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CHAPTER 1

Pathways in time and space

Animal domestication encompasses many kinds of interactions between humans and other species. It is a continuum of stages of a gradually intensifying relationship. This relationship ranges from anthropophily to commensalism, from control in the wild to control of captive animals, from extensive to intensive breeding, and in some cases it extends to owning of pets (e.g., Vigne 2011, Zeder 2012a, b; Larson and Fuller 2014). A fundamental and primary aspect of domesticated animals is their tameness, meaning that they tolerate and are unafraid of human presence and handling. The genetics and the physiological and morphological correlates of tameness have thus been a central focus of studies of domestication. However, tameness alone does not imply domestication, as exemplified by tamed elephants living in close association with humans. Keeping an animal as a pet does not make it domestic. Examples from the Amazon region abound. Changes in reproduction can be seen at the core of domestication (Vigne 2011).

Domestic animals emerged from small groups of individuals of their respective wild form that became increasingly reproductively isolated from the stem forms as a result of the influence of humans. They adapted to the peculiar ecological conditions imposed by an anthropogenic environment and in some cases developed considerable population sizes. Domesticated animals are subject to environmental conditions and selective pressures different from those faced by their wild counterparts. Furthermore, the conditions to which populations of domestic animals are exposed vary greatly (e.g. culling patterns, availability of food, protection from predators). Altered natural selection and continual targeted and non-targeted selection by humans led to divergence from the wild norm in morphology, physiology, and behavior. Domestic animals are increasingly used for economic and leisure purposes in diverse ways. The variety of perspectives by which to characterize domestication (e.g., symbiotic interactions: Budiansky 1992; resulting domesticated phenotype: Price 1984; Kohane and Parsons 1988) make a unique and universal definition a challenging and unrealistic goal (Ladizinky 1998; Balasse et al. 2018).

Traditionally, domestication has been defined and conceptualized from the human perspective, with our species as the domesticator. This view is no longer universally accepted, and in fact different perspectives have contributed to this change. A new look at naturalistic observations demonstrates the active role played

by animals in approaching humans and in looking for benefits resulting from human proximity and interaction. It is thus relevant to examine the reciprocal impact of animals in shaping the trajectory of human biological and cultural evolution (Zeder 2017). Animal-human interactions have been discussed in terms of niche construction, a subject often treated in discussions of an expanded evolutionary synthesis (Smith 2011a; Zeder 2018). Niche construction refers to the evolutionary impact of ecosystem engineering activities that create new or modify existing selection pressures acting on present and future generations (Odling-Smee et al. 2003). Humans have been characterized as the ultimate niche constructors, and cultural niche construction has been discussed in the context of the initial phase of domestication (Smith 2011b). Domestic animals are also niche constructors. Independent of the discussion around the repetitive nature of the subject of niche construction in the literature (Gupta et al. 2017), its relevance to conceptualizing and describing ecological interactions is uncontested.

Another perspective that questions the traditional and human-centered conceptualization of domestication (e.g., Zeuner 1963) is a philosophical/sociological one. People tend to create narratives (Diogo 2017), and we have done so with domestication, in which we present ourselves as central and the makers of destinies of organisms. This notion ignores the active role of the “domesticated” and is a traditional Western European view of our place in nature that is not universal among humans (Ingold 2000; Descola 2013; Figure 1.1). The argument has been made for abandoning the notion of domestication in favor of a continuum of human-nonhuman animal relationships (Russell 2002). Although there is merit in this idea, it does not solve the issue of defining the complex phenomenon we call domestication. It is more productive to discuss the pathways to domestication and the different kinds of interactions entailed by domestication. These reflections should not obviate the recorded cases in which humans have played and directed a one-sided role in domestication, as in the case of canaries native to the Canary Islands brought to Europe and domesticated simply because of their singing (Birkhead 2003).

When the focus is on intense, selective breeding and animal management, the conceptualization of domestication leads to a view in which humans are the sole agents (Fig. 1.1, “Ego”). This view also sees domestication as an intentional and goal-oriented interaction. An alternative view arises if one concentrates on the first steps of the domestication continuum. At this point, people did not have long-term domestication plans, and interactions between humans and other animals were voluntary on both sides; therefore, from this perspective, the agent is not as obvious. The argument has been made that, based on some parameters, some domesticated animals and plants have benefited more from the interaction than humans themselves (Budiansky 1992). The increased distribution and multiplication of species that became domesticated contrast with the many challenges and disadvantages faced by humans following the Neolithic transition. The idea of human demise following the Neolithic transition has an element of retro-romantic thinking. What is needed is a multivariate evaluation and quantification of human prosperity across time, so that a nuanced evaluation of how human life has changed can be attained. Surely the result will show nonlinear changes, geographic variation, and a lack of universals.

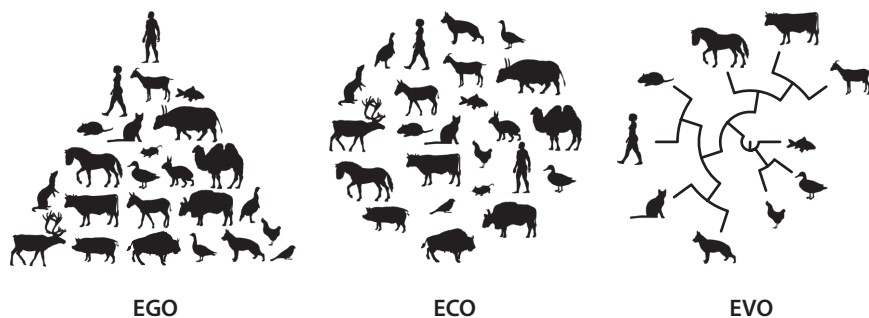


Fig 1.1. Ego, Eco, and Evo views of the human-animal interactions. Only domesticated animals are shown.

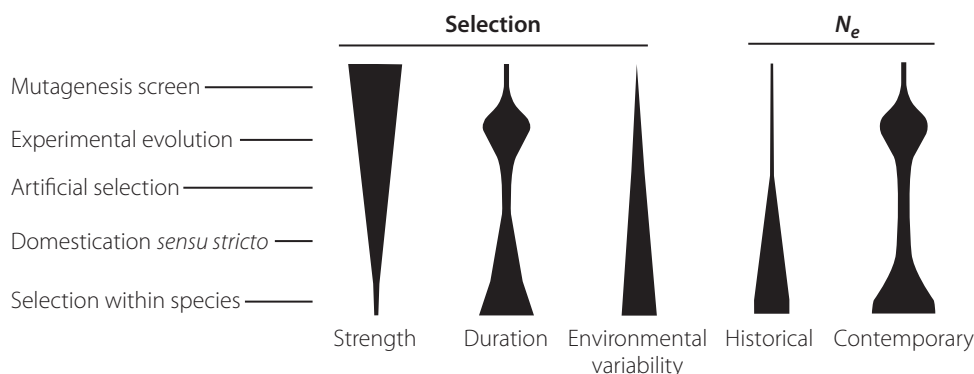


Fig 1.2. Comparison of domestication *sensu stricto* versus artificial selection and other kinds of selection regimes. The geometric shapes represent the relative magnitude of variables shown along the top of the figure. N_e is the effective population size. The historical population size influences the amount of variation present in the population.

It is fundamental to differentiate the intense “artificial selection” typical of the creation and preservation of breeds (“intensive breeding”) from the domestication pathways described below, associated with the initial phase of interaction, in which a dependence of the domesticated form on humans has not yet been established. Mutagenesis screens, experimental evolution, artificial selection, domestication, and selection within species differ in important parameters in space and time (Stern 2011; Figure 1.2). A mutagenesis or genetic screen is an experimental approach used in research to generate a mutated population to identify and select for individuals with a specific target phenotype, providing information on gene function. The difference between domestication *sensu stricto* versus selection for “improvement” traits or artificial selection, as well as with other kinds of evolutionary and human-induced phenomena, becomes evident when comparing degree of selection and population sizes.

There are different pathways to domestication. Likewise, the kinds of interactions at the other end of the domestication continuum (Figure 1.3) are not all the

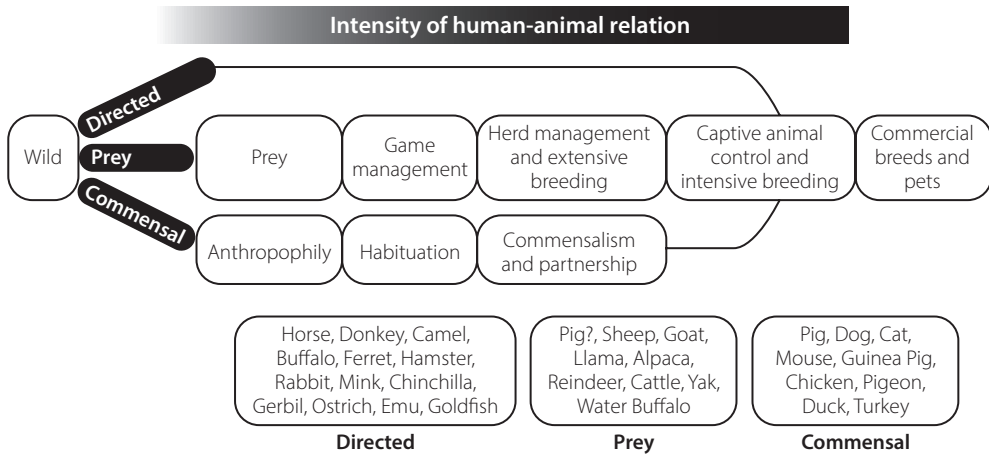


Fig 1.3. Pathways to domestication. Changes in intensity of the human-animal relationship are indicated.

same. Selective breeding, aimed at preserving specific breeds or features, is different from management, which involves manipulation of growth conditions, or the environment that sustains it. The aim of management is to increase the relative abundance and predictability of a population and to reduce the time and energy required to harvest it (Zeder 2015).

Pathways to domestication

Traditionally, domestication has been seen as resulting from goal-driven human action, with narratives about selection for traits that differentiated wild and domestic forms. In reality, domestication of different species has involved different kinds of interactions. Zeder (2012a, b) formally recognized and described three separate pathways followed by animals into a domesticated relationship with humans: a commensal pathway, a prey pathway, and a direct pathway (Figure 1.3).

There is usually no intentionality in the commensal pathway, which involves a coevolutionary process in which a population uses a novel niche that includes another species. That niche could involve human food waste or refuge, which is then taken advantage of by a subset of individuals of another animal species (e.g., wolves) that were less aggressive (i.e., tamer) than the rest. In the absence of human instigation, an interaction could arise, and only later would the human-directed selection that we associate with modern domestic populations have been possible.

