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BEAVERS

ECOLOGY, BEHAVIOUR, CONSERVATION, AND MANAGEMENT

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Ecology, Behaviour, Conservation, and Management

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OXFORD
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Preface

Both species of beavers (the Eurasian beaver [*Castor fiber*] and the North American beaver [*C. canadensis*]) have followed similar histories, from near extinction, largely through hunting, to their recovery being viewed as somewhat of a conservation success story. Beavers have been widely reintroduced across Europe and North America for species restoration, biodiversity, and ecological benefits. Many countries have recently reintroduced beavers in Europe, demonstrating that the beaver's role as a keystone engineer is well understood, with proven abilities to increase the complexity and biodiversity of freshwater ecosystems.

During the last 20 years, there has been a huge increase in the number of scientific papers published about both beaver species, revealing precisely how unique they are. There is no other animal quite like the beaver, which, like humans, has the ability to adapt its surroundings to suit its needs. This makes it a fascinating and exciting animal to learn about and watch. What animals other than humans can act as engineers, forest workers, carpenters, masons, creators of habitats, and nature managers? Beavers build their own houses, with indoor pools, often having winter and summer residences. They have their own 'freezer box' where they store food during cold winter months. They have even been observed using tools, brandishing sticks in territorial displays. Their dams act as bridges for a variety of animals to use, and they create wetlands. They can restore entire forests by selectively clearing trees and allowing natural regeneration, thereby encouraging plant diversity, which in turn supports a whole host of other species.

This book will, for the first time, bring together themes and latest research from behaviour, ecology, conservation, and management for both species. New methods such as GPS and tri-axial accelerometers attached to beavers have moved the field forward in the last few years. In this book, we have focused on scientific publications but have also included results from some important theses, accessible reports, and writings from those working and living closely with these animals.

(Chapter 10), and Gerhard Schwab (Chapters 10 and 11). Special thanks also go to the editors at Oxford University Press.

Finally, Frank wishes to thank his wife Frid Elisabeth Berge and stepdaughter Yrja Skjærum for their patience and support during the writing of this book. Róisín would also like to thank her family, in particular her mum for proofreading, beyond the call of duty, and her sister for her skill and patience with the illustrations throughout the book.

Frank Rosell and Róisín Campbell-Palmer
September 2021
Bø in Telemark
and Pitlochry/Belfast

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Introducing the beaver

1.1 A buck-toothed wonder

Early written descriptions of beavers (*Castor* spp.) are not kind. The openings of Lewis Henry (Morgan)'s iconic writings in 1868, introducing the beaver to a European and colonial American audience, clearly place the beaver at the lower end of mammalian evolution. With descriptions that include 'a coarse vegetable feeder' whose 'clumsy proportions render him slow', 'inferior to the carnivorous and even the herbivorous animals' when comparing to both other land and water mammals, seem somewhat harsh. However, he could not help but be impressed by the beaver's architectural skills, dedicating most of his book to these. Again perhaps somewhat unfairly, the American naturalist and historian Earl Hilfiker (1991) described the beaver's appearance as 'definitely not impressive. It is the things he does rather than his appearance that make him one of the most widely recognized forms of North American wildlife'. More recently, Frances (Backhouse)'s book *Once They Were Hats* (2015) opens with discussing the beaver's image problem: 'a chubby rodent with goofy buckteeth and a tail that looks like it was run over by a tractor tire'. She goes on to elegantly argue for the beaver's rightful place in history, their incredible influences on our ecosystems, and why we should respect this fascinating animal with its uniquely adapted biology and natural history. Saying that, if the reports of some of the objects found in beaver constructions are to be believed, from lengths of pipe, steals from nearby firewood stores, fence posts, beer bottles, drinks cans, tyres, and even a prosthetic leg (Goldfarb, 2018), beavers are also practical recyclers with potentially a great sense of humour!

Beavers are unique, oversized, semi-aquatic rodents with distinctive features such as their flat scaly tail, webbed hind feet, prominent teeth, and luxurious fur (Figure 1.1), and they exhibit specialized behaviours such as damming and tree felling that can transform landscapes. Because of such adaptations, few species, bar humans, can so readily modify their surrounding environments if left to their own devices.

Beavers have a long history of being utilized and eradicated by humans—for food, various body parts, and of course their highly valued fur (see Chapter 2) but also indirectly with their activities providing habitats for numerous species, thereby providing foraging opportunities and ecological benefits such as water storage in times of drought (see Chapter 9). They are a highly adaptable species and can modify many types of natural, cultivated (Schwab et al., 1994), and urban habitats (Pachinger and Hulik, 1999) to suit their needs. Although beavers can also establish in brackish water (Pasternack et al., 2000), especially at higher population density, they are typically a freshwater species, occupying a wide range of freshwater systems including ponds, streams, marshes, rivers, lakes, and even agricultural drainage systems. They thrive in areas stretching from sea level (0 m a.s.l.) to mountain areas (upto 3,500 m a.s.l., including the Rocky Mountains, Colorado), though preferring low-gradient watercourses (Novak, 1987; Osmundson and Buskirk, 1993).

Box 1.1 describes the classification of beavers (*Castor fiber* and *C. canadensis*). Both species play a crucial role in wetland ecology and species biodiversity and can provide important ecosystem services such as habitat creation and water management. This is challenging in modern, often heavily modified landscapes. The history of the beaver represents

Figure 1.1 Beavers are unique semi-aquatic rodents, highly social in family groups, living in actively defended territories against other beaver families. (Photo supplied courtesy of Michael Runtz.)

Box 1.1 Beaver classification

The family Castoridae is not closely related to any modern rodent group. They are represented today by only two extant species in the once-larger Castorimorpha branch.

Beaver classification is as follows:

Class: Mammalia

Order: Rodentia

Family: Castoridae

Genus: *Castor*

Species: *Castor fiber* Linnaeus, 1758 (Eurasian beaver)

           Castor canadensis Kuhl, 1820 (North American beaver)

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important lessons in conservation, as both species were on the verge of extinction solely through human activities. These biodiversity and ecological services benefit that beaver activities can generate are only now being recognized in more modern times (Rosell et al., 2005; Stringer and Gaywood, 2016). Their restoration has offered exciting opportunities for habitat and biodiversity restoration if we are prepared to tolerate, accept and even embrace their activities.

1.2 All in the name

The formal scientific name, Latin '*castor*' and Greek '*kastor*', is thought to originate from the Sanskrit '*kasturi*' meaning musk, though it has also been suggested that the Greeks called it *Castor* from *gastro*, the stomach, given their rounded appearance (Martin, 1892). When formally naming the beaver (1758), recognizing only one species at the time, Carl Linnaeus basically named it '*beaver beaver*', as the genus name '*fiber*' means beaver in Latin (Poliquin, 2015). Kuhl formally described and named the North American beaver in 1820, over two centuries after some of the first fur trading posts were established in Canada (Martin, 1892). The genus name '*canadensis*' represents the North American geographic range (Long, 2000).

The Old Norse for beaver was '*bjorr*', leading to '*bjur*', '*bur*', and '*björ*' in Old Scandinavian. In today's more modern languages, the Norwegian '*bever*', Swedish '*bäver*' (first appearing in Swedish texts from the sixteenth century), Danish '*bæver*', Dutch '*bever*', and German '*biber*' are especially

similar. The Old English term '*beofor*' has at various points also been spelt '*befor*', '*byfor*', '*befer*', and '*bever*'—all presumed to have their origins in the Old Teutonic term '*bebru*', a general reference to a brown animal. Yet another similar word is '*bhebhrú*' meaning brown water animal in Old Aryan (Long, 2000). During the Middle Ages in Britain, '*bever*' or '*bevor*' were words used to describe a drink or snack between meals, leading to the word beverage. The verb to '*bever*' was to tremble or shake. At other times, '*beaver*' or '*bever*' was a type of face guard on military helmets and even undergrowth associated with hedges was called '*beaver*' or '*beever*' (Long, 2000).

1.3 A robust rodent

Beavers are often described as a 'robust' rodent. They are streamlined and thought of as more agile in the water, though are sizeable, chunky animals especially when viewed on land. Both species are remarkably similar in morphology, with body shapes often described as teardrop with short, stumpy limbs. Beaver morphology reflects their adaptations to a semi-aquatic lifestyle (see Chapter 3). Their large webbed hind feet are specialized for swimming, providing forward thrust to quietly propel them through the water, along with a unique tail with a developed caudal muscle attachment to the vertebrae. Their tail is dorsal-ventrally flattened, pretty much hairless, with skin patterning often described as scaly in appearance. Beaver tails (see more in Chapter 3) are fairly large affairs, though slight variability is evident across adults and according to body condition.

Beavers are dominantly brown in coloration, with dark-grey tails, for example accounting for 91.8% of animal observed in Karelia, Russia (Danilov et al., 2011a), though pelage colour can range from almost blonde to reddish-brown to black, with even white individuals known (Baker and Hill, 2003). Very light-coloured beavers have been recorded, but albinism is rare (Novak, 1987). Native Americans attached significant value to the skins of white beavers, which were often made into medicine bags (Martin, 1892). Partial albinism or 'spotted' beavers have been recorded in

North America and Russia, with white appearing as irregular patches especially on the stomach and hind feet (Lovallo and Suzuki, 1993). Isolated beaver populations in Central Asia have also been observed with white spotting on their ventral sides (Busher, 2016). Completely black beavers are more common than white or spotted variations, and these often fetched the highest prices in early fur exploitation in Canada (Martin, 1892). Up until the 1970s it was reported that all beavers residing in the Luga watershed, Leningrad region, were composed of only black individuals (Danilov and Kan'shiev, 1983). Out of 350 North American beavers trapped in Karelia and the Leningrad region, only two were nearly black, with the rest varying in coloration from light- to dark-brown (Danilov and Kan'shiev, 1983; Kanshiev, 1998). Export lists of beaver pelts from sixteenth-century Stockholm note colour variations, with black pelts being the most expensive, suggesting reintroductions from Norway may have lost some of this colour variation during genetic bottlenecking (G. Hartman, pers. comm.). Brown pelage is therefore presumed to be the dominant genetic trait for both species, given the scarcity of other colours and brown offspring being born to black parents (Danilov and Kan'shiev, 1983).

Typical body dimensions vary due to a range of factors, such as time of year and habitat quality, and age class should also be considered (Tables 1.1 and 1.2; Figure 1.2). Newborn kits tend to weigh between 380 and 620 g (mean 525 g in captive Eurasian beavers; Żurowski, 1977) and typically reach between 7 and 9 kg by the end of their first year (Ognev, 1947). Adults (≥ 2–3 years) on average weigh around 18 kg but can reach 26+ kg, though general body dimensions are less variable with age (Grinnell et al., 1937; Leege and Williams, 1967; Aleksiuk and Cowan, 1969; Parker et al., 2012). Mass is used to distinguish subadults (between ≥ 17 and ≤ 19.5 kg) and adults ≥ 3 years (≥ 19.5 kg) (Rosell et al., 2010). Rarer examples of Eurasian beavers weighing 29–35 kg have been trapped in Russia, including a 36-kg female (Yazan, 1964; Solov'yov, 1973; Danilov et al., 2011a). North American adults weighing between 24 and 28 kg are common; more rarely maximum body weights of 37–39 kg have been recorded in North

Table 1.1 Reported average adult body dimensions of the two species (note 2-year olds are included, thus lowering the mean mass).

Parameter	Eurasian	References	North American	References
Body weight	17.8 kg	Danilov et al. (2011a)	17.2 kg	Jenkins and Busher (1979); Baker and Hill (2003); Danilov et al. (2011a) (North American in Karelia)
Body length	80.5 cm	Danilov et al. (2011a)	76.8 cm	Jenkins and Busher (1979); Baker and Hill (2003); Danilov et al. (2011a)
Tail length	26.3–30 cm	Danilov et al. (2011a)	25.8–32.5 cm	Grinnell et al. (1937); Davis (1940); Osborn (1953); Jenkins and Busher (1979); Baker and Hill (2003) Danilov et al. (2011a);
Tail width	13cm	Danilov et al. (2011a)	9–20 cm	Grinnell et al. (1937); Davis (1940); Osborn (1953); Jenkins and Busher (1979); Baker and Hill (2003); Danilov et al. (2011a)

Table 1.2 Age class body dimension breakdown of the Norwegian beaver (Rosell and Pedersen, 1999).

