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Geographical distribution of domestic animals: a historical perspective

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Summary

Our understanding of the history of animal domestication has been built on regular input from archaeozoology. This fast-expanding discipline uses increasingly sophisticated and specialised tools to enhance our knowledge of phenomena dating back, for the oldest species, to the Neolithic Revolution.

This article takes three examples, those of the domestic dog, domestic goat and European rabbit, to illustrate the history of three different domestication processes using the contemporary means available. In each of the three cases, the authors define the location of original domestication, analyse the principal routes of species movements following domestication, discuss the possible reasons for domestication and suggest a few likely epidemiological impacts.

Key words

Archaeozoology – Brucellosis – Dog – Domestication – Geographical distribution – Goat – Rabbit – Rabies.

Introduction

The study and understanding of the phenomenon of animal domestication are far from complete. There are many questions still to be resolved. What was the reason for the transition from subsistence hunting to livestock production? Was it out of necessity, or were the arguments, or reasons, of a conceptual or technical nature, or perhaps a mixture of the above? What explains the choices of species to domesticate? Are there any links between the different known areas in which domestication took place? How did the subsequent gradual invasion of the diverse inhabited regions come about? As the domestication process seems to be associated with only a few geographical areas, how can we explain and describe the way (or ways) in which the practice expanded? Did the new herders 'invade' the lands of neighbouring hunter-gatherers, or did the practice of domestication gradually spread among populations and become adopted by them? Which were the first products to be derived from the various domesticated species? How did we gradually arrive at the point where we find ourselves today?

Studying the contemporary situation allows us to measure the distance separating us from the point (or rather points) of departure. The current widespread use of western practices associated with the advanced globalisation of factory farming systems tends to obliterate any trace of previous phases of domestication. However, data from recent centuries are still fairly easy to access through historical documents. As we travel backwards in time to examine the history of domestication, the first important moment we come to is the period around the year 1500 AD, i.e. at the end of the Middle Ages and the start of the Renaissance period in Europe, when Europeans were travelling to the New World. The phases prior to this period have been ascertained by a variety of means depending on the region of the world, as well as on the records left behind by the civilisations concerned and on their accessibility and comprehensibility. Different tools are needed to examine the Neolithic Revolution period around

11,000 years ago, relying mainly on archaeology and, more specifically, archaeozoology. The farther we travel back in time, the more uncertainty grows, which explains the large number of questions that remain unanswered (6, 7, 11, 15, 24, 31).

In all likelihood, the movement of domestic herds and the gradual invasion of continents by the various domesticated species over past millennia explain the foundations of today's world animal health geography (5, 9, 27, 37). Some phases still remain to be reconstructed, while others are well documented, but what we do know is that today's situation can, in part, be explained by this long history. This article provides a few examples as an attempt to illustrate this. As other articles in this issue of the OIE *Scientific and Technical Review* discuss the case of cattle (17, 26), it is not included here. The examples the authors have chosen are the domestic dog, goat and rabbit. In the case of the rabbit, the presentation complements the other articles in this issue.

Archaeozoology

Methods for reconstructing the stages in the domestication process and in the dissemination of techniques and associated practices rely on a set of tools that have been gradually developed within a discipline that emerged strongly in the second half of the 20th Century: archaeozoology. Several manuals on the subject are now available and provide a good overview (4, 8). They should be distinguished from a host of summaries that are also available on the subject of domestication itself, which describe part of the methodology followed and used (6, 11, 13, 16). These works examine contemporary thinking, and its various stages, concerning issues relating to the transition from subsistence hunting to raising certain animal species. Without going into details about the tools, the authors would simply point out the importance of working on sites that are still largely intact and where the remains examined have been found more or less in their original position. Apart from the basic anatomical and osteological work (identification of types of bone, species, age group and sex), archaeozoology involves a detailed analysis of remains using different analytical techniques to study chemical composition, genetic makeup, etc. The data-processing software available is increasingly effective because it is tailored to these specific situations. There are also ever-more-accurate and less-destructive dating methods being developed and, together with modern molecular biology techniques, this technology enables us to determine, for example, whether an ancient fragment of pottery might have contained goat's milk or cow's milk. A specific discipline of archaeozoology – taphonomy – studies the natural decay of bone remains over time and how they become fossilised, depending on the chemical composition of the soil and the respective position of the bones from a single skeleton, as well as their evolution over time. The amount and quality of information is growing steadily, enhancing our knowledge of the ancient stages of these processes considerably.

The dog

Without wishing to expand upon this point, we merely note that, by convention, the dog has been given a scientific name (*Canis familiaris*) which is different from that of the wolf (*Canis lupus*), even though the dog is a descendent of the wolf. Biologically speaking they can be considered as conspecific. The question of how best to name domestic species has been the subject of various discussions (12). The scientific name for the domestic goat also differs from that of the wild goat, although the domestic rabbit bears the same scientific name as its wild ancestor, the European rabbit (see below). There are a few other cases of naming differences among domestic mammals. However, no domestic bird has received a different scientific name from that of its corresponding wild form (Fig. 1). Oddly enough, this has happened in the case of the silk moth, the domesticated form of which (*Bombyx mori*) goes under a different name from the wild silk moth (*Bombyx mandarina*). Cultural influences have been a constant feature throughout the history of domestication, even influencing how species are named!