The prey pathway involved a human intention to increase the efficiency of resource management. Medium to large herbivores were targeted as prey, including perhaps the case of horses. Although not originally planned as such, domestication resulted from humans altering their hunting strategies toward herd management, eventually leading to control over the animals' diet and reproduction (Zeder 2012a, b). The prey pathway probably took place in human communities

that cultivated plants and did not lead a hunter-gatherer life. The directed pathway involved the deliberate use of a species and its incorporation into human life for uses such as transport, although the species in question were sometimes hunted as prey. A classic example of a directed pathway involving consumption is aquaculture (chapter 9).

The domestication pathway followed by different species is in some cases clear and in some cases debatable (Larson and Fuller 2014). There can be mixed cases, as in pigs perhaps having been domesticated via both a commensal and a prey pathway. The zooarchaeological and molecular evidence used to establish domestication pathways is mostly inconclusive, but mortality profiles may provide clues (Payne 1973) if performed with proper sampling and approach (Bartosiewicz 2015; Bartosiewicz and Bonsall 2018). Although recourse to comparative, ethnological data from hunter-gatherers is important, such ethnological data only provide hints on the plausibility of an explanation by analogy, and never a direct test of what happened.

Domestication in other species?

Different kinds of interactions occur among animal species, and some of these have been compared with domestication (Zeuner 1963). Prominent among these interactions is symbiosis, in which both partners benefit. Certainly common aspects are shared by some interactions and domestication, but by definition and considering the cognitive and social aspects associated with humans, it seems reasonable to see those commonalities as superficial.

The sharing of resources and of defense against predators recorded for baboons interacting with feral dogs and cats in Saudi Arabia are a remarkable case recorded in numerous videos and popular accounts. Indeed, mixed-species associations are known to occur and benefit those involved by increasing foraging success, and by aiding in the detection and deterrence of predators (Venkataraman et al. 2015).

In the case of agriculture, some authors have called the case of humans and crops and the “agriculture” practiced by leaf cutter and other ants a convergence (Conway Morris 2003), but there are profound evolutionary differences between the two (Sterelny 2005; Jablonsky 2017). Agriculture has reportedly evolved in three groups of insects: once in ants, once in termites, and seven times in ambrosia beetles. All three groups produce clonal monocultures within their nests and for generations, with monitoring of gardens and additionally managing of microbes that provide disease suppression (Mueller et al. 2005). Other reports include those of fungus farming by a snail in the marine environment (Silliman and Newell 2003), bacterial husbandry in social amoebas (Brock et al. 2011), and a damselfish (*Stegastes nigricans*) and algae (*Polysiphonia* sp.) in a coral reef ecosystem. But the “agriculture” of these animals is neither associated with cultural changes in the domesticator, nor has it led to major geographic expansions and use of natural resources. Furthermore, the associated cognitive, physiological, and developmental aspects of the organisms involved are different from those of humans.

The diversity of domesticated mammals and birds: patterns in time and space

Roughly 70,000 species of vertebrates have been recognized in the world, of which about 5,500 are mammals and 10,900 are birds. Of these, only a few dozen species have been domesticated. The number of species with populations being managed or kept in captivity is much larger, and many of these have been described as “semi-domesticated” (Mason 1984). Distinguishing wild from domestic forms—to use the simple and not always proper dichotomy—in both the zooarchaeological record and even when considering extant population samples, is not an easy task. One aspect to consider is that lifestyle under domestication is quite variable. A wild population may be more similar in its life conditions to a domesticated one than to another wild population, for example.

When Darwin (1868) published his major work on domestication, hypotheses about which ancestral species led to domesticated ones were being first postulated. Darwin wrote that the diversity of dogs was such that origin from a single species would be highly unlikely. He was wrong—although not quite, if we consider the fact that introgression (gene flow resulting from hybridization) has occurred between wolves and coyotes (Lehman et al. 1991), and probably between some groups of dogs and other canids (Norton 2019). On the other hand, Darwin suggested that pigeons have a single ancestor, a surprising (and correct) hypothesis given how remarkably diverse pigeons are (Hansell 1998; Price 2002b). But things are complicated, as some traits of pigeons have been introgressed from other species (Vickrey et al. 2018). A similar case is known for the many breeds of chickens, originating mainly from the red junglefowl but with some degree of introgression from two other species of *Gallus*, at least in some regions, explaining some of the traits of chickens (Eriksson et al. 2008; Wang et al. 2020). Molecular and archaeological studies have hypothesized with great certainty which wild species were the ancestors for domesticated ones, as well as helped to test hypotheses on when and where major domestication phases occurred (Shapiro and Hofreiter 2014).

Mammalian domesticates

Among mammals, more than 25 species of placentals have been domesticated (Table 1.1). I follow Gentry et al.’s (2004) nomenclature, the one more universally used, in spite of the idiosyncratic nature of this decision given the known history of the animals involved, including hybridization (Zeller and Göttert 2019). Most domestic species are herbivores and, of those, most belong to the artiodactyls, which tend to live in herds and are nonterritorial. These features surely contributed to lend themselves to herding and managing by humans. The pig, although usually characterized as an “omnivore,” also eats mostly plant material, calculated in one study as around 90% of its diet (Ballari and Barrios-García 2014). Some domesticated artiodactyls such as the yak have remained confined to their original areas of domestication, but others, including cattle, sheep, goats and camels, dispersed widely through their association with humans. Pastoralism spread throughout semidesert lands, steppes, and savannas of Eurasia and Africa.

Table 1.1. A selection of domesticated mammals and their wild ancestors

Domestic form	Wild form
Dog, <i>Canis familiaris</i>	Grey wolf, <i>Canis lupus</i>
Ferret, <i>Mustela furo</i>	European polecat, <i>Mustela putorius</i>
American mink, <i>Neovison vison</i>	Wild mink, <i>Neovison vison</i>
Cat, <i>Felis catus</i>	Wildcat, <i>Felis silvestris lybica</i>
Horse, <i>Equus caballus</i>	Extinct lineage of <i>Equus ferus</i>
Ass (plus hybrids mule and onager), <i>Equus asinus</i>	North African wild ass, <i>Equus africanus</i>
Domestic goat, <i>Capra hircus</i>	Bezoar, <i>Capra aegagrus</i>
Domestic sheep, <i>Ovis aries</i>	Mouflon, <i>Ovis orientalis</i>
Pig, <i>Sus domesticus</i>	Wild boar, <i>Sus scrofa scrofa</i>
Bactrian camel, <i>Camelus bactrianus</i>	Bactrian camel, <i>Camelus ferus</i>
Dromedary, <i>Camelus dromedarius</i>	Dromedary, <i>Camelus dromedarius</i>
Llama, <i>Lama glama</i>	Guanaco, <i>Lama guanicoe</i>
Alpaca, <i>Vicugna pacos</i>	Vicuña, <i>Vicugna vicugna</i>
Common cattle, <i>Bos taurus</i>	Auroch, <i>Bos primigenius</i>
Indicine cattle, <i>Bos indicus</i>	Auroch, <i>Bos primigenius</i>
Bali cattle, <i>Bos javanicus</i>	Banteng, <i>Bos javanicus</i>
Gayal or mithan, <i>Bos frontalis</i>	Gaur, <i>Bos gaurus</i>
Domestic yak, <i>Bos grunniens</i>	Wild yak, <i>Bos mutus</i>
Water buffalo, <i>Bubalus bubalis</i>	Asian water buffalo, <i>Bubalus</i> spp.
Reindeer, <i>Rangifer tarandus</i>	Reindeer, <i>Rangifer tarandus</i>
Domestic rabbit, <i>Oryctolagus cuniculus</i>	Wild European rabbit, <i>Oryctolagus cuniculus</i>
Domestic cavy, <i>Cavia porcellus</i>	<i>Cavia tschudii</i> and/or <i>C. anolaimae</i>
Chinchilla, <i>Chinchilla brevicaudata</i> and <i>C. laniger</i>	Chinchilla, <i>Chinchilla brevicaudata</i> and <i>C. laniger</i>
Syrian or golden hamster, <i>Mesocricetus auratus</i>	Syrian or golden hamster, <i>Mesocricetus auratus</i>
Mongolian gerbil, <i>Meriones unguiculatus</i>	Mongolian gerbil, <i>Meriones unguiculatus</i>
House mouse (W Europe) and laboratory mouse, <i>Mus musculus domesticus</i>	Mouse, <i>Mus musculus</i> “group”

Note: Scientific names largely follow Gentry et al. (2004), given the widespread use of that nomenclature (but see Zeller and Göttert 2019). The taxa included follow the review of Larson and Fuller (2014) for the most part, with some modifications, such as adding the gerbil (Stuermer et al. 2003).

The domesticated carnivorans are the dog, the ferret, and the cat, and, more recently, the domesticated mink. Almost half the species of mammals are rodents, but few of them became domesticated. The laboratory rat can be considered domesticated, and together with the mouse and the domestic cavy or guinea pig, they are important in biomedical research.

Some species not listed in Table 1.1 are considered “domesticated” in a most general way, including many species that are simply kept in captivity or managed for diverse economic purposes but were never tamed over generations resulting in the genetic or morphological changes characteristic of domestication, nor were their

reproductive patterns significantly changed (Vigne 2011). In a compendium of domesticated animals, Mason (1984) listed among others the following species: muskox (*Ovibos moschatus*), American (*Bison bison*) and European (*Bison bonasus*) bison, silver fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), Egyptian mongoose, Indian grey mongoose, and the small Asian mongoose (*Herpestes ichneumon*, *H. edwardsi*, and *H. javanicus*, respectively), some civets (*Viverra* spp. and *Viverricula indica*), coypu or nutria (*Myocastor coypus*), capybara (*Hydrochoeris hydrochaeris*), muskrat (*Ondatra zibethicus*), giant pouched rat and greater cane rat (*Cricetomys* spp. and *Thryonomys swinderianus*), and Arctic or white fox (*Vulpes lagopus*).

There are no domesticated marsupials, even though opossums, possums, and kangaroos and their relatives both in the Americas and in Australia have played a role in the culture and traditions of humans (e.g., Smith and Litchfield 2009). Furthermore, no domesticates are included among two of the four large clades of placentals, the xenarthrans (armadillos, sloths, and anteaters) and the afrotherians (elephants, tenrecs, golden moles, sirenians, hyraxes). However, in these groups many species have been important as pets or are being or have been managed in different cultures (e.g., kangaroos), in some cases for centuries.

The evolutionary relationships among the domesticated mammalian species are solidly supported by comprehensive analyses of placental mammals (Francis 2015; Figure 1.4). This phylogenetic framework is fundamental to understanding the commonalities and differences among species of domesticates regarding changes in morphology and life history that result from domestication, as the evolvability and modularity of traits are usually clade-specific. For example, the “domestication syndrome” is not a universal and uniform set of characters, as different clades exhibit different sets of modifications arising from selection for tameness (chapter 3). Likewise, an understanding of the evolutionary relationships and distances among species is important for predicting the likelihood of transmission of infectious diseases between them (Farrell and Davies 2019). It has been speculated that infections from parasites outside their normal phylogenetic host range are more likely to result in death. In fact, the odds of lethality were estimated to double for each additional 10 million years of evolutionary distance (Farrell and Davies 2019).