Age class	Body length (cm)	Tail length (cm)	Tail width (middle point) (cm)
One-year olds	70–80	17–23	5–8
Two-year olds	90–100	23–27	8–10
Adult	100–110	27–31	10–12
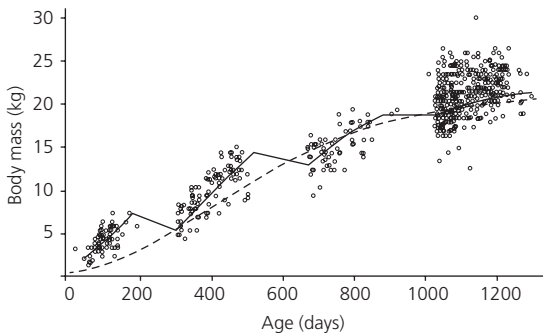
Figure 1.2 Body weight with beaver age. (Reprinted from Campbell, R. 2010. Demography and life history of the Eurasian beaver *Castor fiber*. PhD thesis, University of Oxford.)

America (Grinnell et al., 1937; Schorger, 1953) and even a 44-kg individual (Seaton-Thomson, 1909). Adult body lengths can vary, and though there may be inconsistences with measuring methods, 100–120 cm has been recorded in North American beavers (Grinnell et al., 1937; Osborn, 1953; Jenkins and Busher, 1979).

1.4 The two beavers

The collective term 'beavers' recognizes that there are two species of beavers alive today. Although people have been quite challenged to physically distinguish between them, genetic evidence clearly determines the Eurasian beaver (*C. fiber*) from the North American or Canadian beaver (*C. canadensis*). Both modern species are incredibly similar in appearance and behaviour which can make them hard to distinguish in the field (Rosell et al., 2005; Danilov et al., 2011a). Whilst some differences in skull morphology were first described by Cuvier (1825), historically most zoologists considered that all beavers were either one species or two subspecies (Morgan, 1868). It was not until differences in the number of chromosomes determined fairly late on the existence of the two distinct species: the Eurasian beaver has 48 pairs of chromosomes, whereas the North American has 40 pairs (Lavrov and Orlov, 1973), which clearly distinguishes them as separate species. Captive experiments investigating whether these would interbreed took place, but although copulations were recorded, no hybrid offspring resulted (Lavrov and Orlov, 1973). More recent genetic analysis in developing a rapid DNA assay between the two beaver species determined that SNP positions 1971 and 2473 in the 16-s mitochondrial gene are fixed for nucleotides C/A in Eurasian beavers and G/T in North American beavers, respectively (McEwing et al., 2014). These fixed differences are ideal for species identification purposes and could be used to develop a quick field test.

To the experienced observer, subtle differences in pelage colouring (such as more buff-coloured cheeks and rarity of black individuals in North American beavers) and differences in tail shape (generally slightly rounded, more oval shaped in North American whereas straighter edged, parallel sides of the Eurasian have been noted) have been reported, though setting consistent defining species standards can be complicated (Danilov, 1995). Internal differences in skull morphology are evident; at least seven differences have been reported, including nasal bone structure, depression of basioccipital, and shape of nostril and foramen magnum (Miller, 1912; Ognev, 1947; Figure 1.3a and b). These of course cannot be used in field assessments, and many of these physical differences are only relevant on post mortem examination. One curious and seemingly reliable difference appears to be the colour and viscosity of their anal gland secretions (AGS) (Figure 1.4). Examination of these is a quick and reliable method to determine the sex of a beaver, as external sexually dimorphic features are often lacking across both species (Rosell and Sun, 1999).

Many authors have investigated and postulated over dissimilarities between the species (Table 1.3)
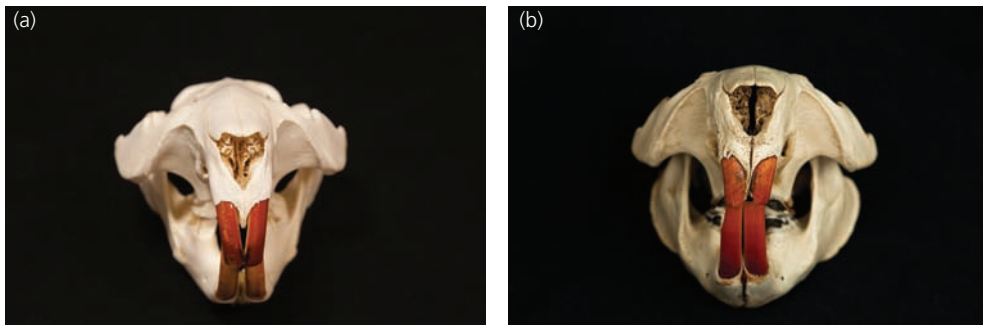
Figure 1.3a and b Differences in skull morphology exist between the two beaver species, the Eurasian (a, on the left) North American beaver (b, on the right), note the more triangular rostrum in the Eurasian. (Photos supplied courtesy of Michael Runtz.)

Figure 1.4 Anal gland secretion (AGS) colour and viscosity vary but can be reliably used to identify species and sexes. (Photo supplied courtesy of Frank Rosell.)

Table 1.3 Main reported differences between the two extant beaver species (Miller, 1912; Ognev, 1947; Lavrov, 1980; Lavrov, 1983; Rosell and Sun, 1999; Rosell et al., 2005; Danilov et al., 2011a; Müller-Schwarze, 2011).

Feature	Eurasian	North American
Genetic		
Chromosome number	48	40
Cranium		
Skull volume	Smaller	Larger
Nasal opening	Triangular	Quadrangular, slightly shorter below than above
Nasal bones	Extend beyond nasal processes of premaxillae	Do not extend beyond nasal processes of premaxillae
Depression between auditory bullae in the lower basioccipital region	Broad and rounded	Ovate
Pterygoid process	Large, 4–6 mm wide	Thin, < 2 mm wide
Least depth of rostrum behind the incisors	Greater than distance from gnathion to end of infraorbital foramen	Nearly equal to distance from gnathion to end of infraorbital foramen
Occipital foramen	Vertically elongated	Horizontally elongated
Foramen magnum	Rounded	Triangular
Cranium width in front postorbital processes	Nearly equals greatest breadth of nasal bones	Greater than greatest breadth of nasal bones
Mandible		
Mandible angular process	Elongately rounded, moderately massive	Short, with rounded edge and very massive
Coronoid process	Strongly bent backwards	Sharpened, bent backwards
Depression between coronoid and angular processes	Prominent	Shallow
Internal		
Uterus masculinus	Present and more consistently identifiable	Not always present and highly variable in form and shape
Anal glands	Larger volume	Smaller volume
Anal gland secretions	Female: greyish-white, paste-like Male: yellow to light-brownish, more fluid	Female: whitish to light-yellow, runny Male: brown and viscous, darker than Eurasian
Tail vertebrae	Narrower, less developed processes	Broader, more developed processes. Deeply bifurcated laminae
Crus bones	Shorter	Longer
External		
Fur	Longer hollow medulla	Shorter hollow medulla
Tail shape	Parallel at midpoint, width 47% of length	Broader across midpoint, width 56% of length
Vertical posture	Assumed less often due to crus bone morphology	Assumed more often due to longer crus bones
Life history		
Sexual maturity	Later typical	Earlier possible
Average fetus number	~2.5	~4.0
Average litter size	1.9–3.1	3.2–4.7
Average family group	3.8 ± 1.0	5.2 ± 1.4
Behavioural		
Dam building	Similar	Similar—greater falsely reported
Lodges	Bank lodges numerous	Free-standing lodges numerous
Scent mounds	Smaller	Some 'giant' mounds recorded

and whether these permit one to have a competitive edge over the other, but general conclusions appear unified (for example, Danilov, 1995; Dewas et al., 2012; Parker et al., 2012; Frosch et al., 2014). Over the years, various studies have reported ecological and life history trait differences. Such comparison studies are particularly relevant where both species are meeting along several fronts, such as in parts of Finland and Russia. For example, studies of adjacent populations of both species living in north-western Russia and Ruusila stated that North American beavers built more dams and stick-type lodges (Danilov and Kan'shiev, 1983), other North American biologists claiming at one point that the greater building activities of North American beavers assisted in giving them a competitive edge (Hilfiker, 1991; Müller-Schwarze, 2011). More recent investigations have reviewed a wide range of ecological features across numerous populations of both species and not found any significant differences, including diet, habitat use, and construction types (Danilov et al., 2011b; Parker et al., 2012). The latest conclusions are that both species build the equivalent frequency and degree of dams and lodges under the same habitat conditions in south Karelia (Danilov and Fyodorov, 2015). Therefore, the niche overlap of both beavers is considered as virtually complete unless further information from sympatric populations comes to light (Parker et al., 2012).

Typically, North American beavers were often presumed to be bigger, raising concerns that this may give them a competitive advantage in body size and aggression in territorial disputes, therefore enabling them to outcompete the native Eurasian. However, body length and masses are highly comparable (Danilov et al., 2011a). It has long been believed that the North American beaver becomes sexually mature faster and has higher fecundity rates (Müller-Schwarze, 2011), with the combined effect of higher fetus numbers (*C. c.* ~4.0, *C. f.* ~2.5) and mean litter sizes (*C. c.* 3.2–4.7, *C. f.* 1.9–3.1). Logically this leads to differences in mean family group sizes (*C. c.* 5.2 ± 1.4, *C. f.* 3.8 ± 1.0) (see Chapter 6). This was thought to give North American beavers a competitive edge and

to explain their more rapid population expansion compared to Eurasian beavers in Finland (Nummi, 2001). However, this is contested by other researchers; moreover, as the two species meet in various parts of Finland and Russia, there are no clear winners and the picture is more complex (see Chapter 2). Actual differences in age of sexual maturity may not be accurately distinguished but rather confounded with data on first age at reproduction, in turn more influenced by population density as opposed to fundamental species differences in reproductive biology. It is therefore not clear if the two beaver species would eventually coexist or be excluded by the other (Petrosyan et al., 2019). Interestingly, several studies report immunophysiological differences between the species, also demonstrated where they both occupy the same habitat. North American beavers appear to have a higher susceptibility to tularaemia and to be a significant reservoir (Mörner, 1992), whereas the Eurasian beaver is reported only sporadically a host (Girling et al., 2019). During tularaemia outbreaks among wild rodents in Voronezh province, Russia, between 1943 and 1945, over half of the North American beavers held at the research centre died, whilst local Eurasian beavers held at the same facility were unaffected (Avrorov and Borisov, 1947).

1.5 Fossil beavers

All rodents share a common ancestor around 57–76 million years ago (myr), with the early beaver-like animals diverging from the scaly-tailed squirrel *Anomalurus* and first appearing around 54 myr (Horn et al., 2011). Therefore, the animal we know today has an incredibly long evolutionary history, though questions still exist around its evolution and closest relatives, as rodent phylogenetic relationships are still difficult to decide (Korth, 1994; Horn et al., 2011). Today's beavers are evolutionary distinct—the only remaining members of the once much larger and diverse family of Castoridae, which dates back nearly 40 myr. The diverse fossil taxa were thought to include up to 30 genera, with more than 100 species at one point (McKenna and

Bell, 1997; Korth and Samuels, 2015; Mörs et al., 2016; Li et al., 2017). In China alone at least ten species of extinct beaver spanning eight genera have been determined from sediments spanning the Early Oligocene to the Pleistocene (Yang et al., 2019), originating from a mouse-related clade, which contains several families including Anomaluridae (scaly-tailed squirrels), Geomyidae (burrowing rodents like gophers), Dipodidae (such as jumping mice), Heteromyidae (such as burrowing rodents, e.g., kangaroo rats), Muridae (true mice), and Pedetidae (springhares) (Huchon et al., 2002; Adkins et al., 2003; Huchon et al., 2007; Blanga-Kanfi et al., 2009). Some debate remains as to whether beavers are more closely related to the scaly-tailed squirrels (Horn et al., 2011) or the Geomyidae (Blanga-Kanfi et al., 2009). The extinct Eutypomyidae are proposed to be the closest related group to Castoridae (Wahlert, 1977). Castoridae varied greatly, from small burrowers around 1 kg in size such as *Palaeocastor* spp. found in the Late Oligocene and Early Miocene to the bear-sized giant beavers of the Pleistocene (Korth, 2001; Rybczynski, 2007).

