishers (Powell 1979b) and weasels (Chappell et al. 2013) remains 26% and 35–37% higher than predicted for other terrestrial quadrupeds, respectively. American mink show similar greater-than-expected running costs that reduce as they change from walking to bounding gaits (Williams 1983b). Lastly, North American river otters, the most aquatically adapted mustelid for which running energetics have been measured, show the greatest difference between measured and predicted values. The minimum net transport cost is 6.63 J per kg per min for river otters running at 1.43 m per s, and is 34–46% higher than predicted for similarly sized terrestrial mammals (Williams et al. 2002).

Swimming imposes even higher energetic costs for aquatic mustelids. In general, the metabolic cost of surface swimming in semi-aquatic mammals, including American mink, is 2.4–5.1 times that of marine mammal specialists (Williams 1999). This is due primarily to two factors, elevated hydrodynamic drag associated with surface-wave generation, and low propulsive efficiency coincident with thrust-recovery propulsion (Fish 1993). The total cost of transport ($\mathrm{COT}_{\mathrm{TOTAL}}$) for semi-aquatic surface-swimming mammals is:

$$\mathrm{COT}_{\mathrm{TOTAL}} = 26.81 \text{ body mass}^{-0.18} \qquad (1)$$

where $\mathrm{COT}_{\mathrm{TOTAL}}$ is in J per kg per minute and body mass is in kg (Williams 1999). By submerging and changing to undulatory swimming, transport costs are reduced significantly for aquatic mustelids. Consequently, the minimum transport cost for sea otters decreases by nearly 60% when they change from surface to underwater swimming (Williams 1989). Similar decreases were demonstrated for submerged swimming by Eurasian otters (Pfeiffer and Culik 1998). However, the energetic costs of swimming for Eurasian and sea otters remain higher than predicted for highly adapted marine mammals, such as pinnipeds and cetaceans (Williams 1999).

Despite the biomechanical and energetic challenges of a semi-aquatic lifestyle, many mustelid species move successfully between terrestrial and aquatic habitats. This includes species other than North American mink and otters that have traditionally not been thought of as semi-aquatic. For example, ferrets are proficient swimmers capable of foraging for fish and demonstrate a transport cost for swimming similar to those of semi-aquatic mammals (Fish and Baudinette 2008). Similarly, stoats appear to move easily between the mainland and offshore islands of New Zealand in search of prey (Taylor and Tilley 1984; King et al. 2013; King et al., Chapter 10, this volume), such that they are now considered significant wide-ranging predators of native shorebirds in wetland areas.

Skeletal adapations for swimming

Swimming imposes challenges for carnivoran skeletons and it is not surprising, therefore, that otters' body form is hydrodynamic with a fusiform shape. The cervical vertebral segment is shorter than the thoracolumbar vertebral segment for body streamlining and to provide stronger support for propulsion (Taylor 1989). Active swimming requires strong propulsion and imposes constraints on hindlimbs, so that otter femora and tibiae are particularly stocky bones. Femora are straight and short, while tibiae are longer and curved to maximize hindlimb muscle insertion (especially those involved in dorsiflexion, inversion, and plantar flexion). The gluteus muscles provide strong propulsion, hence the greater trochanter and femoral tuberosity are well developed (Schutz and Guralnick 2007). Schutz and Guralnick (2007) noted that the tibia shaft is unusually curved for the broadening of the flexor hallucis longus groove. This region allows passage of tendons of the posterior leg muscles involved in dorsiflexion, inversion, and plantar flexion.

In the otter forelimb, the humeri are also curved midshaft for increased muscle attachment to the anterior forelimb, with large heads and expanded medial epicondyles, as are the olecranon process and tibial tuberosities, while the metatarsals are elongated (Samuels et al. 2013). The expanded distal humerus allows for large attachment areas for muscles that flex, pronate, and supinate the forearm, and flex and extend the wrist (Schutz and Guralnick 2007). The radius and ulna are also curved midshaft and the metacarpals are characteristically short relative to the metatarsals (Taylor 1989). All these modifications relate to improvement in propulsion by the action of the forelimbs and paddling by the hindlimbs (Schultz and Guralnick 2007).

The sea otter is more adapted to an aquatic lifestyle than other musteloids. It has a higher bone density than that of other terrestrial mustelids, but bigger animals exhibit higher bone densities (Fish and Stein 1991). The sea otter's forelimbs are poorly developed compared with its hindlimbs, with short metacarpals and poorly developed insertion surfaces on the humerus, whereas the femur is robust, but very short, and the distal hindlimb elements are elongated for specialized hindlimb propulsion (Tarasoff et al. 1972; Mason and Macdonald 1986; Mori et al. 2015). Therefore, the sea otter's hindfeet show extreme modification to provide efficient paddling in water. The sea otter's hands have very short digits, used primarily for manipulating food; they are held against the body during swimming. As a result sea otters seldom go more than 75 metres from the shore, owing to their poor adaptations for terrestrial locomotion (Rosevear 1974; Taylor 1989; Lambert 1997). Overall these features make the sea otter a fully aquatic mammal, contrasting with all other semi-aquatic Lutrinae. In contrast, the American mink is often considered semi-aquatic, although studies by Williams (1983a, b) demonstrated that it is not as well adapted for swimming as otters due to its typical streamlined musteline body shape.

Conclusion

The diversity of form and function among the musteloids is remarkable among carnivorans, and provides unique opportunities for understanding the morphological, behavioural, and physiological trade-offs associated with successful exploitation of different ecological niches. The mustelids, in particular, are highly successful in terms of species diversity and global distribution. There are several morphological and physiological adaptations that are key to their diversification, including a small, elongated body plan with short legs allowing exploitation of a wide array of niches, a highly insulating pelage that can be moulted seasonally allowing survival at high latitudes, powerful teeth and jaws for killing often larger prey, anal sacs that are effective in intraspecific communication at low population densities and/or utilization as chemical weapons to deter predators, and a combination of superovulation and delayed implantation, allowing females to choose (and find) when and whom to mate with, but synchronizing births in the spring. Although none of these is exclusive to the mustelids among carnivorans, they form a unique combination for their global success.