Avian domesticates

Poultry are birds kept by humans for their eggs, meat, or feathers. Most of these birds are members of the Galloanserae (fowl), especially the Galliformes, including chickens, guinea fowls, quails, and turkeys, which are a sister group to the Anseriformes, which include ducks, Muscovy ducks, and geese. All these constitute the sister group to the Neoaves, including the pigeons in the Columbiformes and the great radiation of Passeriformes, examples of which are the Bengalese or society finch and the canary among domesticates (Table 1.2, Figure 1.5).

In addition to the species listed in Table 1.2, the budgerigar (*Melopsittacus undulatus*), the zebra finch (*Taeniopygia guttata*), and the ostrich (*Struthio camelus*) are considered domesticates by many authors. Several bird species are usually kept in

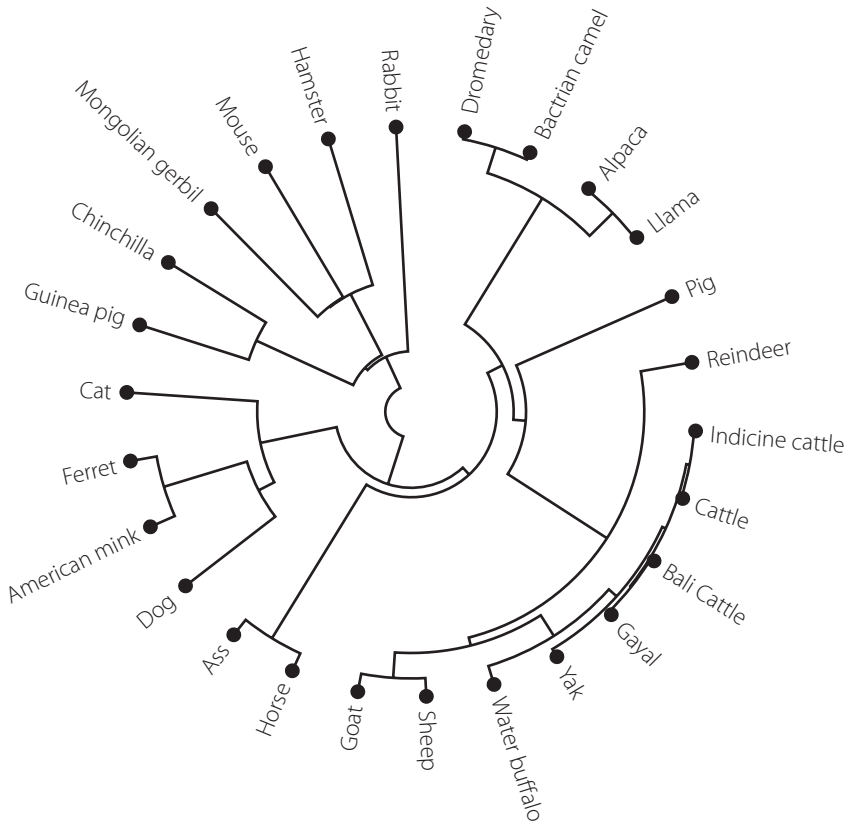


Fig 1.4. Evolutionary relationships among species of domesticated mammals. In some works, the yak is hypothesized as a sister group to the cattle/indicine cattle. Branch lengths are proportional to the estimated distance in time among species.

captivity or managed for diverse economic purposes. Mason (1984) listed the following species as semidomesticated, or routinely captive-bred: Barbary dove (*Streptopelia risoria*) domesticated as the African collared dove (*Streptopelia roseogrisea*), African lovebirds (*Agapornis*), cockatiel (*Nymphicus hollandicus*), mute swan (*Cygnus olor*), peafowl (*Pavo cristatus*), including Indian peafowl (*Pavo muticus*), green peafowl (*P. m. spicifer*), and Burmese form (*P. m. muticus* and *P. m. imperator*), pheasants (*Phasianus colchicus*, common pheasant, and *P. versicolor*, green pheasant), as well as partridges: grey (*Perdix perdix*), red-legged (*Alectoris rufa*), rock (*A. graeca*), and chukar (*A. chukar*).

One peculiar human-bird interaction involves the great cormorant (*Phalacrocorax carbo*) and fishermen in rivers in many countries in Asia, a few countries in Europe, and perhaps Peru in the fifth century of the current era (Leight 1960). In a traditional method now disappearing, fishers tie a snare near the base of the bird's throat, preventing the swallowing of large fish. When a cormorant has caught a fish

Table 1.2. A selection of domesticated birds and their wild ancestors. Additional species are discussed in the text.

Domestic form, common and scientific name	Wild form, common and scientific name
Domestic fowl / chicken, <i>Gallus gallus domesticus</i>	Red junglefowl, <i>Gallus gallus</i> Guinea fowl, <i>Numida meleagris</i>
Domestic guinea fowl, <i>Numida meleagris</i>	Mexican wild turkey, <i>Meleagris gallopavo gallopavo</i>
Domestic turkey, <i>Meleagris gallopavo</i>	Japanese quail, <i>Coturnix coturnix</i>
Japanese quail, <i>Coturnix coturnix japonica</i>	Green-headed mallard, <i>Anas platyrhynchos platyrhynchos</i>
Domestic duck, <i>Anas platyrhynchos</i>	Muscovy duck, <i>Cairina moschata</i>
Muscovy duck, <i>Cairina moschata</i>	Greylag goose, <i>Anser anser anser</i> , and Swan goose, <i>A. cygnoides</i>
Goose, <i>Anser anser</i> and <i>Anser cygnoides</i>	Rock dove / rock pigeon, <i>Columba livia</i>
Pigeon, <i>Columba livia</i>	Canary, <i>Serinus canarius</i>
Canary, <i>Serinus canarius</i>	Striated, white-rumped, white-backed or sharp-tailed finch, manikin or munia, <i>Lonchura striata</i>
Bengalese or Society finch, Munia, Uroloncha, <i>Lonchura striata</i>	

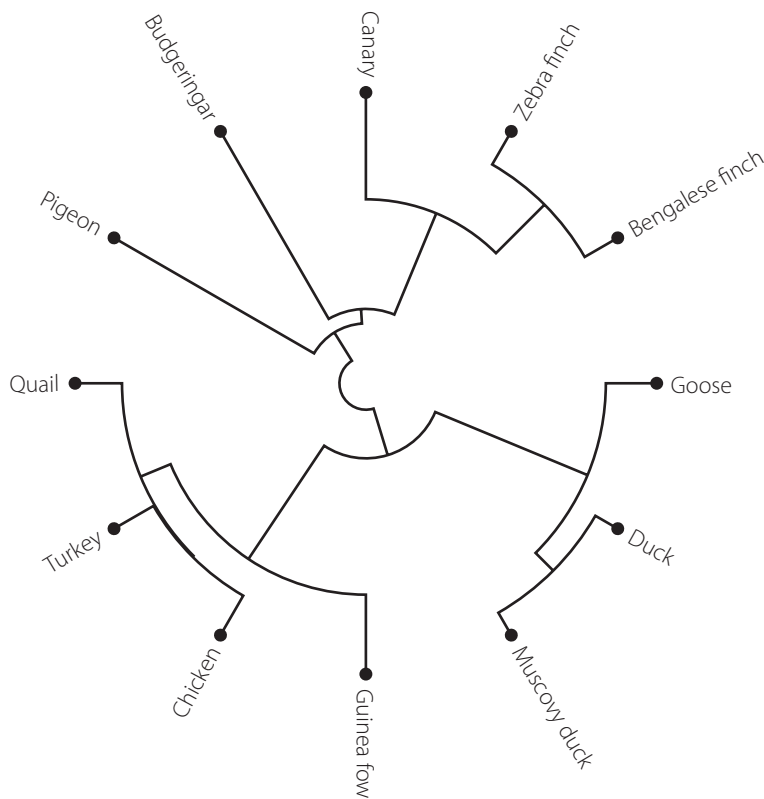


Fig 1.5. Evolutionary relationships among main species of domesticated birds. Branch lengths are proportional to the estimated distance in time among species.

in its throat, the fisher brings the bird back to the boat and has the bird spit up the fish. This peculiar and close interaction requires careful management, but to my knowledge it has not led to any generational changes in reproduction. There may have been rapid evolution of morphological features (Schilthuizen 2018), but longitudinal studies of skeletons or other organ systems are unlikely to be feasible.

The beginnings and antiquity of domestication and transitions from wild to domesticated

Concerning the antiquity of the (complex, continuous, ongoing) domestication process, it is important to avoid the term “event,” as domestication is complex and entails multiple and parallel events and population admixtures (Larson and Fuller 2014). It may be more appropriate to ask questions in terms of “transitions,” as in matters with a strong historical dimension such as those in evolutionary biology and developmental biology. Fixing a specific time and place for the origin of domestication of a species is not possible. What is possible is to provide a general framework of minimal ages, an approximation of reliable documentation of domestication in diverse species, as has been done for many mammals and birds (Figures 1.6, 1.7).

The search for and excessive focus on oldest occurrences as a leitmotif in archaeological research, tied to a progressivist rhetoric, endure in the mass media, but zooarchaeology and related fields dealing with domestication are better off having other foci (Gifford-Gonzalez and Hanotte 2011; Sykes 2014). The archaeological record is fundamental but of limited assistance in providing definitive earliest dates of domestication. This record will never be complete, as the first domesticated individual (actually, if there were such a thing, which is quite questionable, as discussed above) is unlikely to be recorded archaeologically (Perreault 2019). The oldest record of domesticated forms fails to represent the first domestication phase, but instead an approximation of that, and a minimum date. Paleontologists are faced with an analogous situation, what has been coined the Signor–Lipps effect. Given that the fossil record of organisms is incomplete, it is very unlikely that the first or the last organism of a given taxon will be recorded as a fossil (Signor and Lipps 1982).

Our knowledge of the earliest phase of domesticated animals consisted, until recently, of educated guesses based on reasonable but in many cases untested assumptions about morphological changes and mortality profiles suggested by zooarchaeological studies and limited studies of a few genes. Advances have been made over the years, both methodological and conceptual (Vigne et al. 2005a, b). As quantification and more data have become available, it is now more evident how little we know for sure. Furthermore, recognition of varying degrees of intensity in the animal-human relationship—as opposed to an oversimplistic dichotomous categorization of wild versus domestic—has also been a major step forward (Balasse et al. 2016). These categorizations also vary depending on the geographic region and the species in question.