The origin of the Castoridae, genus *Agnotocastor* (Stirton, 1935), is found in North America at the end of the Eocene (37 myr) representing species that could produce, store, and dispense castoreum (Korth, 2001; Rybczynski et al., 2010). These were also found in Asia and France (Hugueney and Escuillie, 1996) in the Oligocene, suggesting they originated in North America and then radiated out into Asia and wider Eurasia, but this remains debated (Horn et al., 2014). Fossil remains of Castoridae have been found in the Middle East from around the Lower Oligocene and Upper Miocene (Turnbull, 1975). Either way, this occurred via the Beringia isthmus. This was an Arctic land bridge, existing throughout most of the Cenozoic, and although subject to climatic change it enabled 'faunal interchange' and mammalian dispersal between Eurasia and North America (Beard and Dawson, 1999; Gladenkov et al., 2002). This is demonstrated by fossil beaver finds in the Yushe basin, China, which are characterized by long lineages of *Dipoides*, *Trogontherium*, and *Sinocastor* (considered a subgenus of *Castor*), the majority dating back to the Pliocene, with some *Dipoides*

species occurring in the Late Miocene (Xu et al., 2017). These early castorids then gave rise to the burrowing Palaeocastorinae (Martin, 1987; Hugueney and Escuillie, 1996; Korth, 2001; Korth and Rybczynski, 2003). The first animals closely related to beavers and often described as the direct ancestors of contemporary beavers of Eurasia are the genus *Steneofiber* (Geoffroy, 1803), appearing in the Late Oligocene (Hugeney, 1975; Lavrov, 1983; Savage and Russell, 1983). Though they were around the size of marmots (genus *Marmota*), they share morphological similarities, especially in molar structures (Lavrov, 1983). Fossil remains of a family found in France, presumed as ten individuals, were discovered in close proximity and displayed various teeth development, from worn adult teeth to erupting premolars, indicating family structure and breeding patterns parallel to extant beaver species (Hugueney and Escuillie, 1996). The genus *Castor* in Europe has been dated back to between 10 and 12 million years (Lavrov, 1983).

It is thought that up to 30 genera once existed up until the Miocene in Eurasia and up to the Late Pleistocene in the rest of the northern hemisphere (Korth, 2001; Rybczynski, 2007; Rook and Angelone, 2013), so that beavers in the past were much more diverse than today. The palaeocastorine beavers tend to refer to those fossorial beavers restricted to North America and represent an Early Oligocene–Miocene radiation (Stefen, 2014). Around 30 myr palaeocastorines diverged into approximately 15 species (Martin, 1987); this radiation was thought to be associated with a climatic shift, the appearance of more open, grass-dominated habitats, and burrowing adaptations (Strömberg, 2002; Samuels and Valkenburgh, 2009). Table 1.4 shows the approximate beaver timeline based on fossil finds.

It was not until the Early Miocene (24 myr) that the familiar traits of modern beavers—wood cutting and swimming—evolved (Rybczynski, 2007). Prior to this, ancestral beavers tended to be small burrowers (a bit larger that a prairie dog) and are thought to have originated from *Palaeocastor* in the Late Oligocene and Early Miocene (~25 myr) which were adapted to fossorial habits in more upland and arid habitats not associated with

Table 1.4 Approximate fossil beaver timeline (years ago) (Pilleri et al., 1983; Müller-Schwarze, 2011).

Period	Pleistocene	Tertiary				
		Pliocene	Miocene	Oligocene	Eocene	Palaeocene
Years before present	1.9 million–8,000	5.3–1.9 million	23.9–5.3 million	33.7–23.9million	55–33.7 million	66–55 million
Key events	Both extant species coexisted with giant forms	*Castor* arrives in North America, speciation of extant species	Wood cutting and swimming evolve	*Palaeocastorine* species divergence	Common rodent ancestor exists. Split from *Anomalurus*	
North America	*Castoroides ohioensis* *Castor canadensis*	*Dipoides* *Amblycastor* *Castor* *Eucastor*	*Eucastor*	*Palaeocastor* *Agnotocastor*	Earliest beaver-like fossils recorded in California, Germany, and China	
Eurasia	*Castor fiber* *Trogontherium*	*Trogontherium* *Steneofiber* *Castor* spp.	*Castor* spp. *Palaeomys* *Steneofiber eseri* (not adapted to aquatic lifestyle)	*Steneofiber fossor* (underground lifestyle)		

wetlands. Canonical analyses of a wide range of extinct beavers have demonstrated that skull morphology was highly adapted for digging behaviours, though these fossorial features demised around 20 myr (Samuels and Valkenburgh, 2009). Some of these burrowing beavers (three species are associated: *Palaeocastor fossor*, *P. magnus*, and *P. barbouri*) dug unusual, deep, helical burrows, ending in an inclined living chamber (Martin and Bennett, 1977). When first discovered, these structures were described as silicified sponges or extinct plants and named '*Daimonelix*' (Barbour, 1892; Barbour, 1895). Later, Cope (1893) and Fuchs (1983) proposed these were rodent burrows, with plant material being roots of various plants gnawed during burrow construction, which was later validated (Peterson, 1906; Schultz, 1942). Several thousand of these unusual structures ('devil's corkscrews'; Figure 1.5), which can descend to a depth of nearly 3 m and were often found in clusters or 'towns', have now been identified in North America (Martin, 1994).Various theories have been proposed as to why these ancient beavers dug such energetically expensive and complex burrows requiring so much effort to construct (Meyer, 1999). This unusual shape was proposed as an efficient space utilization design (Martin and Bennett, 1977), though this was later ruled out as neighbouring burrows are clustered together apparently randomly (Meyer, 1999). Neither did they seem to offer increased predator protection, as the remains of both predated beavers and various predators have been found in these burrows (Martin and Bennett, 1977; Martin, 1994). In the end they concluded that excavated deep, helical burrow systems in arid grasslands maintained a more consistent subsurface temperature and humidity and may even have trapped some water. All burrowing beaver species (up to eight coexisting species known) disappear from the fossil record around the same time, ~20 myr, with those utilizing a more semi-aquatic lifestyle becoming more successful (Hugueney and Escuillie, 1996).

The *Eucastor* gave rise to *Dipoides*, another former member of the family Castoridae, sharing the trait of tree exploitation and possessing the wood-cutting abilities of the genus *Castor*, and therefore our modern beavers (Rybczynski, 2007). Though
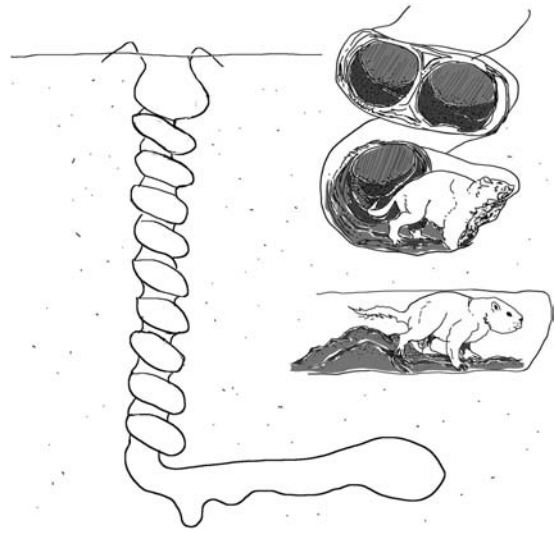
Figure 1.5 'Devil's corkscrew' burrows of ancient fossorial beaver ancestors. (Illustration provided courtesy of Rachael Campbell-Palmer, redrawn after Martin & Bennett, 1977.)

Castor and *Dipoides* share a common wood-cutting ancestor, thought to have been a burrower, which can be traced back at least 24 myr, they are not close relatives but share a semi-aquatic clade (Rybczynski, 2007). Their respective gnawing marks on fossilized tree remains may be difficult to distinguish without careful examination. *Dipoides* are considered less advanced, producing smaller and more overlapping cuts due to their smaller and more round incisors, compared to the more evolved chisel-like ones seen in beavers today (Tedford and Harington, 2003). The wood-cutting abilities of *Castor* are more efficient as their straight edge incisors produce larger cuts, taking fewer bites to fell equivalent sizes of woody material than *Dipoides* with their strongly curved incisors (Rybczynski, 2008). Fossil remains of intertwined cut sticks have also been found in association with them, implying 'nest-type' structures that could be evidence of early lodge and/or dam building activities (Tedford and Harington, 2003). Evidence of dam building behaviours and impacts on geomorphology in extinct Castoridae appears lacking, though wood cutting pre-existed modern beavers (Plint et al., 2020).

Modern beavers (genus *Castor*) first appeared during the Late Miocene and Pliocene (11–2.5 myr) as one common species around the Palaearctic region (Xu, 1994; Rekovets et al., 2009; Rybczynski et al., 2010) from their close relative species *Steneofiber* (Xu, 1994; Rybczynski, 2007; Flynn and Jacobs, 2008). *Castor praefiber* (Depéret, 1897) for example is considered an intermediate species in *Castor fiber* evolution thought to have first appeared in the early Pliocene (Rekovets et al., 2009). The genus *Castor* is believed to have emerged in Eurasia and then penetrated into North America via the Bering land bridge (Lavrov, 1983; Lindsay et al., 1984; Xu, 1994; Hugueney and Escuillie, 1996; Flynn and Jacobs, 2008) during the Pliocene around 4.9–6.6 myr (Lindsay et al., 1984; Xu, 1994). The earliest *C. fiber* is known from is the Early Pleistocene (Barisone et al., 2006; Rekovets et al., 2009), and it is thought to have overlapped with *Castor plicidens* (Cuenca-Bescós et al., 2015).

Trogontherium was a congener of modern beavers; these were the giant beavers of Eurasia, though widely distributed throughout the Palaearctic, comprising three species, *T. minutum*, *T. minus*, and the largest *T. cuvieri*, in the Upper Pliocene (Mayhew, 1978; Fostowicz-Frelik, 2008). Their fossil remains have been discovered regularly with those of the genus *Castor* in both Europe and Asia from the Early Pleistocene (~2.4–0.13 myr), and the recent finding of a specimen in China has extended its extinction date to the Late Pleistocene (Yang et al., 2019). It appears that modern beavers lived alongside or were possibly locally extirpated by the slightly larger *Trogontherium cuvieri*, as the prevalence of the two forms at archaeological sites demonstrates an inverse relationship (Mayhew, 1978). Additionally, this places the survival of this giant beaver as overlapping with Pleistocene people and therefore a candidate with the other extinctions of large Ice Age mammals caused by human activities (Yang et al., 2019). Figure 1.6a and b shows comparison sizes.

More recent genetic studies have determined that divergence between our two modern species occurred around 7.5 myr (Horn et al., 2011). The Bering land bridge would have permitted animal movements between Eurasia and North America. After the land bridge disappeared this most likely triggered the speciation into *C. fiber* and *C. canadensis* as they became completely isolated from each other (Horn et al., 2011). The Eurasian beaver is therefore thought to be around twice as old, dating back around 2 myr. Genetic differences and lack of hybridization are evident, but their biology,

(a)
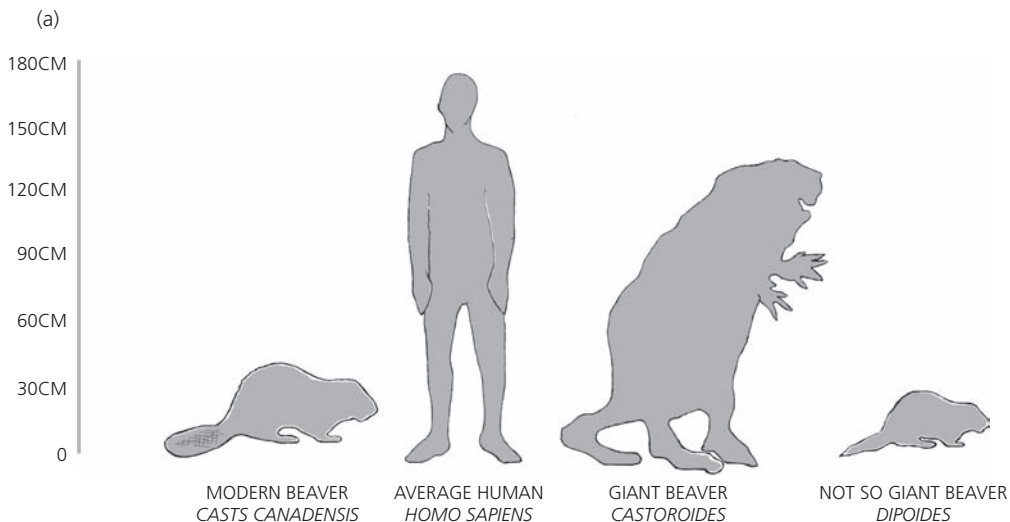
Figure 1.6a Modern beaver size in relation to *Homo sapiens*, their giant ancestor *Castoroides*, and *Dipoides*. (Illustration provided courtesy of Rachael Campbell-Palmer, redrawn after Scott Woods, Western University, Canada.)

(b)

Figure 1.6b Giant beaver replica skull in comparison to beavers today. (Photo supplied courtesy of Michael Runtz.)

morphology, and physiology remain remarkably similar, along with their shared ancient, coevolved parasites, the beaver beetle *Platypsyllus castoris* and stomach nematode *Travassosius rufus* (Lavrov, 1983; see Chapter 8).

Today's beavers are the second largest species of rodent in the world (the largest being the capybara, *Hydrochoerus hydrochaeris*, from South America), although the now-extinct giant beavers (genus *Castoroides*) really capture the imagination. It is believed that giant beavers and modern beavers shared most of the same range, with fossils found from Alaska to Florida (Kurtén and Anderson, 1980). These giant beavers existed in North America during the Pleistocene and were one of the last megafauna (typically defined as animals with body weights > 44 kg; Martin, 1984) to go extinct near the end of this epoch—thought to be due to a combination of climatic and anthropogenic impacts (Boulanger and Lyman, 2014; Cooper et al., 2015). One such giant beaver *Castoroides leiseyorum*, was thought to reach adult body sizes of 2.5 m in length and weigh between 150 and 200 kg (Kurtén and Anderson, 1980) and was known to exist throughout the southeastern USA (Parmalee and Graham, 2002). Another, *Castoroides ohioensis*, thought to have been one of the last of the giant beavers, disappeared around 10,000 years ago (Boulanger and Lyman, 2014). There are conflicting theories on giant beaver ecology, especially regarding their tree cutting and dam and lodge building abilities, as little evidence of these structures exist (Rybczynski,

2008), though their large body size and short limbs are thought to have made them poorly adapted for terrestrial life (Plint et al., 2019).

However, very recent palaeodietary studies have used stable carbon and nitrogen isotope analysis of bone collagen to confirm these beavers were likely to be cold-tolerant and highly dependent on submerged and floating macrophytes, a significant factor allowing *C. canadensis* to coexist, as they would have exhibited complementary dietary niches (Plint et al., 2019). This dietary analysis did not support tree material consumption, which is consistent with their dental morphology (Rinaldi et al., 2009), both indicating giant beavers had to rely on significant existing wetlands (Plint et al., 2019). Fossil finds display rounded incisors with blunt tips, and this has prompted researchers to believe these teeth were used to cut off and grind coarse swamp vegetation rather than trees (Kurtén and Anderson, 1980).

Evidence for the last known giant beaver populations is concentrated in the Great Lake Basins, northern USA, and Ontario, Canada, where they are thought to have hung on before their final extinction (Boulanger and Lyman, 2014). Although there is evidence of giant beavers and humans overlapping in these areas for ~1,000 years, no evidence of them hunting these animals currently exists (Boulanger and Lyman, 2014). It is therefore concluded that changes to warmer and drier climatic conditions resulted in suitable wetland habitat loss through reduction in glacial melt water and sediment infilling, with associated changes in woody vegetation and giant beavers being reduced to small, isolated populations that eventually died out completely (Plint et al., 2019); on the other hand, *Castor* spp. possessed incisors, allowing tree felling, taking advantage of woody tree species, and would have had the ability to create new habitats, giving them a competitive edge (Plint et al., 2019).

1.6 Modern beavers

Extant beavers were first named and described as *Castor fiber* by Linnaeus (1758), while Kuhl first named and described *Castor canadensis* (1820). Fossil

evidence of Eurasian beavers has been found in Italy, Spain, Turkey, Syria, Iraq, Israel, and Iran, but the species is thought to have gone extinct in southern Eurasia by the Late Holocene (Linstow, 1908; Legge and Rowley-Conwy, 1986; Barisone et al., 2006). For example, fossil evidence of Eurasian beaver from Spain documents their presence from the Early Pleistocene ~1.4 myr, but then there is a great absence of remains during the Middle Pleistocene when human occupation intensified and suitable habitat most likely became scarcer (Cuenca-Bescós et al., 2015). Both beaver species remained widespread in suitable freshwater habitats throughout the northern hemisphere successfully until human populations grew and began to exploit them, beginning in Eurasia (see Chapter 2). The mass exploitation of beavers, to the point of near complete extinction, has impacted on both their modern distribution and subspecies classification. For both species the usage of subspecies names is complicated by inconsistent application in the literature, with some names not following the rules of the International Code of Zoological Nomenclature and based on contested scientific data such as differences only in relict population survival location (Gabrys and Wazna, 2003). Table 1.5 shows the historical classification of subspecies for both extant beaver species.

The greatest impact on Eurasian beavers, with the most rapid period of decline, occurred in the nineteenth century, by the end of which this species was on the verge of becoming extinct and reduced to a handful of populations in fragmented refugia left after the fur trade, thought to number 1,200 individuals overall (Veron, 1992; Nolet and Rosell, 1998). As a side note, in some early taxonomical descriptions the Eurasian beaver was classified as two species—the eastern beaver, *C. fiber*, and the western beaver, *C. albicus*—by Matschie (1907) based on craniological differences (Lavrov, 1981; Lavrov, 1983). Most zoologists at that time, however, recognized only two contemporary species, the North American and a single Eurasian species (Figure 1.7a Eurasian and Figure 1.7b North American), so this third species (*C. albicus*) was rejected and placed in subspecies classification, which themselves underwent several debates (Gabryś and Ważna, 2003). Ancient beaver DNA

analysis does not provide any evidence to support defined substructure categories, instead forming part of a continuous clade (Horn et al., 2014; Marr et al., 2018), though divergence in mtDNA haplotypes is evident (eastern and western phylogroups), caused by population retreat into glacial refugia during the last Ice Age (~25,000 years ago) (Durka et al., 2005). So enough defined, it was recommended they be managed as separate evolutionary significant units (ESU) (Durka et al., 2005). ESUs are largely defined as reciprocally monophyletic mtDNA units exhibiting significant divergence of allele frequencies at nuclear markers and in regard to conservation management can suggest sourcing for reintroductions (Moritz, 1994; Frosch et al., 2014). Ancient beaver populations were pretty much continuous across the whole of Eurasia and although the two main lineages were apparent, so too was a higher degree of haplotype diversity, and later differences determined in the remaining relict populations were not as stark (Horn et al., 2014). Comparison of DNA from fossil beavers with modern beavers (using samples ranging from several hundred to 11,000 years old) demonstrates Eurasian beavers have suffered a significant genetic bottleneck, losing at least a quarter of their unique haplotypes (Horn et al., 2014). This loss of genetic diversity occurred during the Holocene, when human populations expanded (Horn et al., 2014), with the most recent impact and distribution strongly linked with human activities (Halley et al., 2020).

These nine relict populations, characterized by low genetic variability and a low proportion of polymorphic loci (Ellegren et al., 1993; Babik et al., 2005; Ducroz et al., 2005), were previously considered to be distinct subspecies based on morphological skull measurements, disjunct distribution (Lavrov, 1981; Heidecke, 1986; Frahnert, 2000), and mitochondrial differences, including proportion of assignment to eastern or western clades (Durka et al., 2005). The Belarus refuge has more recently been determined to be the most genetically diverse compared to all the other relict populations, given its larger population size and more complex distribution remaining at isolated locations across several water basins while it passed through this genetic bottlenecking (Munclinger et al., in prep).

Table 1.5 Historical subspecies classification for both extant beaver species. Note many of these are no longer formally recognized as a subspecies or referred to as a fur trade refugia (Gabryś and Ważna, 2003; Pelz-Serrano, 2011).

Species	Subspecies	Region	References
C. fiber	*C. f. albicus*	Germany (Elbe), Poland	Matschis (1907)
	C. f. galliae	France (Rhone)	Geoffroy (1803)
	C. f. fiber	Norway	Linneaus (1758)
	C. f. belarusicus	Belarus, northern Ukraine	Heidecke (1986)
	C. f. orientoeuropaeus	Russia (Voronez), Belarus	Lavrov (1981)
	C. f. pohlei	Western Siberia, Urals	Serebrennikov (1929)
	C. f. tuvinicus	South-central Siberia	Lavrov (1969)
	C. f. birulai	Southwest Mongolia, China	Serebrennikov (1929)
	C. f. vistulanus	Vistula, Poland	Matschis (1907)
C. canadensis	*C. c. acadicus*	New Brunswick, New England, Nova Scotia, Quebec	Bailey and Doutt (1942)
	C. c. baileyi	Humboldt River, Nevada	Nelson (1927)
	C. c. belugae	Yukon, Alaska	Taylor (1916)
	C. c. caecator	Newfoundland	Kuhl (1820); Banngs (1913)
	C. c. canadensis	Canada, British Columbia	
	C. c. carolinensis	North Carolina, Louisiana, Mississippi	Rhoads (1898)
	C. c. concisor	Colorado, Mexico	Warren and Hall (1939)
	C. c. duchesnei	Duchesne River, Utah	Durrant and Crane (1948) Mearns (1898)
	C. c. frondator	Rio San Pedro, Mexico border	
	C. c. idoneus	Oregon, Washington	Jewett and Hall (1940)
	C. c. labradorensis	Labrador rivers	Bailey and Doutt (1942)
	C. c. leucodontus	Vancouver Island, British Columbia	Gray (1869)
	C. c. mexicanus	New Mexico, Texas	Bailey (1913)
	C. c. michiganensis	Michigan, Wisconsin, Minnesota Saskatchewan, Manitoba,	Bailey (1913)
	C. c. missouriensis	Missouri, Dakota	Bailey (1919)
		Washington, British Columbia,	
	C. c. pacificus	Idaho	Benson (1933)
	C. c. pallidus	Raft River, Utah	Durrant and Crane (1948)
	C. c. phaeus	Pleasant Bay, Alaska	
	C. c. repentinus	Grand Canyon, Arizona	Heller (1909)
	C. c. rostralis	Red Butte Canyon, Utah	Goldman (1932)
	C. c. sagittatus	British Columbia, Yukon, Idaho	Durrant and Crane (1948)
		Shasta Mountains, California	
	C. c. shastensis	California	Benson (1933)
	C. c. subauratus	Big Wood River, Idaho	
	C. c. taylori	Cummings Creek, Texas	Taylor (1916)
	C. c. texensis		Taylor (1912)
			Davis (1939)
			Bailey (1905)

Since the 1900s, beaver numbers have recovered throughout much of their former European range as a result of a combination of legal protection (species and habitat), reduction in hunting pressure and increased regulation, land-use shifts including farmland abandonment, proactive reintroductions/ translocations, and natural recolonizations (Deinet et al., 2013; see Section 2.8.1). Genetic analysis of mitochondrial DNA and major histocompatibility complex (MHC) DRB gene sequences demonstrates low diversity within these refugia populations, though distinctions between them do exist (Babik

Figure 1.7a Adult Eurasian beaver (*Castor fiber*). (Photo supplied courtesy of Frank Rosell.)

Figure 1.7b Adult North American beaver (*Castor canadensis*). (Photo supplied courtesy of Jan Herr.)

et al., 2005; Ducroz et al., 2005; Durka et al., 2005). Despite large geographical distances, there was no significant genetic differentiation between Mongolian and eastern Russian beaver populations (Ducroz et al., 2005). No major variations in haplotypes have been found within central European relict populations (Durka et al., 2005). However, some skull morphometric analyses suggest some evidence for relict population differentiation (Frahnert, 2000) and behavioural discrimination studies indicate lesser recognition and reactions to anal gland secretions between, *C. f. fiber* (relict Norwegian) and *C. f. albicus* (relict German), different Eurasian subspecies (Rosell and Steifetten, 2004). Whilst distinctive eastern (Russia, Belarus, Siberia, and Mongolia) and western (relict France, Germany, and Norway) clades based on genetic differences based on mtDNA have been found (Durka et al., 2005; Horn et al., 2014), as for many European mammals following the last Ice Age, hybridization zones are also apparent. Recent genetic studies dismiss these differences as being significant enough to warrant subspecies classification, as the remnants of a once much more diverse, mixed, and expansive population, now relegated to the artefact of human hunting and recent anthropogenic genetic bottlenecking rather than previously separated subspecies (Horn et al., 2014). This has been supported by nuclear and mitochondrial analyses (Frosch et al., 2014; Horn et al., 2014; Senn et al., 2014). Recent genetic analysis has concluded that much of Europe and Russia is now populated by admixed beavers, resulting in increased genetic diversity leading to viable and successfully expanding populations,

indicating that outbreeding depression is not a significant impact (Munclinger et al., in prep). Some authors still argue for the recognition of certain subspecies/populations, for example Siberian beavers, *C. f. pohlei*, defined as possessing a specific haplotype marker (Saveljev and Lavrov, 2016), and *C. f. tuvinicus* and *C. f. birulini* populations in Mongolia and China given their long period of isolation (Munclinger et al., in prep).