Several years ago most genetic data sets were restricted to mitochondrial sequences, a non-recombining maternally inherited DNA, which by itself cannot be used to identify or quantify hybridization between wild and domestic populations

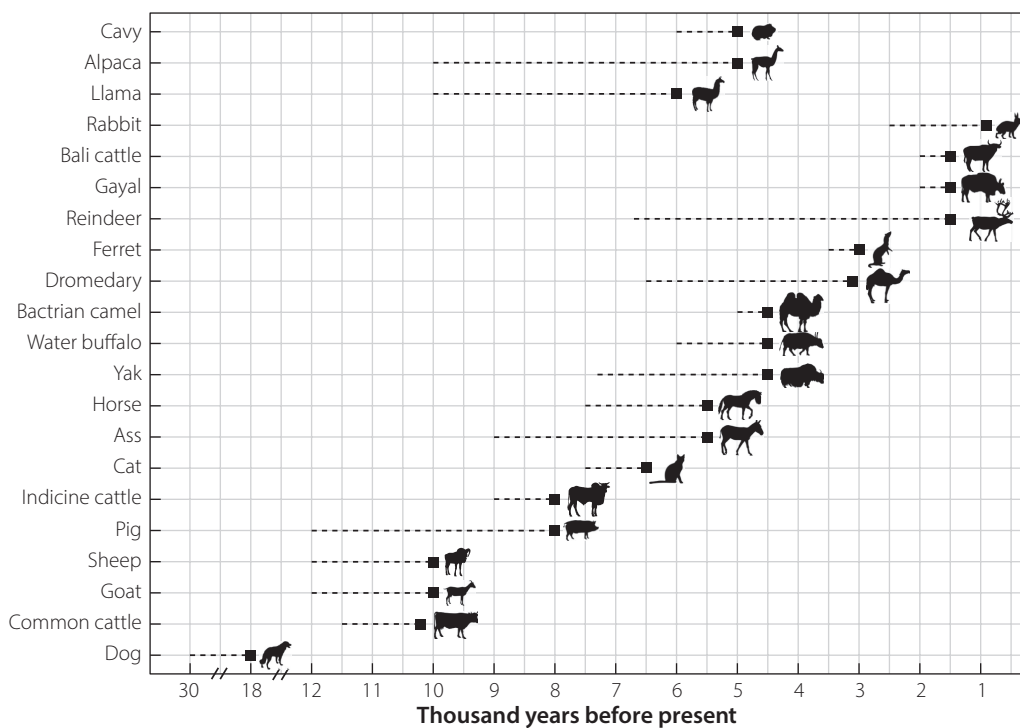


Fig 1.6. Estimated time line of domestication of selected mammalian species.

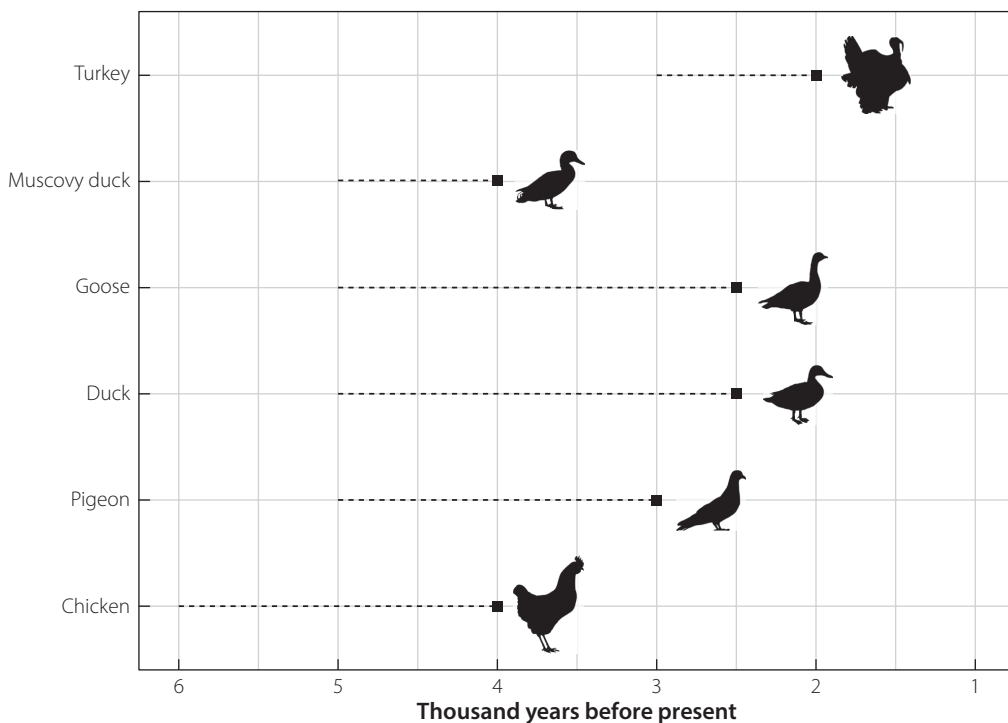


Fig 1.7. Estimated time line of domestication of selected bird species.

or among geographically differentiated domestic populations. This lack of discriminatory power led to false claims of independent and multiple events of domestication for pigs (Larson et al. 2005), goats (Luikart et al. 2001), sheep (Pedrosa et al. 2005), horses (Vilà et al. 2001), and cattle (Hanotte et al. 2002), based on the presence of divergent mitochondrial haplotypes in domestic populations. With current genomic data, including population genetic studies of nuclear DNA sequences, it is possible to determine whether those haplotypes result from an independent domestication process involving genetically divergent wild populations or from introgression of a wild population into domestic stock (Larson and Burger 2013; Gerbault et al. 2014). Gene flow is common not only between domestic and wild populations, but also among geographically diverse domestic populations of the same species (Larson and Fuller 2014; Frantz et al. 2019). Genetic data as currently analyzed can also be used to date domestication phases, migrations, and mixing of populations, in spite of the caveats and challenges these estimates involve (Sykes et al. 2019; Frantz et al. 2020).

Zooarchaeologists have documented changes in the management strategies of hunted sheep, goats, pigs, and cows in the Fertile Crescent by measuring the size, sex ratios, and mortality profiles of assemblages of animal remains (Zeder 2012b). By 10,000 ybp, some people were preferentially killing young males of a variety of species and allowing the females to live to produce more offspring.

Traditionally, two alternative explanations have been offered for the beginning of domestication—here meaning management and some kind of selective breeding. One hypothesis suggests that domestication started independently of any population–resource imbalances (Smith 2011a, b; Zeder 2012c) and was driven by intentional management of wild resources and experimentation. The intentionality aspect of this hypothesis is often questioned. An alternative hypothesis is based on predictions from foraging theory models and behavioral ecology, and assumes that domestication arose at times of need, of Malthusian population–resource imbalance, which led people to try to acquire more food from the environment (Hawkes and O’Connell 1992). It is possible that different mechanisms operated in the many places where domestication occurred, without a universal driving force in all of them. Thus, empirical studies of specific areas and a broad and pluralistic framework seem justified, one firmly based on our knowledge of human behavior and evolutionary biology (Gremillion et al. 2014). The domestication of plants that occurred in Eastern North America approximately 5,000 ybp was associated with population–resource imbalances, as inferred based on changes in radiocarbon date density and site counts as proxies for human population data (Weitzel and Codding 2016). Larger populations, along with decreased resource abundance, may have led to domestication in this area of the world. For other regions, other conditions and dynamics were probably involved.

A different kind of question concerns the earliest domestication phase, one of close human–animal interactions. A combination of ethnographic and anthropological data, and a refreshed view of the zooarchaeological record are needed to address this (Sykes 2014). It seems that nonutilitarian aspects drove those interactions, and this is reflected in the archaeological record of many species that had a close contact with humans, some of which were never domesticated later. This could

be the case for the monk seal (*Monachus monachus*), of which a burial on the island of Rhodes in Greece is known (Masseti 2012). Francis Galton (1865) related a story of a tamed seal from the Shetland islands (it must have been either the common seal *Phoca vitulina*, the grey seal *Halichoerus grypus*, or the fur seal *Arctocephalus gazella*) and speculated on the possibility of populations of this species becoming domesticated.

The translocation of a species outside its native range can be used as circumstantial evidence for domestication. Morphological traits of domestication are not detectable in the archaeological record of sheep, goats, cattle, pigs, and cats before 10,000 ybp, but populations of these species were translocated to Cyprus at least 10,600 ybp, suggesting that management of some kind occurred back then (Vigne et al. 2012).

Identifying morphological changes associated with domestication has been a major interest among zooarchaeologists, aiming at finding signs in isolated and often fragmentary bones and teeth that can be used for this purpose. The artifacts of preservation and the impossibility of separating the many factors involved make the search for universal or even species-specific markers of the first phase of domestication an almost hopeless task. Experimental studies are one approach (Harbers et al. 2020a, b); improvements in the zooarchaeological record will surely help as well.

Given the diverse evolutionary (phylogenetic) background of the different groups of species of domestics and therefore different evolvability of skull modules, kinds of tissue, and organs, it is unrealistic to expect universal features (e.g., changes in size) or simple markers of a clear wild-versus-domestic dichotomy. More importantly, there are fundamental if not insurmountable challenges in such a search.

Complete skeletons of the earliest domesticates will never become available. A standard approach to identifying morphological changes associated with domestication has been to compare wild and domestic modern forms of the same species, assuming that the current populations accurately reflect both the ancestral wild form and the domesticated counterpart in its first phases of differentiation (Price 2002a). We can arrive at approximations by looking at populations of domesticated forms that have not diverged much from the wild ones, as done in a study comparing growth series of skulls (Sánchez-Villagra et al. 2017). However, hybridization, feralization, bottlenecks, and the complex interactions between natural and artificial selection pressures can introduce considerable noise to such a standard approach. In fact, no living population is any group's ancestral population. Furthermore, in many cases, wild populations of a domesticated form no longer exist, as in the case of cattle and camels, and likely also the horse.

Many genetic studies compare the wild form with current domestic ones, sometimes a specific breed, or even a wide array of them, and discuss the finding as revealing selection for that gene and the associated trait in domestication, even for the early phases. Given the antiquity of domestication and the different intensity of the interaction, it is clear that there will be biases in such studies. This was discussed and demonstrated for genetic features of chickens (Girdland Flink et al. 2014). Over the past 2,000 years there has been variation in two genes in ancient European chickens: the *BCDO2* gene, which underlies yellow skin, and the thyroid stimulating

hormone receptor gene *TSHR*, related to the control of development of the thyroid gland and its functions, affecting the regulation of growth, brain development, and metabolic rate. The study of these genes showed that a mutation thought to be associated with domestication was not subjected to strong human-mediated selection until much later in time than what all experts agree was the start of chicken domestication. This is an example of the challenge of addressing any issue concerning the process of (early) domestication with existing and consequently “derived” forms, known as breeds. Studies of ancient DNA—combined with sound morphological studies from zooarchaeological studies (Evin et al. 2017b; Evin 2020)—may help in making more meaningful wild-domestic comparisons, if the goal is to address domestication *per se* and not some aspect of selective breeding.

The study of ancient DNA recovered from remains of different time periods can be used to reconstruct patterns of genetic variation and admixture at earlier stages of the domestication process, get better estimates of the time when initial stages took place, or more specifically provide insights into whether specific variants were already present in past populations, for example coat color mutations (Frantz et al. 2020).

In the case of forms from which milk is consumed, there is another approach to domestication research: detecting milk residue in pottery (Evershed et al. 2008). This approach has provided evidence of early horse domestication, studying organic residue analysis using $\delta^{13}\text{C}$ and δD values of fatty acids (Outram et al. 2009). Furthermore, it is possible to use proteomics to differentiate yak, cattle, and goat milk (Yang et al. 2013). Another approach has been to detect residues in the dental calculus of humans, thus directly showing consumption from dairy livestock. The protein β -lactoglobulin (BLG) is a species-specific biomarker of dairy consumption of cattle, sheep, and goat milk products and is preserved for example in human dental calculus from the Bronze Age, circa 3000 BCE (Warinner et al. 2015).

The anatomy of hair can be informative about taxonomic allocation and domesticated status (De Marinis and Asprea 2006). Through the identification of hairs, the oldest evidence for domestic goat in Neolithic Finland was reported, from a pastoral herding economy, the Corded Ware Culture, dated ca. 2800–2300 BCE (Ahola et al. 2018). The study consisted of microscopic analyses of soil samples collected during the 1930s from a grave.

Material culture associated with domestication can also be used to provide evidence of the latter in the archaeological record. An example is provided by artifacts that were parts of headgear worn by transport reindeer, remains of these dating back to around 2,000 ybp (Losey et al. 2020).

Dental signs of domestication in pigs and dogs

Given the high preservation potential of teeth and that teeth are taxonomically informative and they consist of the most mineralized tissues of the body, efforts have been made to find signs of domestication in them. Here I discuss pigs and dogs, which have been intensively studied.

A study of molar teeth of current wild and domestic West Palearctic pigs compared maximum length, size, and shape variables from 2D geometric morphometrics

(Evin et al. 2013). Size was a poor indicator of wild and domestic status, whereas shape provided a high degree of confidence distinguishing the two. The authors concluded that geometric morphometrics is a better alternative to traditional biometric techniques. This and most other similar studies described differences between modern wild and domestic forms. It is a major improvement when additional categories are used—that is, feral, hybrid, captive, and insular, as in a study of diversity of dental size, shape, and allometry (Evin et al. 2015a). Although the amount of variation among domestic pigs does not exceed that of their wild counterpart, domestication has produced new dental phenotypes not found in wild boar. Domestic breeds can be distinguished by distinct dental phenotypes, and captive and insular pigs are also distinctive in dental shape (Evin et al. 2015a).

Tooth crowding in domestic dogs in contrast to wolves has been proposed as a criterium to infer the process of domestication in the zooarchaeological record (Bencke 1994a). A comprehensive test of this hypothesis using landmark-based metrics examined 750 modern dogs versus 205 modern wolves from across the modern geographic range of the latter and 66 Late Pleistocene wolves from Alaska (Ameen et al. 2017). This study found a higher than expected frequency of crowding in both modern (~18%) and ancient (~36%) wolves, thus questioning assumptions linking tooth crowding with the process of early dog domestication. The strength of this study is supported by its examination of alternative approaches to quantify and compare tooth crowding, which show that the results are reliable.

Osteological signs of domestication in dogs, pigs, goat, and sheep

Geometric morphometrics of wild and domestic pig crania reveal strong discrimination among wild, domestic, and hybrid pigs that applies to both the complete and the subsections of the crania (Owen et al. 2014). Based on a study of adults of 42 modern domestic pigs representing six European domestic breeds, 10 wild/domestic first-generation hybrid pigs, and 55 wild boars, it was possible to discriminate among the breeds on the basis of cranial morphology (Figure 1.8). The skull of first-generation hybrid wild/domestic pig more closely resembles that of wild pigs than domestic. As with dental metrics, it was concluded that geometric morphometrics can provide a quantifiable separation between wild and domestic pigs, even when considering partial cranial remains. As in other wild-domestic pairs (chapter 7), the variation in skull shape in domestic pigs is larger than that of wild boar.

A potential osteological marker of domestication in mammals is the petrosal or periotic bone, a small, compact bone at the base of the skull. Even though goats and sheep are closely related taxa that may not be obviously distinguished based on fragmentary osteological material, an anatomical and metric study of the petrosal bone showed that it was possible to discriminate between these two species (Mallet et al. 2019). Distinguishing wild from domestic forms within the same species pair, or from other categories such as feral or hybrids, can be more complicated, as small differences could also result from phenotypic plasticity.

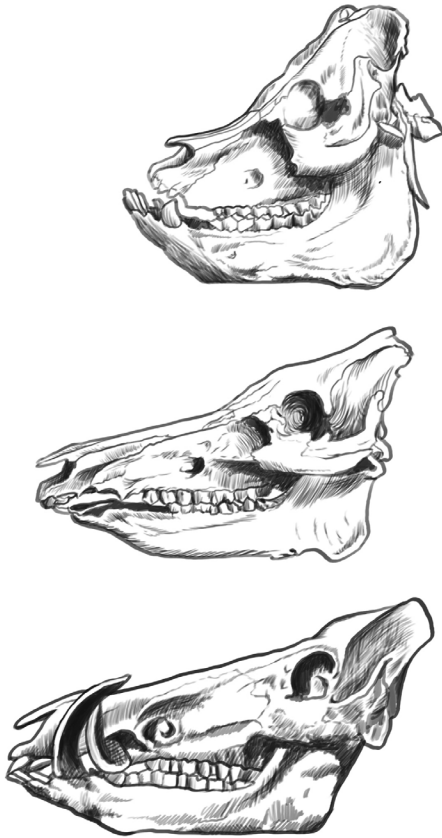


Fig 1.8. Domestic pig skulls (top and middle) and wild boar (bottom). The skull of domestic forms is easy to distinguish from the wild counterpart even in less derived forms. But distinguishing the two based on fragmentary skull parts in individuals from the early phases of domestication, in which hybridization occurred as it still does today in many regions, is a challenge.

Studies of dogs using microcomputed tomography and 3D geometric morphometrics have attempted to discern differences in the organs of hearing and balance located within the petrosal bone (Figure 1.9). The interspecific variation of the inner ear is well documented for many groups of mammals. The proportions among canals and their shape, and the number of cochlear coils are variable features, and this variation is correlated with locomotory habits and hearing frequencies (Ekdale 2016). An investigation of a sample of 24 wolves, 8 dingoes, 39 modern domesticated dogs from 20 different breeds, and 21 prehistoric domestic dogs reported that shape variance is slightly higher for the different parts of the inner ear in domestic dogs than in wolves, but these differences are not significant (Schweizer et al. 2017). The variation detected in inner ear shape was size-related, and this work did not identify criteria by which to differentiate between domestic dog and wolf inner ear. Although wolves have smaller levels of size variation than dogs, they show a greater level of variance in the angle between the lateral and the posterior canal than domestic dog breeds (Schweizer et al. 2017).

The study of a different sample of inner ears using an alternative 3D geometric morphometric method led to contrasting conclusions (Janssens et al. 2019b). This study measured 20 modern Eurasian wolves and 20 modern dogs of comparable skull length and reported that dogs had on average a significantly smaller bony

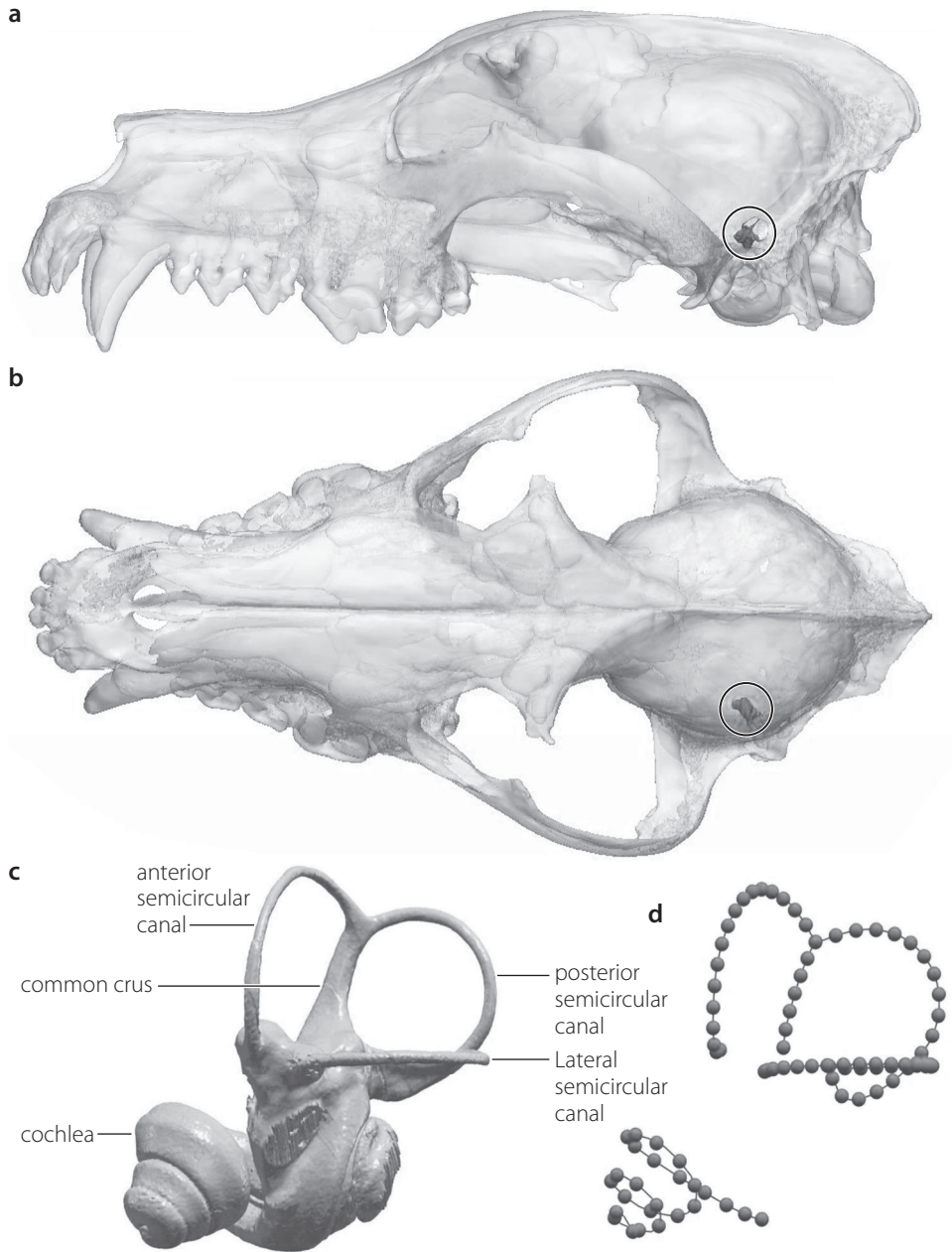


Fig 1.9. Bony labyrinth location in a mammalian skull and its main features. Location in a wolf skull of the bony labyrinth, (a) lateral, and (b) dorsal views based on 3D reconstruction of computer tomographic images. Also illustrated are (c) the bony labyrinth and (d) the location of semilandmarks along the cochlea and the three semicircular canals.

labyrinth than wolves. Furthermore, the shape space of the two groups forms two nonoverlapping clusters, with dogs having a smaller relative size of the vertical canals and oval window, larger relative size of the lateral semicircular canal, and shorter relative cochlea streamline length, with a more anteroventrally tilted modiolus. The authors discussed how these shape differences are not related to allometric effects and could therefore potentially lead to recognition of dog-specific features useful in the identification of samples in the zooarchaeological record. However, the significance of this important study needs confirmation in view of the limited sample evaluated, one that may reflect phenotypic differentiation following selective breeding and not the first phase of domestication.