Genetic screening of modern-day Eurasian beaver populations demonstrates that the degree of mixing between eastern and western lineages is already so advanced (Frosch et al., 2014; Senn et al., 2014) across several areas in Eurasia that it seems pointless to try and maintain this former glaciation and geographically induced clade separation, especially as anthropogenic translocations continue and naturally population expansion leads to secondary contact and mixing across their native range (Frosch et al., 2014). Recent genetic analysis of the current population determined that mitochondrial DNA (mtDNA) and nuclear microsatellites reflected the composition of the founder animals and that admixture zones occurred (Minnig et al., 2016). Recent recovery through both natural spread and reintroductions demonstrates that beavers from these relict populations are meeting and admixing (Frosch et al., 2014). Poland for example is a modern-day mixing zone, where as a result of natural range expansion and multiple translocations, admixed populations now exist, with both lineages represented (Biedrzycka et al., 2014).

One of the most detailed genetic analyses of the Eurasian beaver genome was undertaken by Senn

et al. (2014), through the identification of 306 single nucleotide polymorphisms (SNP) genotyping derived from restriction site associated DNA (RAD) sequencing data (Senn et al., 2013) comparing samples from across Europe. Several key outcomes were established: the Norwegian *C. f. fiber* and French *C. f. galliae* are distinct populations with no evidence of mixing with any other populations; there is no evidence of *C. f. albicus* remaining as a separate identity with a high degree of introgression with other populations; *C. f. belorussicus* and *C. f. orientoeuropaeus* from Belarus and Russia share a common genetic cluster; and beavers from Bavaria and Switzerland clearly display multiple genetic origins and represent admixed populations (Senn et al., 2014). After they were extirpated at the start of the nineteenth century, reintroductions of 141 individuals to Switzerland occurred between 1956 and 1977. These beavers were sourced from the Rhone valley in France (*C. f. galliae*) released into the Rhone and Rhine catchment areas in the west, beavers from the Telemark region in Norway (*C. f. fiber*), and beavers from the Voronezh province in Russia (*C. f. orientoeuropaeus*) were released into the eastern Rhine catchment (Stocker, 1985), though haplotypes of French, Norwegian, and German (*C. f. albicus*), due to secondary contact, were later determined genetically (Minnig et al., 2016).

It has been clearly demonstrated that genetic diversity is highest in populations involving the reintroduction of mixed sourced animals, compared to those composed solely of remaining fur trade refugia (Frosch et al., 2014; Senn et al., 2014). In addition, these studies provided evidence that the genetic difference between the previous eastern and western clades was not as distinct as the haplotype data suggested and subsequent mixing is fairly extensive as beaver populations meet along varying fronts. However, in some populations relatedness between individuals is still high, e.g. parts of Britain (Campbell-Palmer et al., 2020) and Switzerland where some closely related individuals were found up to 50 km away (Minnig et al., 2016) (Figure 1.8).

A very similar story occurred with the North American beaver; at one time 24+ subspecies were recognized (Jenkins and Busher, 1979). Previously widespread across Canada and North America,

from the Arctic to the Rio Grande, until they were commercially removed by the fur trade, *C. c. acadicus*, *C. c. canadensis*, *C. c. carolinensis*, and *C. c. missouriensis* were considered to be the most widespread North American subspecies (Hall, 1981). Repeated and widespread reintroduction and restoration projects have led to mixing of many of the more isolated and potentially discrete populations (Baker and Hill, 2003). The pattern of hunting, then subsequent reintroductions and mixing has essentially made many of these categorizations redundant. Some flexible mating strategies of beavers, including extra-pair mating (Crawford et al., 2008) and equal dispersal between the sexes (Sun et al., 2000), suggest they are socially monogamous but opportunistically promiscuous, which should promote mixing and genetic diversity. However, genetic structure comparison analysis has been undertaken between different Illinois populations, one acting as a small population with single family units, whilst the other had larger family numbers and size, with multiple breeding adults on a less linear system (Sun, 2003; Crawford et al., 2008). These mating and ecological differences had clear influences on genetic population structure—for example, groups of animals in non-linear systems proving more difficult to scent mark and defend, and multiple families presenting more opportunities for interactions (Crawford et al., 2009). They also found evidence of female philopatry; however, parental genetic analysis was suggestive of dispersal between populations and promiscuous mating systems (Crawford et al., 2008). Therefore, some gene flow was maintained, even though families functioned as fairly distinct breeding units (Crawford et al., 2009; see also Chapter 6). The authors conclude that despite reintroductions occurring previously to Illinois (Pietsch, 1956), beaver populations are acting as fairly isolated units with some limited dispersal between them, a fact to consider in longer-term beaver population management. Overall, North American beavers are now once again present in all the states and provinces they previously occupied, with numbers still growing (see Section 2.8.2).

To try and unravel the genome of the North American beaver, a beaver volunteer called Ward, descended from wild stock originating in Quebec, was undertaken by geneticists in Ontario (Lok et al.,
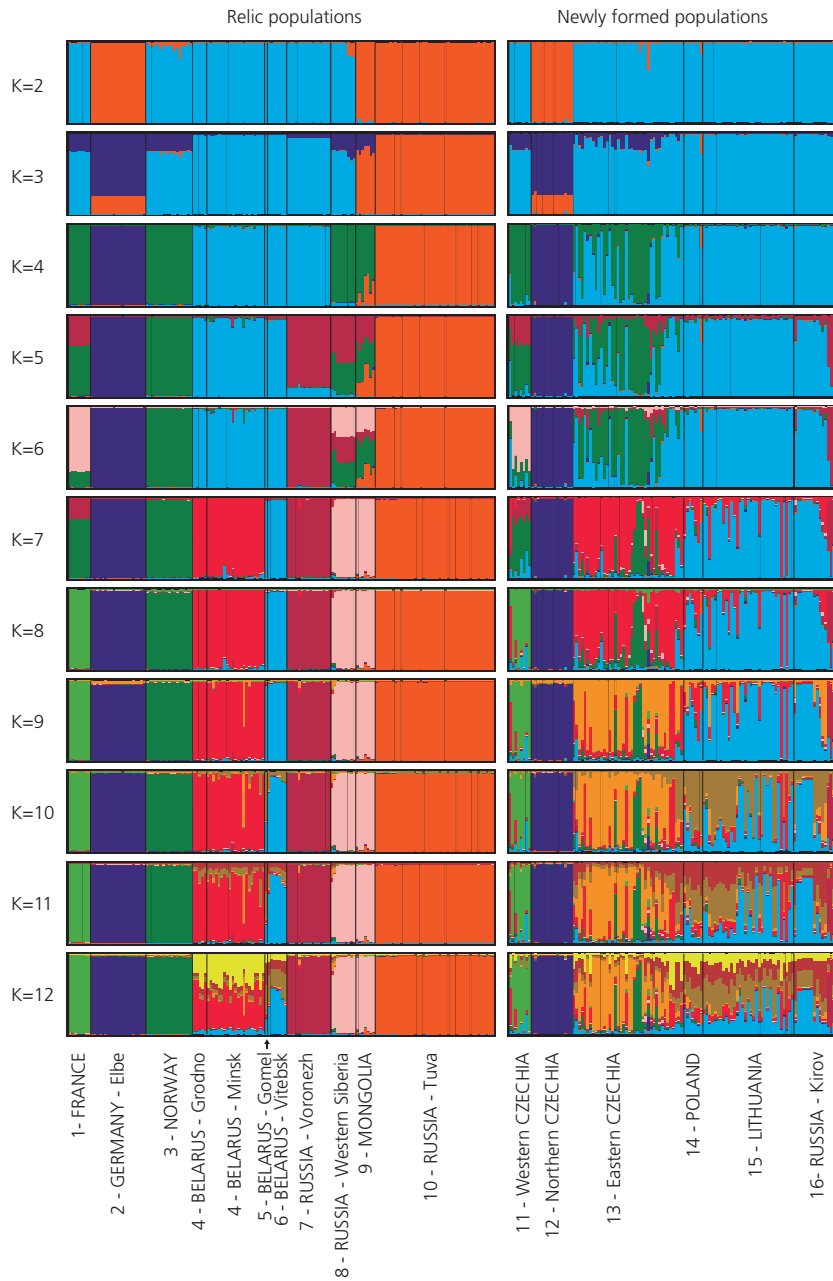
Figure 1.8 Structure analysis of microsatellite data for K (number of assumed groups) from 2 to 12. Newly formed populations display a greater degree of admixing in contrast to relict populations. Newly formed populations are viable and expanding and typically display higher genetic diversity and hybrid vigor, outbreeding depression does not appear to be a significant issue. (Figure supplied courtesy of Pavel Munclinger.)

2017). Despite being almost made extinct, with remaining populations small and dispersed, high levels of genetic diversity appear to have been retained with no strong indication of recent genetic bottleneck, known to have occurred ~100 years ago (Pelz-Serrano et al., 2009; Lok et al., 2017). Microsatellite studies have found mean heterozygosity ranging from 66.3 to 74% in tested populations, though the degree of gene flow possible amongst all the various geographic locations is questioned (Crawford et al., 2009; Lok et al., 2017). Beavers sampled (*n*=117) from Alabama, Arizona, Maine, Minnesota, South Carolina, Texas, and Wisconsin and tested across nine microsatellites found them to be highly polymorphic, again finding mean heterozygosity around 74%, with Alabama displaying the lowest and Texas populations the highest (Pelz-Serrano, 2011). Therefore, the North American beaver has not appeared to have lost the same extent of genetic diversity as the Eurasian beaver.

Analysis of mitochondrial DNA does indicate that past climatic and geological events, predominantly ice sheet coverage, determined phylogenetic relationships, with evidence of multiple Pleistocene refugia, including in Texas and the Rocky and Appalachian Mountains (Pelz-Serrano, 2011). Rapid population recovery, potentially due to the greater expanses of remaining and less human-populated landscapes along with larger remaining population size, as compared to Europe, could explain the lesser loss of heterozygosity. There have been investigations on whether this mass persecution, followed by a series of translocation and reintroduction efforts to compensate for this loss serve to enable the evaluation of these human impacts on current genetic diversity of populations today. Genetic analysis (based on nine microsatellites) of seven North American geographic areas subject to historic translocations (Alabama, Arizona, Maine, Minnesota, South Carolina, Texas, and Wisconsin) concluded that high genetic diversity at the mitochondrial DNA has remained, though this doesn't mean that other parts of the genome have not been negatively impacted, and high gene flow rates among some of these geographic areas are lacking (Pelz-Serrano et al., 2009). For example, Russian populations of Eurasian beaver demonstrated a high degree of polymorphism at the microsatellite but not MHC loci, whilst both were extremely low in Scandinavian beavers (Ellegren et al., 1993). The Alabama population for example seem composed of alleles from both the Texas and South Carolina populations (probably due to historical translocations); therefore current populations are a result of ancestral populations, admixed with modern translocations, though natural dispersal is also contributing to low levels of genetic flow as these populations do not exist in complete genetic isolation (Pelz-Serrano et al., 2009). Early, interregional translocations have most certainly aided the preservation of genetic diversity and recovery of this species, though that is not to say some genetic distinctions and specialized local adaptations have not been lost.

1.7 Mistaken identity

Even for such a distinctive species it is surprising how often and how variable misidentification of beavers can be. A number of semi-aquatic mammals utilize and simultaneously overlap occupation of freshwater riparian habitats (Hood, 2020). Identifying swimming animals in particular seems to cause some confusion. This is not entirely surprising as regular and clear viewing of beavers can still be an elusive experience to many. Not only may beavers be misidentified as other species, but also other species, especially those commonly utilizing swimming and burrowing near to freshwater environments, can often be labelled as beavers. Particularly where beavers are relatively new recolonizers of areas, any swimming mammal (and sometimes even a duck!) can be enthusiastically assigned as a *Castor* species. Depending on which continent you are in (and recognizing that some of these species are now common introduced invasive animals), otters (*Lutra lutra*), coypu or nutria (*Myocastor coypus*), muskrat (*Ondatra zibethicus*), and even water voles (*Arvicola amphibius*) may be commonly mistaken (Figure 1.9a–d). In North America, beavers, coypu, and muskrat are important furbearing semi-aquatic mammals, which can be confused for each other by a casual observer as their ranges commonly overlap.

Figure 1.9a Both the Eurasian (*Lutra lutra*) and North American (*Lutra canadensis*) otter can be confused for beavers, especially when swimming, but otters move quite differently, with much more slender bodies and completely different tails. (Photo supplied courtesy of Kirsty Taylor-Wilson.)

Figure 1.9b The coypu or nutria (*Myocastor coypus*) looks the most similar to beavers apart from their tails, but they are completely unrelated. (Photo supplied courtesy of Leopold Kanzler.)

Figure 1.9c Swimming muskrats (*Ondatra zibethicus*) can look especially like swimming beaver kits, but out of water their tail is clearly different. (Photo supplied courtesy of Leopold Kanzler.)

Figure 1.9d Though much smaller, swimming water voles (*Arvicola amphibious*) have also been mistaken for beaver kits. (Photo supplied courtesy of Kirsty Taylor-Wilson.)

A naming confusion may come with the mountain beaver (*Aplodontia rufa*) also known as a sewellel, found in western North America and which of course is not a beaver at all. They are small (~20–46 cm long and weighing 0.8–1.2 kg), burrow-dwelling rodents, with a short furry tail which is largely non-visible, living in forest with dense understories, and confusingly not aquatic or found in the mountains (Kays and Wilson, 2010). They eat a range of vegetation, including bark and small branches, which is thought to be how they got their name (Long, 2000).

It is perhaps the beaver's tail, a common and distinctive feature of both species, that tends to set it apart from other species—not only in shape and size but also in the fact it is generally hairless bar the odd, short and scattered bristles. Their tails' fish-scale-like appearance was once falsely accredited to their pescatarian diet, and this is still a surprisingly commonly held belief. Perhaps the most similar looking species is the coypu, which both in and out of the water is uncannily comparable. This South American species has been introduced to both North America and parts of Europe as a productive, furbearing mammal. This confusion with beavers occurs to such an extent that many media stories concerning beavers are often illustrated with photos of coypu. The key difference is undoubtedly the tail, being round, long, thin, and sparsely covered with bristle hair; whereas the beaver tail is uniquely beaver! On land these two animals move completely

differently and hopefully if you are seeing them out of the water then the tail should be immediately obvious.

Beavers are often described as cumbersome on land, walking on all fours with the tail dragging behind in a purposeful direction but not at great speed, unless they feel in immediate danger. Coypu are more agile and can almost be described as being able to scuttle on land, rather than plod along. Coypu are also much smaller, with average weights of ~5.4 kg, though they can reach 9.1 kg, and body lengths of ~61 cm (LeBlanc, 1994), being more similar to a 1-year-old beaver. Facially they have a more truncated snout than beavers and possess noticeable white whiskers around the muzzle. They share webbed hind feet, though in coypu the first four toes are connected whilst the outer toe is free, as opposed to being fully webbed in beavers; therefore tracks, especially the hind paws, can be differentiated. They also possess prominent orange incisor teeth which can range into a deeper, more red-orange than beavers in coloration (LeBlanc, 1994). Field signs (especially burrows and feeding signs) from both these species can also be hard to distinguish and can overlap. Their scats are also distinct from beavers as they produce dark green to almost black cylindrical faeces (~5 cm long) marked by deep parallel grooves (LeBlanc, 1994). Life history traits also vary, with coypu being shorter lived, reaching sexual maturity at a much younger stage (~4 months), and having multiple litters throughout the year (LeBlanc, 1994). Lactating coypus have more visible nipples than beavers, which are set high on the female's side.

Muskrats and beavers can be confused. Though native to North America, muskrats have been introduced to parts of Europe and share the same aquatic habitats. It is proposed that some degree of commensal relationship may exist as they sometimes co-inhabit beaver burrows and lodges, and the muskrat nest or 'push-up' can look like a mini-beaver lodge (MacArthur and Aleksiuk, 1979). Misidentification can happen especially with a swimming animal, though muskrats are significantly smaller (overall length 46–61 cm with average weights of 1.1 kg) than beavers and coypu (Miller, 1994). They could be mistaken for a beaver kit, though they can swim much faster. Facially the

muskrat's snout tends to be more pointed, with no visible white whiskers. Again, the tail is distinctly different from beavers, being scaly and laterally flattened but long and thin in shape and when swimming makes a clear undulating motion. Coypu and beaver tails on the other hand are still while surface swimming. Muskrat and water vole feeding signs on green vegetation (as opposed to woody vegetation) could be mistaken for beaver feeding (Strachan et al., 2011); however, alternative field signs in close proximity should aid identification. When out of the water and eating, for example, their digits are visually more elongated with longer, often lighter nails than beavers. Their tracks are significantly smaller than both beaver and coypu, and they possess skin folds between the toes of their hind feet (partially webbed) as opposed to clear webbing between toes (Miller, 1994).

On occasions, otters have been confused for beavers and vice versa. there are few physical similarities, though they do share a similar semi-aquatic lifestyle and are often seen swimming in the same freshwater habitats (Woodroffe, 2007). Either the excitement of knowing beavers may be recolonizing an area, mixed with at times poorer viewing conditions, such as seeing a swimming animal in the dusk, can fool the observer. Many of their behavioural and habitat use traits differ, due to their carnivore and vegetarian diets respectively. Otters are faster, agile, energetic swimmers capable of changing direction and speed abruptly, with elongated bodies and prominent whiskers (e.g. Erlinge, 1968), whereas beavers tend to be more set on their course—yacht to tanker comparisons come to mind! Otters have been reported to use abandoned beaver burrows and sometimes even active lodges (Vorel, 2001). Otters tend to hold their heads higher out of the water while swimming, whereas when beavers swim on the surface only the upper part of their head (eyes and above) are visible.

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Utilization and distribution of beavers

2.1 An ancient relationship

Humans have an ancient relationship with beavers (*Castor* spp.) which has ranged broadly over time from the supply of food and fur, through the inspiration of religious and cultural beliefs, to a contemporary recognition of the species' critical role as a maintainer of ecological balance. This often-forgotten association is seldom recognized at a time when their modern populations are now just beginning to recover. Without exaggeration, beavers can be afforded the distinction of being one of the key wild animal species that have influenced history (Coles, 2006). Many of the Native American indigenous people have a long history of utilising beavers as a source of food and warmth, with legends relating to beavers, and even keeping more amiable individuals as pets (Schorger, 1965; Dolin, 2010). Beavers were a commonly hunted mammal dominant in the diets of Neolithic and Early Bronze Age humans across the East Baltic region (Daugnora and Girininkas, 1995; Antanaitis-Jacobs et al., 2009). They are also depicted in prehistoric art. Their behaviour and castoreum (their unique scent from the castor sacs; chapter 3.2.9) were discussed by the Roman naturalist Pliny the Elder (*c.* 77 BCE); Strabo (*c.* 63 BCE–24 CE), a Greek geographer and philosopher, states castoreum (which was actively traded in Roman times) from Pontus, where it was called the '*Pontic dog*' (now northern Turkey, near the Black Sea) was superior to that from Spain; and beavers are also included in the medieval Iranian text of *Bestiary* (1297–1298).

Strange theories regarding their behaviours and biology were commonly held. Early North American explorers told exaggerated tales of their building capabilities. They described them using their tails as spatulas to plaster their homes and spoke of their organized colonies where strict laws and social structures were maintained. While some individuals ruled, others had set jobs such as guards, ditch diggers, or carpenters (Denys, 1672). Across their range, similar beliefs about beavers as nature's 'workaholics' are held by people, while sayings such as 'to be as busy as a beaver', 'eager beaver', and 'beavering away' refer directly to their obvious work ethic. In contradiction, it was also thought that their industrial traits could result in confusion, conflict, and selfishness in their determination to finish their tasks (Lake-Thom, 1997)!

Wars have been waged, laws enshrined, religions spread, and new countries established on the glossy backs of beavers. The complex interweaving of the fur trade and colonial expansion is best exemplified in history by the formation of Canada and colonization of North America (Gerstell, 1985; Dolin, 2010). The *Beaver Wars* of the eighteenth century were predominantly fought between the early British and French colonialists in an effort to secure the most lucrative trapping areas and trading routes.

In 1975, Canada received Royal assent and, acknowledging its beaver escutcheon, its symbol of sovereignty incorporates the beaver's heritage and economic and cultural importance (Lok et al., 2017). The beaver is depicted on countless emblems, seals, and government and military badges; for example, the public seal of New Netherland used from 1623 (Martin, 1892). Though the Canadian five cent famously depicts the beaver on one of its faces

(a)

Figure 2.1a The Canadian five cent coin depicts the beaver in recognition of its economic and cultural importance. (Illustration provided courtesy of Rachael Campbell-Palmer.)

(b)

Figure 2.1b The illegal $5 'beaver coin'. (Illustration provided courtesy of Rachael Campbell-Palmer, drawn from photo of coin.)

(c)

Figure 2.1c The crest of Bjursås a municipality of the Swedish city of Härnösand, city seal depicting the hard work ethic of the beaver.

(Figure 2.1a), it was not the first coin to bear the beaver image. In 1849, the gold $5 'beaver coin', showing a beaver standing on a log on one side (Figure 2.1b), was produced by a private mint following growing frustration at the US government's lack of establishment of a countrywide currency system; it was later deemed illegal (Crutchfield, 2018). The first Canadian postage stamp issued in 1851, the '3p beaver', depicts a beaver rather than Queen Victoria, which was a significant break from the customary practice of the British Empire at that time (Lok et al., 2017). As such it was the first animal to ever appear on an official stamp (Poliquin, 2015).

In other countries and states, the beaver appears on crests and coats of arms, such as the London School of Economics, and the state flag of Oregon,

on the reverse of which a golden beaver is depicted, the state animal. In *Fairbairn's Book of Crests of the Families of Great Britain and Ireland*, an extensive listing categorizing all surnames known at the time, the beaver appears on the crest of 25 families (Fairbairns, 1892, Vol. 1, plate 134; Box 2.1). More recently, *Amik* (originating from the Anishinaabe word for beaver) was the beaver mascot chosen for the Montreal Summer Olympics of 1976, while the logo for the National Parks of Canada (Parks Canada) is a beaver—symbolic of hard work, self-reliance, peacefulness, and an ability to tackle challenges!

2.1.1 Early human interactions

The largest rodent ever to have existed in North America and now extinct, the giant beaver (*Castorides ohioensis*) is believed to have appeared at the dawn of the Pleistocene and has been embedded in Native American legends (Martin, 1867; Powell, 1948; see Section 2.2). However, historical evidence of both modern species is widespread. Extensive beaver burrows have been identified from the Late Palaeolithic site of Grabow in the floodplain of North Germany (Tolksdorf et al., 2017). Prehistoric digs in Somerset, England, have determined that humans were attracted to beaver sites, building plank walkways in shared habitats, with beaver bone remains found in nearby caves from 12,700 to 8500 BCE (Coles, 2006).

Box 2.1 Beaver crest family names

Family surnames including beaver in their crest (Fairbairns, 1892).

Alexander, Baynham, Beaver, Beevor, Bell, Besook, Bevers, Beynham, Brookes, Brooks, Coram, Corham, Danskine, Dimsdale, Eaton, Fenwick, Howel, Howell, Maclagan, McLagan, Molineux, Sadleyr, Symcock, Symcott, Trowell.

Common surnames deriving from beaver in some form include:

Beverley or *Beverly* 'beaver stream' in Old English and derived from a settlement in England.

Bieber 'beaver' German and Jewish origin, could also be a nickname for a hard worker.

Bjurström (Swedish spelling) or *Bjurstrøm* (Norwegian and Danish spelling) are Nordic surnames derived from *bjur* 'beaver' and *ström* 'river'.

One '*gost*' (a title awarded only by the tsar to represent a very wealthy merchant), Vasili Bobr, is known for building a brick church in the 1480s near to Red Square in Moscow today, presumed to have made his money from beaver pelts, given his surname (Monahan, 2016).

Three main human-related activities found in beaver remains have been described (Lebreton et al., 2017). Evidence of various cut marks on the bones demonstrates (1) the use of a sharp-edged tool, producing small perpendicular marks as evidence of skinning; (2) disarticulation via deep marks, made again by a sharp tool to separate limbs from the axial skeleton; and (3) defleshing, evident through short incisions in a regular pattern left by axe-shaped tools to separate meat from the bone. Butchery at numerous prehistory human sites such as Dalmeri, Italy (Fiore et al., 2001), Kettig, Germany (Baales, 2002), and multiple sites in Finland (Forstén and Lahti, 1976) clearly indicates that beavers were consumed quite normally alongside many other animals. A burnt beaver tooth from this same period has been found at Medzhibozh in the Ukraine (Stepanchuk and Moigne, 2016). In the Middle Palaeolithic, human cut marks have been identified on beaver remains in Grotta San Bernadino, Italy (Fiore et al., 2004) and at Taubach and Lehringen in Germany (Gaudzinski, 2004). Multiple beaver remains, including burnt and cut bones have been

dated from the Early Holocene at several sites in France (Dibble et al., 2009; Rendu, 2010; Silmak et al., 2010). Just over 5% of total mammal remains in the Rhone Valley and Danube basin from this time have been identified as beaver (Kind, 2009). In northern European Mesolithic sites, beaver bone fragments are much more numerous, for example they comprise 30–60% of mammal remains at some Estonian (Veski et al., 2005) and Russian (Chaix, 2003) sites. At one Russian location, a beaver skull with the remains of a harpoon head has been uncovered (Zhillin, 2004). In North America near Lake Huron, butchered beaver bones with clear knife cuts have been aged as being 3,700 years old and the remains of a beaver pelt which was once wrapped around a copper axe has been aged to 2,500 years, found in a burial mound (Backhouse, 2018).