A quantification of the variation of the wild form is paramount in studies aiming at finding osteological markers of domestication. This was shown for wolves versus dogs in a comprehensive review of several skull and dental parameters (Janssens et al. 2019a). Clearly, further work needs to be conducted in this area, as the implementation of geometric morphometrics and anatomical characterizations of additional species with appropriate samples has only just started. The question arises as to what functional, biomechanical, or other kinds of processes might underlie morphological differences between wild and domestic forms. This is a challenging area of research, as it requires samples of great quality in order to discern subtle differences among populations.

Perhaps as gross morphological features of the skeleton are affected by domestication, so are bone microstructure features. Examination of wild and domesticated sheep bones in petrographic thin sections seemed to identify characteristics that distinguish the two: increase in lacunar size, higher preferential alignment of hydroxyapatite crystals, thicker trabeculae, and a sharp transition between compact and spongy bone (Drew et al. 1971). However, later examinations of the subject showed that aspects first described as differences were linked to diagenesis and to individual variation. Furthermore, the original work assumed naively a dichotomy between wild and domestic unsuitable for the studied samples (Watson 1975; Gilbert 1989). The older and the more recent literature on comparative mammal and bird bone microstructure includes much information on domestic forms (Enlow and Brown 1956; Zedda et al. 2008), but no systematic comparisons with wild forms have been attempted. Studies of bone microstructure may provide information on life history variation (chapter 6).

Isotopic markers of domestication

Whether zooarchaeological specimens are from individuals living in the wild in close proximity to humans or from fully domesticated ones, their status cannot always be assessed based on anatomical or morphometric comparisons alone; this often requires the use of additional approaches. Stable isotope biochemical analysis of animal remains can be used to investigate ancient human-animal relationships. However, the methods involved are plagued with issues of sampling and interpretation; thus establishing uniform protocols and terminology is essential (Roberts et al. 2018).

Potential domesticates differ isotopically from other wild taxa because of different diets, water consumption, and properties of the soil on which they live. Isotopic values represent an average of dietary patterns over many years, given that bone collagen is replaced slowly throughout the life of an organism. In some localities the consumers of the potential domesticates will also be isotopically distinct from consumers of other taxa. The isotopic approach, based on C4 and C3 values in different plants, can be used to study human remains and establish whether diets included domesticated crops (Barton et al. 2009).

The broad dietary plasticity of pigs makes them an excellent subject for isotopic analysis, as it is possible to distinguish among wild, feral, extensively herded, and household pigs, the last being more dependent on domestic sources of animal protein (human consumption leftovers). Various dietary sources can be traced through analysis of stable nitrogen isotope ratio ($\delta^{15}\text{N}$) of bone, which significantly increases with each trophic level in a food web (Ervynck et al. 2007). This approach was used in a detailed study of pig husbandry in the city of York, England, with a long and more or less continuous zooarchaeological record in handling of pigs from the foundation of the city at the end of the first century AD until post-medieval times. Further examples of studies of this kind are those on Neolithic China (Cucchi et al. 2016), a Celtic village in France (Frémondeau et al. 2015), and Chalcolithic Romania (Balasse et al. 2016). They all documented varying degrees of intensity in the pig-human relationship.

It is possible to combine studies of dental microwear and oxygen isotopes, as in the examination of herding practices of sheep in Çatalhöyük East, in central Anatolia, one of the largest Neolithic sites in southwest Asia (Henton 2013). The two data sets situated an individual sheep in its environment at different points of its life with good resolution. Different models of herding were associated with different shapes, ranges, and summer isotopic values. Those models were characterized as follows: “Sheep raised year-round near settlement on the plain—Marl steppe, alluvial fan, sand-ridges”; “Sheep raised year-round in perennial stream valleys, cutting through terraces and lower hill-slopes”; and finally “Vertical transhumance to higher hill-slopes in summer or pasturing near springs fed by averaged groundwater.” Consideration of seasonality in dental wear and reconstructed diet and in the life history of these animals provided a look at mismatches with the natural environment (and the cycles recorded by wild forms living in it) that can characterize conditions of managing of domesticated forms (Henton 2013).

By studying carbon, nitrogen, and oxygen isotopes, it was hypothesized that animal trade and possible captive animal rearing occurred in the Maya region of Ceibal, Guatemala (Sharpe et al. 2018). This study examined animal specimens across almost 2,000 years (1000 BC to AD 950), and the strontium isotope analysis revealed that the Maya brought dogs to Ceibal from distant highlands. Contextual evidence indicated that domesticated and possibly wild animals were deposited in the ceremonial core, showing an association of these managed animals with special events, activities interpreted to have been important in the development of state society (Sharpe et al. 2018).

Cultural evolution and reconstructing the history of domestication

An underexplored and potentially useful tool for examining congruence between cultural and biological data in the history of domestication is the use of statistical techniques to study myths and folktales. A database of 23 myths concerning dogs and 22 geographic areas was analyzed with a neighbor-joining tree based on Jaccard distances (d'Huy 2015). The application of phylogenetic methods showed a correlation between history and geography, and the approach made it possible to reconstruct the paleolithic mythology around dogs.

Another rich area of research is the study of the biological information stored in parchment documents made of animal skin (Ryder 1958). Information about book production can provide data on livestock economies and handling, and provenance of the animals. Advances in molecular methods can make this biological approach a highly relevant discipline in manuscript studies (Fiddymet et al. 2019).

The Neolithic transition

Homo sapiens originated approximately 300,000 ybp, but the domestication process of several species started only around 10,000 ybp. Why then? This is a fundamental issue in human history and biology, so it is justified to propose reasonable hypotheses and even speculations.

The standard account goes that at the start of the Neolithic a transition from a life of hunting and gathering nomadism to farming sedentism occurred in many populations. It was not universal (everywhere, everybody) and, as in domestication (“wild” versus “domestic”), human ways of living cannot be encased in dichotomies (Sykes 2014). Hunting for semi-domesticated forms occurred. The coupling of farming and long-term sedentism is not straightforward, as each of the two shows degrees, and diverse and simultaneous lifestyles most likely occurred in early Neolithic times, with the first cities located in wetlands in which productivity and mobility were both high. The development of multiple cities postdated the first records of domestication by several thousand years (Scott 2017).

For decades the Near East was considered the major center of domestication of plants and animals around 10,000 ybp in what used to be called the “Neolithic revolution” (Childe 1936). We now refer to this as the “Neolithic phase or transition.” Many geographic areas of early domestication of plants or animals, or both, were areas of analogous and independent places of transitions to new modes of human life, including many in the Americas (Smith 1998; Piperno and Pearsall 1998; Zeder et al. 2006).

The Neolithic transition happened at the end of the Pleistocene, when the onset of warmer and wetter climates was accompanied by an increase in CO₂

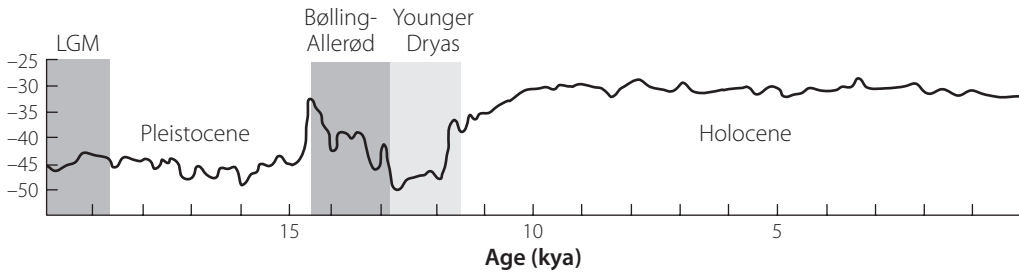


Fig 1.10. Climatic curve, reconstructed from the GISP2 ice core in Greenland. The vertical axis (*left*) refers to temperature (°C). LGM=Last glacial maximum.

levels and the establishment of more stable weather patterns (Figure 1.10). In the temperate latitude zones, productive ecosystems emerged and human societies developed in areas of high human-carrying capacity, especially along river floodplain corridors and lake and marsh/estuary margins. A wide spectrum of plant and animal species were utilized in these early Holocene environments, subject to varying degrees and forms of manipulation and life-cycle changes (Zeder 2012c). Vegetation clearing and the presence of water-management features are recorded in the archaeological record from these regions (Smith 2011a). There were new forms of social learning (Laland and Brown 2011) and interactions associated with sustained economic utilization, including ownership, with a shift by small-scale societies to territorial defense of resources (Dyson-Hudson and Smith 1978). The archaeological record presents evidence of multigenerational corporate ownership of resources, including group burial features and other ceremonial structures.

The Neolithic transition and environmental crisis

In 1928, the renowned archaeologist V. Gordon Childe (1892–1957) stated that domestication provided one of the great moments in prehistory, “that revolution whereby man ceased to be purely parasitic and, with the adoption of agriculture and stock-raising, became a creator emancipated from the whims of his environment.” (Childe 1928, p. 2). This view dominated for decades in Western Europe and the United States. After almost 100 years our views have changed dramatically—from celebration of domination to well-founded concern. The age in which we live is arguably one of environmental crisis, and domestication is at the center of it (Ceballos et al. 2015). It all started with the Neolithic transition some 10,000 ybp, but the tipping point in the exponential acceleration of a process of habitat degradation came about when selective breeding became industrialized, tied to excessive consumption and exponential population growth.

Changing patterns of food consumption and human resource use in Western societies have produced an unprecedented reconfiguration of the Earth’s

biosphere and in many cases of populations of individual species. The domesticated broiler chicken is a classic example of this reconfiguration (Bennett et al. 2018). Human selective breeding has led to a doubling in body size of domesticated chickens from the late medieval period to the present. In the case of the broiler, there has been a fivefold increase in body mass since only the mid-twentieth century, besides the changes in skeletal morphology, pathology, bone geochemistry, and genetics discussed in this book. Broilers cannot survive without human intervention. The huge increases in population sizes mean that broiler chickens have a combined mass exceeding that of all other birds on Earth (Bennett et al. 2018).

A detailed census of the overall biomass composition of the biosphere among all kingdoms of life showed that the mass of humans is an order of magnitude higher than that of all wild mammals combined. Furthermore, there has been an enormous impact of humanity on the global biomass of prominent taxa, including mammals, fishes, and plants (Figure 1.11).

Domestication and agricultural practices impact the evolution and ecology of not only domestic animals themselves but also the wild forms (Turcotte et al. 2017). Special traits of domesticated forms can alter the selective environment of wild species. Domesticated animals can become invasive species; aided by humans, these move to places where they are non-native and can have a detrimental effect on the environment, including effects on populations of other species (Doherty et al. 2016).

Furthermore, the introduction of domesticated animals into new environments can produce a cascade of effects on plants. For example, farming of domestic animals can lead to megafaunal local extinction, which can in turn decrease the dispersal of seeds of plants and consequently their survival

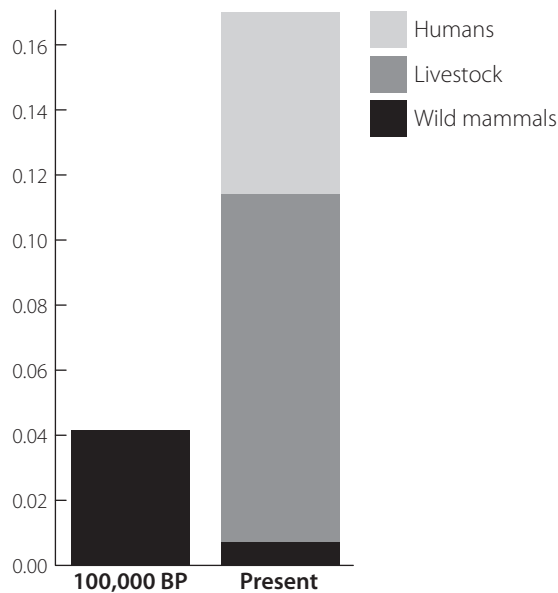


Fig 1.11. Estimated biomass of wild mammals before the rise of domestication and at present. The great proportion of livestock is dominated by cattle. The vertical axis (*left*) refers to gigatons of carbon.

(Onstein et al. 2018). Islands provide many examples, as in the case of diverse native grasses in New Zealand. These evolved in the absence of grazing mammals, and exhibit the strategy of old leaf abscission, a rare characteristic in grasses (Antonelli et al. 2010). This feature increases plant productivity but reduces protection against mammal grazing. Following the introduction of sheep, cattle, and rabbits in the nineteenth century, these endemic grasses were highly affected (Rose and Platt 1992).

The Neolithic transition: mismatches and human health

Intensive selective breeding can and has led to mismatches of past adaptations of humans with the environment, particularly since the industrial revolution. These mismatches concern epidemiological, nutritional, and demographic matters. They have greatly affected human ecology and biology, leading to changes in life history traits including fertility, life span, and age and size at maturity (Corbett et al. 2018), and may lead to gene variants linked to higher fitness in the past now predisposing us to disease. This change in fitness can occur through pleiotropic effects and can predispose humans for example to cancer and coronary artery disease.

It is usually claimed and generalized that the Neolithic transition brought major changes in time management by humans, with mostly an increase in working hours in agricultural societies (Harari 2011). However, a dichotomy of hunter-gatherer versus agricultural is too simplistic to capture the diversity of subsistence styles, and generalizations on their consequences are also multivariate (Higgs and Jarman 1969). The dimensions of “hunter-gatherers” or foragers vary depending on geography and cultural history (Kelly 2013). Notwithstanding this variation, it is highly likely that the activity patterns of the first farmers changed from those of pre-farmers, and their skeletons changed as a result (MacIntosh et al. 2016). Being rather sedentary, farmers’ lives strongly contrast with those of foragers, for whom walking, running over long distances, and carrying heavy loads (Carrier 2002; Stock and Pfeiffer 2004) are common activities. The rise of the farming lifestyle has traditionally been associated with a decline in health, and even in physical prowess (Larsen 2006). Greater population densities, as well as greater reliance on domesticated crops and the vagaries of farming contributed to the spread of infectious diseases (Verano and Ubelaker 1992; Steckel and Rose 2002; Scott 2017). The first farmers may have suffered from hunger (Bowles 2011). The relationship between sedentism and the global obesity pandemic is however not simply related to a change in activity and exercise, as cross-cultural studies of metabolic rates have shown (Pontzer et al. 2012).

The patterns of change among the people who experienced the Neolithic transition may not have been universal. The variations among populations and sites and the relations between lifestyle and disease are complex (Carlson and

Marchi 2014; Ash et al. 2016; Ruff 2017). Mortality risks and food shortages can also be substantial among mobile hunter-gatherers.

Nutrition, disease, hormones, and mechanical loading can influence bone development (Hall 2015). It follows that studies of skeletons of past populations can provide clues to their lives. Studying markers of developmental instability during childhood and embryogenesis could offer insights into health and the effects of disease and famine (ten Broek et al. 2012).

The geography of domestication

Not only the old notion of a domestication “event” has been abandoned, but also that of a “center” of domestication. Domestication is a process, a transition, without clear boundaries in place and time. Because of the biases of the archaeological record and the nature of domestication, centers of domestication can refer only to general areas in which domestication was practiced to such an extent as to leave demographic or morphological markers.

The Fertile Crescent was surely an important area for domestication of mammals, but other regions of the world need to be studied to gain a balanced record of the earliest livestock and crops (Figure 1.12). In fact, crop cultivation probably began independently in as many as 20 regions worldwide (Fuller 2010), whereas early animal domestication is associated mainly with just the Middle East, central China, and the Andes. Later cases of animal domestication in antiquity took place in many areas, decoupled from centers of plant domestication. The exponential growth of aquaculture in the last decades is a worldwide phenomenon (Duarte et al. 2007).

The geographic range of wild forms was wide for some species, as in the case of the wild boar, ranging from southeast Asia (where genetic evidence shows it first originated) to Western Europe, or restricted, as in the case of the original distribution of wild sheep and goat in the Middle East. Some of the wild forms are now extinct, such as the aurochs (von Lengerken 1955; Van Vuure 2005).

Concerning the domestication of birds, any geographic pattern is of course conditional on what is assumed to be a domesticated bird, and here there is no consensus. However, a general pattern exists. The subtropical and warm-temperate regions of Asia contributed most, Africa and the middle and high latitudes of Eurasia comparatively less (Donkin 1989). The guinea fowl, *Numida meleagris*, and for some authors also the ostrich, *Struthio camelus*, are the two domesticated bird species from Africa. In the New World, the Muscovy duck, *Cairina moschata*, and the turkey, *Meleagris gallopavo*, were domesticated. The canary, *Serinus canaria*, is a particular case; this song bird is originally from the Macaronesian islands in the Atlantic Ocean, from where it was taken to Europe.

The Americas were the last continents, aside from the polar regions, to be occupied by humans. After the discovery—and at last general acceptance—of several archaeological sites precluding the Clovis phase, the dates of the earliest occurrence of the peopling of the Americas have been moved back in time to at least 15,000 ybp

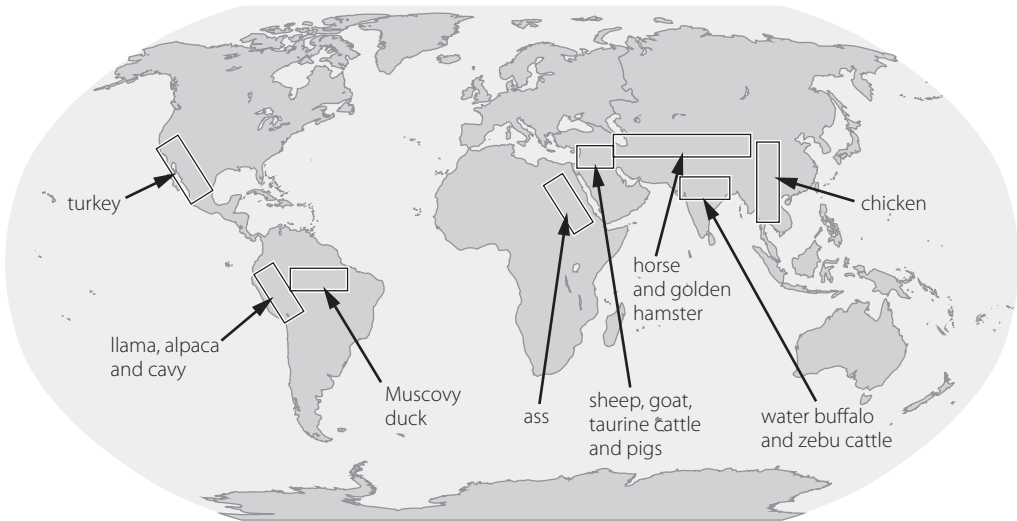


Fig 1.12. Sites of domestication of the main domesticated mammals and birds.

(Waters and Stafford 2013). The human-animal interactions that occurred since then include domestication. Only a few endemic mammals and birds were and still are domesticated in South America. Several New World mammal species had intense interactions with humans in the past, such as the hutia rodent in the Caribbean (Colten et al. 2017). The dog was already domesticated when it arrived in the Americas with human populations in pre-Columbian times (Leonard et al. 2002).

There is no quantitative geography of breeds of domesticated species and their origins. A survey could serve to factor the surface of the regions and human population density in relation to the diversity of local breeds and landraces. It might reveal that areas thought to be poor for domestication, for example some in Africa, are not so. In plants, there are analogous examples of how the domestication process may have started in some region, but the process extended to other areas of even more prolific diversification. The classic example is the tomato, originating in the Andean region, becoming domesticated and selected in Mexico, and after colonial times finding its way into southern Italy, and to all corners of the world, including Ukraine, where delicious varieties are produced (Mann 2011).