In the Neolithic period, northern European tribes were also creating symbolic representations of beavers. Petroglyphs (rock carvings) of beavers have been found at Lake Onega and near the White Sea, in northwest Russia (Danilov, 1976). These representations are believed to have been drawn from a hunter's perspective, looking down on a swimming beaver from above (Danilov et al., 2011; Figure 2.2a and b). Further beaver remains at the Etruscan sanctuary of Podere Ortaglia, in Italy, are believed to have been part of a ritualistic offering to Artemis, the goddess of the hunt (Sorrentino and Landini, 2005). Whilst beavers are featured as part of cultural belief systems, occurring widely in Native American totem carvings as important animal spirits (Marcuzzi, 1986; Figure 2.3).

2.1.2 Beaver place names

Apart from Hawaii, every other American state and Canadian province possesses place names relating to beavers (Backhouse, 2018). Nearly 3,500 geographical locations with 'beaver' in their name have been recorded, including 61 swamps, 331 lakes, and 1,373 creeks (Long, 2000). Wherever beavers have been numerous they were an important feature of value in the landscape and were as such recognized by people.

A similar pattern of place name records exists in Europe. The Old French word for beaver being '*bièvre*' is recorded in towns such as Monthou-sur-Bièvre
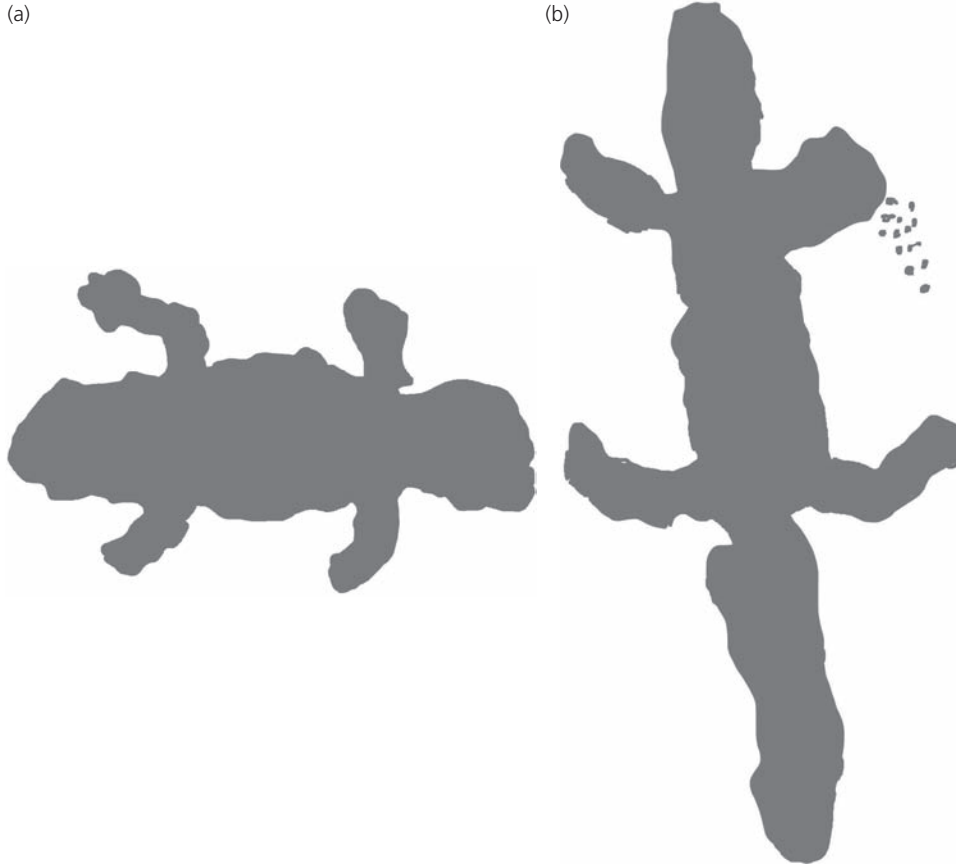
(a)   (b)

Figure 2.2a and b Representations of rock carving depicting a swimming beaver from a hunter's perspective looking down.
(Illustrations provided courtesy of Rachael Campbell-Palmer, redrawn after Savvateev, 1970.)

and Bièvres, whilst Beverley in England was named through the combination of '*beofor*' and '*leac*' which are the Old English words for beaver and stream respectively (Figure 2.4). In Germany, the municipality of Biberbach means beaver creek and there are also two Biber rivers elsewhere. The Polish word for beaver '*bóbr*' is recorded in the River Bóbr and the towns of Bober and Bóbrka (Poliquin, 2015). Similarly, the villages Bobr, Bobroviníky, and Bobrová can all be found in the Czech Republic. The Nordic '*bjur*' is found in numerous place names including Bjurälven (beaver river), site of the first beaver reintroduction in Sweden 1922. Throughout the whole of Sweden there are numerous derived place names including Bjurängen, Bjursås, Bjurbäck, and Bjuön.

In Karelian, Finnish, Sámi, and Vespian the word for beaver is '*majova*', '*majava*', '*mádjit*', and '*maji*', all of which sound very similar. Various place names, including the rivers Maija and Maya, the lakes Maima, Maimjärvi, and Maijezero, and numerous Karelia villages such as Maiguba and Mayaniemi (Danilov et al., 2011), take their root from these. Other names have proved more controversial. For example, the confirmed Old Welsh name for beaver is '*llostlydan*' meaning broadtail, which appears in the 'Laws of Hywel Dda' known as the Medieval Welsh Law Codes, dating back to 940 CE (Charles-Edwards, 1989), though no place names associated with this are known today. From around the seventeenth century the Welsh term for beaver more commonly becomes '*afanc*', also spelt

Figure 2.3 The beaver is often represented in the Native American belief system as a creator of life. (Photo supplied courtesy of Alicia Leow-Dyke.)

'*afangc*' or '*avanke*', with place names including Llyn-yr-Afanc, meaning beaver pool, and Bedd yr Afanc, meaning Grave of the Afanc, still evident (Coles, 2019). In early Welsh the term '*afanc*' refers

to a water monster (Aybes and Yalden, 1995), variably described as anything from a crocodile-like creature to a giant beaver and even a hybrid between the two (A. Leow-Dyke, pers. comm.)!

2.2 Myths, folklore, and religious beliefs

Many folklore and numerous myths are associated with the beaver, including counting as a fish meal on religious holidays but also eating fish themselves, working in huge teams to build dams, and self-sacrificing body parts (often mistakenly referred to as their testicles, whilst meaning their castor sacs) to appease hunters (Wilsson, 1971; Poliquin, 2015; Figure 2.5a). Medieval writers, such as Dante Alighieri, believed beavers not only ate fish but also could lure them by waving their tails in the water and releasing an attractive fatty substance (Holbrook, 1902; Figure 2.5b), with Buffon, a French natural historian, even stating a beaver's scaly tail was caused by fish eating. Other myths such as an ability to predict the weather may be based on the biological realities of extra fur growth and larger food caches in harsh winter conditions. Many such as sleeping with their tails dipped in the water to detect its changing levels or their tail slapping leading to thunder (Newman, 1985) relate more to fairy tales than having a scientific basis, but wherever beavers exist, there are stories.

Figure 2.4 The English town of Beverley, named after the Old English for beaver and stream. (Photo supplied courtesy of Derek Gow.)

Many Native American tribes considered beavers to be superior animals, with a central role in their belief regarding the creation of the world. '*Beaverman*' was believed by indigenous Alaskans to have redesigned the animals we know today from their previous forms (Long, 2000). The Sioux have four creative gods, one of which is the beaver. The Amikonas 'People of the Beaver', an Algonquin tribe of Lake Huron, have long-standing myths about the giant 'great original father' beaver, which they claim to be descended from (Martin, 1892). *Castoroides ohioensis* was a giant beaver species which occurred in the Pleistocene when humans and the now extinct megafauna overlapped in time?. The Cherokee thought that giant beavers helped the Great Spirit to create the Earth (Rue, 1964). The northeastern Algonquin tales talk of *Quahbeet*, the giant beaver, whose tail slapping produced thunder (Martin, 1892). The super mythical figure *Gluskap* was common in many tales of epic chases and hunts of giant beavers (Beck, 1966). Many of these credit the formation of the Great Lakes to the giant beaver when it dammed the Saint Lawrence River. *Gluskap* also created all animals, including people whom he made last and then presented to the other creatures. Those who

showed no respect to his newest of beings he reduced in size by a stroke of his hand. While this worked for some, the crafty beavers were swift to escape and another epic chase began. Numerous bays and islands were formed from the paddle strokes of *Gluskap* chasing the beavers in his canoe and from the rocks he threw at them during these battles. Slight variations in this story and topographical features change, but its telling is fairly consistent amongst the indigenous people of this region (Beck, 1972). The Dene tribe of the Great Slave and Artillery Lakes tell stories of *Xachogh*, a hunter who killed giant beavers for food, while the Pocumtuck tribe believes the Pocumtuck hill range of the Connecticut River valley to be the petrified remains of a giant beaver that tried to eat people when it ran out of fish. The people called on the spirit *Hobomock* to chase the giant beaver back into the water and kill it (Poliquin, 2015). The commonality of giant beaver tales among various northeastern Algonquin tribes overlapped with the distribution of Pleistocene remains of this extinct animal represent a fossil memory of shared existence (Beck, 1972).

The Cherokee credit the beaver for creating the antlers that are now borne by deer, which they won after a contest with the rabbit as to who was the
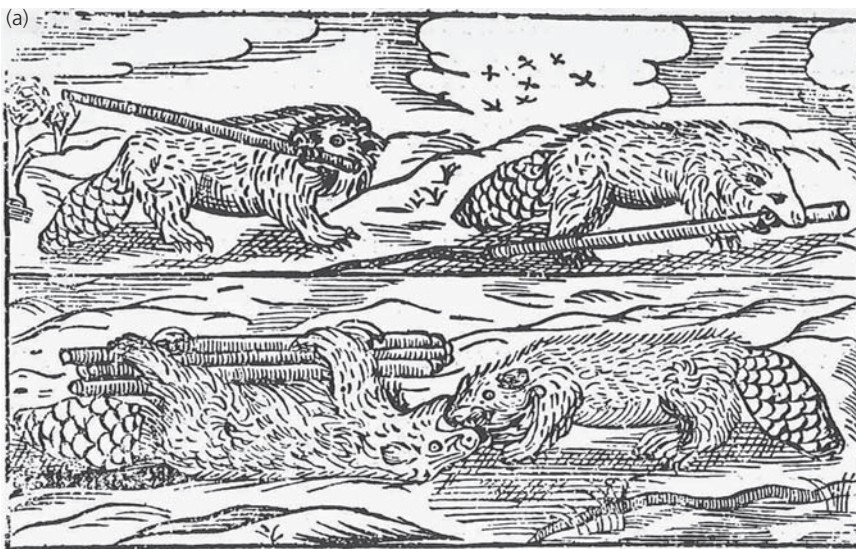
Figure 2.5a Old females or slave beavers could be recognized as they have bald backs as they were used for transporting trees. Johannes Bjurberg illustration, 1687, University of Uppsala.

Figure 2.5b   Notice beavers are fishing with their tails in the water in this illustration of beaver hunting from the '*History of the Nordic People*', Olaus Magnus around 1550.

faster animal (Lake-Thom, 1997). With variations, many tribes believe that in the beginning the Earth was covered in water and it was the beaver that dived to bring up mud from which the Great Spirit Manitou formed the land. Manitou removed their power of speech as a punishment. One Cheyenne clan believes the father of all humans to be a great white beaver who retains the power to gnaw through the wooden post that holds up their world if he is angered. As a result, touching the skin or eating the meat of ordinary beavers would make you sick (Long, 2000).