On domesticated species, breeds, and landraces – nomenclatural issues

It is regrettable that there is no uniform nomenclature across biological disciplines to refer to domesticated animals, with some exceptions. In both the domestication and the zoological literature, domestic rabbits have the same name, *Oryctolagus cuniculus*. On the other hand, the most widely accepted standard of mammalian taxonomy, *Mammal Species of the World* (Wilson and Reeder 2005), considers the dog a subspecies of the wolf, whereas the literature on domestication

assigns different species names to the two, following Linnaeus (1758). Linnaeus (1758) also gave different names to other wild–domestic pairs, as in the aurochs (*Bos primigenius*) and domesticated cattle (*Bos taurus*). The most widely accepted nomenclature for many domestic animals in the literature on domestication is one in which, for many cases, the domesticates constitute different species from the wild form (Tables 1.1, 1.2).

The type species designations of several mammals are based on domestic animals (Gentry et al. 2004). For 16 mammals the name of the domestic form antedates or is contemporary with that of the wild ancestor, as in the case of the wolf and the dog. The contrary case does also occur, as for *Sus scrofa* Linnaeus 1758 for the wild boar predating that for the domestic form, *Sus domesticus* Erxleben 1777 (Gentry et al. 2004).

Even though the nomenclatural separation of wild and domestic for many pairs does not make much sense biologically (Zeller and Göttert 2019), I follow it here for the sake of stability (Tables 1.1 and 1.2). Some authors have argued in favor of naming the domestic forms the same as the wild forms and adding “forma domestica” (Herre and Röhrs 1990), others have suggested categorizations below the species level to differentiate domestic from wild forms (Bohlken 1961). The long, tedious history of discussions on the proper nomenclature to use when referring to wild and domesticated forms (Gautier 1993) teaches us that attempts to make the nomenclature uniform across disciplines and research traditions have consistently failed.

A different name for the domesticated form could be interpreted as implying reproductive isolation, but hybridization is rampant among breeds within a domestic form and between wild and domestic individuals. Thus, a biological concept (based on reproductive isolation) is problematic at best when used for domestic forms. Many concepts are used for species (Zachos 2016), and the pragmatic decision to give new names to populations that have significantly and measurably diverged morphologically from the wild forms has had influential advocates (Gentry et al. 2004). A species can be considered a distinct cluster of individuals that are morphologically and ecologically similar. This “vernacular” species concept is used, for example, when considering the diversity of cichlids from African lakes (Salzburger 2018). In the case of domesticates, the historical distinction and morphological divergence from the wild form have been given much weight. Ecologically, domesticated forms can be also seen as distinct.

Addressing the multiplicity of definitions and in search of consilience, one can define a species as a divergent lineage, with a morphological or ecological discontinuity, and/or a reproductive isolation having arisen during speciation (de Queiroz 1998). These features could have been attained sequentially. Populations in the process of speciation (whatever that may mean!) may have different morphological features and yet not be isolated reproductively. On the other hand, cryptic species may be different ecologically or reproductively and yet be morphologically similar. As Darwin (1859, p. 469) stated, “no line of demarcation can be drawn between species . . . and varieties.”

Since wild and domestic forms are in most cases recognizable entities by virtue of their phenotypes, and in some cases and for many populations there is imposed

reproductive isolation from each other, it is practical to separate them by nomenclature when distinct names exist, which is also justified for the sake of stability.

The categories of landraces and breeds are used for some domestic animals. Landraces result from the culling or disposal of unwanted individuals; they are thus the product of natural selection and postzygotic selection, without direct control over the individual's reproduction. To create breeds, in contrast, there is deliberate mating of preferred animals to perpetuate an observable phenotype that is therefore the result of pre-zygotic selection. A definition of breed was provided by J. A. Clutton-Brock (1999, p. 40): "A breed is a group of animals that has been selected by humans to possess a uniform appearance that is inheritable and distinguishes it from other groups of animals within the same species." But determining what a breed is and what is not is a matter, to a great extent, of convention.

Conventions for defining breeds are particularly established in dogs. Some recognized dog breeds were created when individuals from regional landrace populations were removed and sexually isolated, and then registered as breeds with international kennel clubs; examples include the Italian Maremmas, the French Great Pyrenees, and the Turkish Anatolian Shepherds (Lord et al. 2016). Breeds are recognized by kennel clubs (the British one dates from 1873, the American Kennel Club from 1884, the Fédération Cynologique Internationale from 1911) and have been subject to selective breeding regimes with strict requirements and closed bloodlines.

In some regions of the world, breeding of a particular kind of domesticated animal has been ongoing and has led to a certain singularity, which can then lead to an official request for formal recognition. This is the case of the Ovejero Patagónico or Patagonian Sheepdog from southern Chile's Magallanes region (Barrios et al. 2019). It originated from European breeds, including the extinct British breed Old Welsh Grey, and several varieties of Collies (Fuenzalida 2006). It is highly distinctive in its phenotype (Tafrá et al. 2014) even when some of its variation is considered (Figure 1.13). Another example of differentiation leading to a singular and recognized breed is the Colombian Paso horses, whose gait types, genetics, and phenotype have been thoroughly documented (Novoa-Bravo 2021).

Cattle exemplify a case of historical significance concerning the matter of breed recognition. Darwin (1845) wrote quite a bit on a short-snouted cow he encountered in his travels in Argentina and Uruguay, the *vaca ñata*, deemed since then brachycephalic (Veitschegger et al. 2018). The name *ñata* refers to nose in a variation of the local Spanish (used in several tango songs). This breed was included in the writings of Richard Owen (1853), the influential anatomist and contemporary of Darwin, and of the Swiss zoologist Rüttimeyer (1866) in his classic treatises on cattle (Figure 1.14). A DNA analysis based on 2,205 single-nucleotide polymorphism (SNP) loci genotyped five *ñata* samples (Veitschegger et al. 2018) and included 134 other cattle breeds (Decker et al. 2014). The analysis showed clustering of all the *ñata* samples within taurine breeds, indicating a unity there, as opposed to the independent generation of the peculiar anatomy in diverse individuals (Veitschegger et al. 2018). Furthermore, the anatomical study and that of 3D geometric morphometrics of cattle and aurochs skulls showed all these *ñata* individuals to be singular and sharing several unique features.

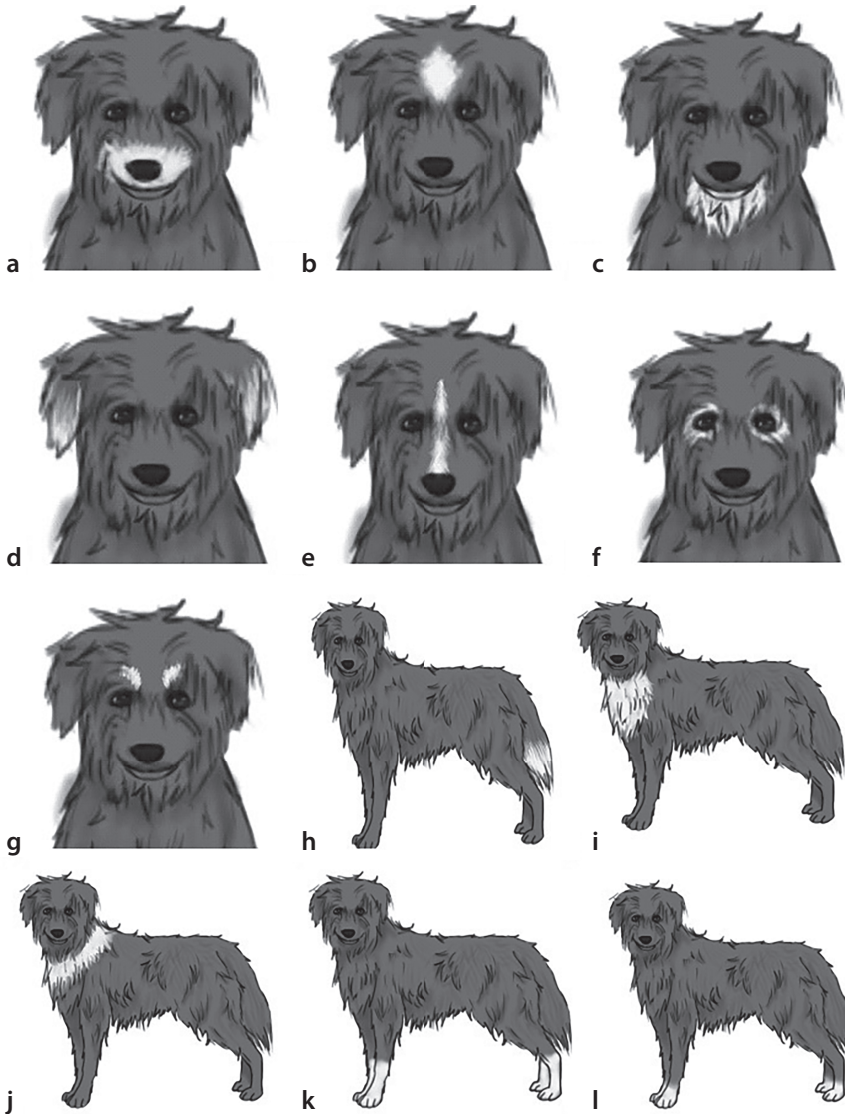


Fig 1.13. Phenotypic variation in the Patagonian Sheepdog.

On the extinction of local breeds

“Men have forgotten this truth,” said the fox. “But you must not forget it. You become responsible, forever, for what you have tamed.”

—Antoine de Saint-Exupéry, *The Little Prince*

Many domesticated animal species show great diversity in local breeds, and this diversity is usually tied to cultural identity, in addition to the biological properties that match local conditions, or production goals in the case of livestock. Works



Fig 1.14. The skull of the *vaca ñata* (front), in contrast to that of standard cattle (back). Skulls displayed in the exhibits of the Museo de La Plata, Argentina.

documenting local breeds of several species come from Greece (Plassará 2005), Japan (Hongo 2017), China (Epstein 1969), Nepal (Epstein 1977), and Africa (Epstein 1971), to name a few examples. Treatises on breed diversity of given species are also available (e.g., Porter 2002).

Industrialization and globalization, with associated urbanization and migration to cities, led to the extinction of many local breeds. There are many examples in cattle, for which, as with many other domesticated forms, phenotypic and genetic diversity are becoming reduced, driven by selection for some productive breeds, with extinction of many regional forms. An example is the extinction of the “Freiburgerkuh” in Kanton Freiburg in Switzerland, a cattle breed well adapted to winter conditions, meager pastures, and unaided birthing in low alpine landscapes. This breed has been replaced by larger and superficially similarly colored Holstein cattle, which are high-production dairy animals. The “Freiburgerkuh” was transported many decades ago to southern Chile around Punta Arenas, with current populations of free-ranging cattle in that southern Patagonian landscape encountering physiological challenges similar to those of Freiburg. Therefore, the “Freiburgerkuh” may either still be around, or may have left significant genetic legacy. Studies by the ProSpecieRara organization of Switzerland have sadly confirmed the extinction of the local Swiss breed also in Chile.

Local movements across the world aim to preserve local breeds and along with them, important cultural and genetic heritage. Examples are the organizations in the

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