In the USA Midwest, it was believed that human spirits were trapped inside beavers and that these would return to their human forms when they were killed. The Crow thought they were reincarnated humans (Rue, 1964) and as a result not all Native American tribes will hunt or eat beavers. So strong was this consideration for the Blackfeet that they refused to trade in their furs with the European colonists. Mistassini Cree ideology holds the beaver in higher regard than other animals (Cox, 1988). Utilizing and respecting their entire carcass required that even the often-purposeless forelegs were decorated and hung in trees to prevent their con-

sumption by scavengers (Speck, 1923; Tanner, 1979). Other tribes believed beaver bones should be burnt as a mark of respect. The Tlingits thought that feeding beaver meat to their dogs would result in the dead beaver complaining to the spirits of the living beavers with regard to their fate and that as a result the spirit animals would punish their hunters with reduced yields in the future.

The discovery of beaver artefacts at religious sites and graves from ancient European sites also indicates that the species retained an almost holy status for early people (Wilsson, 1968). Some of the first written accounts of beavers and their activities were provided by Giraldus Cambrensis 'Gerald of Wales'. In 1188, this historian and Cambro-Norman archdeacon described beaver castles and other more curious aspects of their behaviours. He stated that when moving large logs, they would work in a team, with some lying on their backs while others loaded logs onto their stomachs. They would then drag their load back to the water. A widespread European medieval literary cycle or fable *Reynard the Fox*, first appearing in the later twelfth century, includes a series of animal characters with defined personalities, including Bockert the beaver, considered wise and

well educated, who acts as the secretary and translator at the court the trickster fox is called to (G. Hartman, pers. comm.). One of the first natural history accounts of North American beavers was written by Denys (1672). He described their collective workings and told how they came together in highly regimented units of over 400 individuals where labour divisions (lumberjacks, diggers, masons, etc.) were strictly enforced and overseen by commanders (Denys, 1672).

One of the oldest and most commonly held myths relating to beavers is believed to originate from one of Aesop's legendary fables, first written down in 1484 (Caxton, 1484). Aesop was believed to be an African native enslaved in ancient Greece around 620–564 BCE, whose fables have been widely translated and told for centuries throughout the world. The beaver fable describes how a beaver chased by a huntsman and his hounds will bite off and offer up its castor sacs, which were often mistaken for testicles, as they know the hunter will spare their life if they sacrifice these organs valued for their castoreum. Several varying morals were taken from this tale over time. The original has been translated as 'if only people would take the same approach and agree to be deprived of their possessions in order to live lives free from danger: no one, after all, would set a trap for someone already stripped to the skin' (Gibbs, 2002); in another, that 'wise [men] know to sacrifice possessions over their life' (Calabritto, 2002). The Roman satirist Juvenalis (AD 60–130) likens the behaviour of the character Catullus on saving his ship and crew from near-certain death as that of a beaver: 'For when the hold was half of water, and the waves rocked the hull from side to side, so that the white-haired skipper, with all his skill, could bring no succour to the labouring mast, he resolved to compound with the winds like the beaver, who gives up one part of his body that he may keep the rest: so conscious is he of the drug which he carries in his groin. "Overboard with everything!" shouted Catullus.' Medieval and Christian moral overtones link the tale with casting away of 'vices and shameless acts' and therefore sin, and castration was practiced by some priests at the time (Curley, 1979). This belief of beaver self-castration came from classical Greek naturalists, passing into Roman folklore, Christian teachings

(popularized in the medieval period by Isidore of Seville and the Latin *Bestiary*) (Raye, 2014), and numerous ancient natural history texts throughout Eurasia, until published anatomical studies by early French naturalists such as Guillaume Rondelet (around 1566) and Moyse Charas (around 1668) dismissed its possibility, clearly distinguishing between testes and castor sacs (Poliquin, 2015).

A similar story of the self-sacrificing nature of beavers is told by the Midwestern Omaha tribe: when a beaver family has no food to offer a guest, their youngest child will on its own behalf offer itself for dinner. As long as its bones were respected and not broken, the beaver child could then regenerate and return good as new. If, however, the guest was careless or dishonest while eating and cracked even a small bone, when the young beaver reappeared it would have a broken toe, and as a result all beavers carry two split nails on a single hind toe as a reminder of this possibility (Backhouse, 2018).

In medieval times the Catholic Church classed beavers as '*aquatilia*', along with other water-dwelling animals like seals (Phocidae), otters (*Lutra lutra*), and turtles (Chelonia). These creatures were all believed to be more fish-like in nature and as such could be consumed during religious holidays and periods of penitence when meat was forbidden. In parts of Italy, beaver remains related to the diets of seventh- to ninth-century monks have been found in a number of monastic complexes such as San Vincenzo al Volturno, Molise and the Piazza della Signoria in Rome (Salari et al., 2019). The eleventh-century German monk Ekkehard IV has been credited with writing '*sit benedicta fibri caro piscis voce salubri*', roughly translated as blessed be the fish-like flesh of the beaver.

2.3 Beaver territories as resources

It is worth noting that beaver activities in themselves have multifunctional uses for humans and historically have provided an important resource. In modern times their habitat modifications have often been used to justify reintroduction programmes, encourage wetland restoration, and implement a sustainable process of ecosystem services (see Chapters 9 and 11).

Beaver-generated environments generate a broad range of resources readily utilized by humans (Coles, 2006). Early hunter gatherers were drawn to wetlands as these were full of prey (game, water fowl, fish, and small mammals) and complex environments. At a time when there were many large predators in the wider environment, islands surrounded by complex channels were preferentially sought. The vast amount of dead wood generated by the beavers provided a ready fuel resource when dried, which ranged from larger logs cut from felled trunks to the near wood powder generated by gnawed chips. Charred material with beaver tooth marks has been identified and found at a number of archaeological sites (Coles, 2006). Further beaver-cut material of appropriate dimensions was variously used for fence posts, shelters, door stops, paper weights, and even walking sticks (Coles, 2006). The rod-straight regrowth of coppiced tree stumps from species such as willow (*Salix* spp.) must surely have prompted people to initially utilize and then replicate the production of this resource which was essential for wattle fencing, basket weaving, and trap construction (Backhouse, 2018).

Beaver dams can be significant structures and humans have been recorded using them as walkways through wetlands. Perhaps one of the most significant functions of beaver dam systems in our modern world is water retention. This natural function has significant ecological benefits (see Chapter 9), which are now increasingly linked to important economic and conservation gains. The renowned beaver ecologist Glynnis Hood has documented through her numerous studies the hydrological capabilities of beaver-generated environments (see Chapter 9). The impoundment of water behind their main dam structures coupled with a wider retention capacity in extensive networks of excavated canals hold huge volumes of water under drought conditions. This function directly benefited cattle ranchers whose stock could still drink in beaver ponds and graze on the lush availability of associated vegetation in otherwise arid Canadian landscapes (Hood and Bayley, 2008; Hood, 2011).

Beaver meadows, formed from the combination of silts and sediments layered behind their dams over millennia, have also been widely used by humans as environments for cultivation through much of the beaver's former range. As the beaver was hunted out of Eurasia and North America, not only did this leave 'a wealth of place names which no longer made much sense' but ever-expanding colonists used their abandoned dams as sites for water mills and the land left behind broken-down dams was used as rich fertile fields for crops or farming livestock (Cronon, 1983). Henry Wansey, an English traveller to the eastern USA, recognized the high hay production gained from farming these beaver meadows when he noted in 1794 that, 'it is a fortunate circumstance to have purchased lands where these industrious animals have made a settlement' (Wansey, 1798; Backhouse, 2018). In Sweden, a traditional superstition states if you rub a beaver's incisor along your axe then the clearing you make with it in the wood would stay open, most likely an interpretation of people noticing that beaver meadows remain open for long periods of time (G. Hartman, pers. comm.).

2.4 Cultural value of beaver teeth and bones

Entire beaver mandibles or their single long sharp incisor teeth were commonly used as woodworking tools during the Mesolithic. While the mandibles were employed as scrappers or chisels (Ewersen, 2006/2007; Zhillin, 2004), the incisors were typically joined to a simple wooden shaft with pitch and have been found in lowland European sites (Schacht and Bogen, 2001). Beaver incisors were used for carving various artefacts by Northwest Native Americans (Stewart, 1973). Numerous tribes including the Ingalik of Alaska continued such practices well into the twentieth century (Osgood, 1940), while, in particular, Pacific Northwest tribes, such as the Clayoquot of British Columbia, made dice from their molars, decorating them with carvings and colours for gambling games (Dorsey, 1901).

Their large long incisors were widely sought for ornamental pendants, which have been found in Mesolithic sites on the eastern Baltic and in western Russia (Schmölcke et al., 2017). The high value of these pendants for their symbolic and spiritual significance was demonstrated at a large burial site

(~6,400–6,000 BCE) on Lake Onega in northwestern Russia, where many women had been buried with them (O'Shea and Zvelebil, 1984). Beaver ornaments have also been discovered in the graves of children and women in Anglo-Saxon (sixth to seventh centuries) graves in central and eastern England (Coles, 2006). Several theories to explain their symbolism have been considered. Variations in the wear patterns associated with the bodies of growing children and pregnant women may indicate a belief rooted in medical folklore linked to dental health (Meaney, 1981). Alternatively, given the resemblance of the Latin for chastity *castitas* with *castor*, these pendants may represent the virginal status of those they were buried with (Blair, 2005). The Cherokee believed that when a child lost a baby tooth, they had to run around their home four times saying 'beaver put a new tooth into my jaw' before throwing it onto the roof (Long, 2000). Beaver tooth pendants were also worn by Vikings (Schmölcke et al., 2017), while the Romans in Gaul had beaver incisors as amulets, a custom continued in some parts of modern Italy to ward off the evil eye (Pilleri, 1986).

Astragalus (ankle bone) pendants were found in Mesolithic graves in Latvia (Eriksson et al., 2003) and their wider use is of interest as their symbolic value from the Estonian Vikings through to the early French Christians (sixth to seventh centuries) is likely to be different. The commonality of their use in graves either suggests a protective meaning or may be reflective of social status (Schmölcke et al., 2017). Beaver bones have also been found as suspected funeral offerings of German tribes (Pilleri, 1986).

The full symbolic value of the widespread discoveries of beaver teeth and astragalus has resulted in considerable speculation regarding their use, which ranges from common items such as trap markers (Jonuks, 2005) to economic tokens (Luik, 2010), oracles and amulets, and gambling tokens (Nikulina and Schmölcke, 2007; Nikulina and Schmölcke, 2008), and even proves the existence of 'beaver cults' (Fehner, 1963). Beaver teeth were also powdered and made into soup-like substances to be consumed for the prevention of a range of diseases, though castoreum was believed to have the most healing powers.

2.5 Castoreum and its creative uses

Though not used today for medicinal purposes, castoreum has long been employed in traditional medicine. In 500 BCE Hippocrates, the Greek 'Father of Medicine', was credited with describing diseases as natural rather than caused by the gods (Garrisson, 1966) and he fully recognized the healing properties of castoreum (Martin, 1892). Celsus (*c.* 30 CE), a Roman encyclopaedist, details the medicinal value of castoreum in his writing *De Medicina*, whilst Solomon III, King of Israel, is said to have obtained castoreum from Spanish beavers to cure his headaches (Westcott, 1989). Numerous early medical texts, originating with Baccius's *Castrologica* (1685), pronounce now somewhat outlandish claims for the medicinal properties of castoreum. Castoreum is believed to have analgesic and analeptic properties (Leung and Foster, 1996) and has been utilized in the treatment of a range of conditions including all sorts of fevers, toothache, preventing insomnia, stomach complaints, hysteria, and even insanity. Historical testimonies towards its power have included the curing of ear-ache and even deafness, tumours of the liver, gout, sciatica, lethargic people, maladies of the spleen, and a girl with complete memory loss, destroying fleas, stopping hiccoughs, both inducing and preventing sleep (presumably different doses!), as an antidote to the stings of scorpions and spiders, and even as doing 'much good to mad people' by clearing the brain (Martin, 1892). In fairness, castoreum may possess some analgesic properties, being mainly derived from beavers' ingestion of the salicin in the bark of the willow, meadowsweet (*Filipendula ulmaria*), and poplar (*Populus* spp.) trees which then concentrate in their castor sacs (Rainsford, 2016). Where present, beavers will readily select and consume meadowsweet plants with great enthusiasm. Acetylsalicylic acid produced from salicin derived from meadowsweet (at that time its botanical name was *Spiraea ulmaria*) led to the development of aspirin by Felix Hoffmann in 1897 (Jeffreys, 2008). However, no modern medicinal uses for castoreum are recognized (Figure 2.6).

It was also used in perfumes, soaps, and creams and as an oil base and fixative agent in cosmetics to increase the length of time scent lasts, as was ambergris from sperm whales and civet cat musk