The dog is the oldest of all the domesticated species, perhaps dating from just before the Neolithic Revolution when agriculture emerged. It is tricky to date precisely the transition from wolf to dog. A 1997 article based on genetic analyses (34) suggested that it was 100,000 years

Fig. 1
Helmeted guineafowl (*Numida meleagris*), South Africa
West African populations of this species (*N. m. galeata*) gave rise to the domestic guinea fowl
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ago, but errors of methodology preclude such an ancient origin. However, the hypothesis of a multiple origin rather than a single origin has been postulated. A series of articles published in 2002 proposes a set of elements (14, 28, 29) that could be summarised as follows. The dog was probably first domesticated from local wolf populations (*C. lupus*) around 15,000 years ago in East Asia, in a region corresponding roughly to modern China. It is here that genetic variability is the greatest. Every dog breed ever tested, from the smallest to the largest, on every continent, has been shown to have been bred from the wolf. A further study sought the origin of the dogs that accompanied the first humans travelling to the Americas via Beringia (the land bridge connecting present-day Alaska to Siberia during the Pleistocene ice ages). An analysis of genetic traces in ancient dog remains from the late Pleistocene Epoch, found together with human remains, shows that these humans arrived with their dogs from Asia. North American wolves did not contribute to American dog breeds, or to those of the American Indians, or those of the Europeans who followed after the 16th Century. Moreover, it seems that the Europeans, who brought their own dog breeds with them, systematically avoided crossing their breeds with those of the American Indians. Indeed, the study revealed a breeding line specific to the dogs of the American Indians. It proves that the dog populations of North America remained isolated from those of Asia for long enough to diverge from them, but this clade was not found in the sample of contemporary North American dogs tested. The Amerindian canine breeding lines have been lost. In fact Chihuahuas, Mexican hairless dogs, Alaskan huskies and Chesapeake Bay retrievers all descend from the dogs introduced by Europeans (19).

In parallel with their movements towards the north east, Beringia and the Americas, people of the Pleistocene Epoch also travelled to southern Asia, Indonesia, New Guinea, Australia and the islands of the Pacific. Dogs accompanied them. What are assumed to be the most primitive breeds all appear to have come from the same native home in the East. This is the case with the New Guinea Singing Dog, the Australian dingo (Fig. 2) and even the African Basenji. In the latter case, the colonisation movement is of course totally different. The dingo must have arrived in Australia 4,000 years ago with human invaders, but not with the first of them. It represents an interesting phase in the domestication process because, while some individuals then returned to the wild, other dingoes remained in contact with humans. Like the wolf, the dingo has an annual breeding season, whereas the female dog has two cycles per year. The dingo never reached Tasmania. Its impact on the local fauna must have been considerable. It is partially blamed for the extinction of the thylacine, or Tasmanian tiger (*Thylacinus cynocephalus*), which was known to the first humans but had been extinct for around 2,000 years everywhere except in Tasmania, where

Fig. 2
Dingo, Kakadu National Park, Northern Territory, Australia
This is a dog returned to the wild that arrived with humans several thousand years ago
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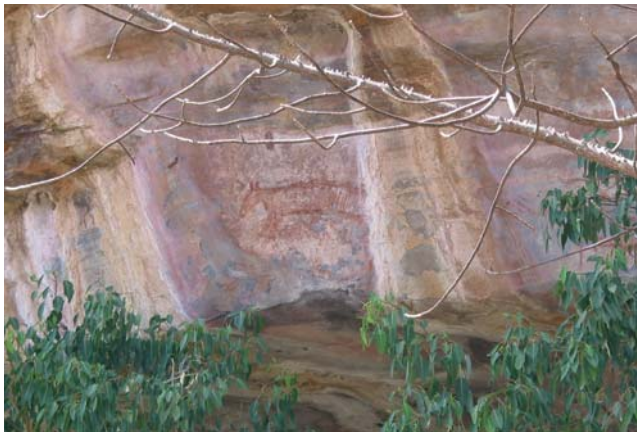

Fig. 3
Thylacine (*Thylacinus cynocephalus*), Kakadu National Park, Northern Territory, Australia
An ancient cave painting of a species that became extinct after the dingo arrived
© V. Besnard & F. Moutou

Europeans wiped it out shortly before 1950 (25) (Fig. 3). The dog must have been introduced into New Guinea only 2,000 years ago, after the arrival of the dingo in Australia and in a form resembling the dingo. The astonishing choruses of this New Guinea breed explain why they have been dubbed 'singing dogs' (10).

Numerous hypotheses attempt to reconstruct the phases in the domestication process that led from wolf to dog. Two species of predatory mammal, humans and wolves, both highly opportunistic, certainly both carrion-eaters on occasion, hunting the same prey in the same hunting grounds, may have helped one another (intentionally to

some degree on the part of humans), with one breed occasionally eating the leftovers from the other's hunt. That is a distinct possibility. Another is that humans may have picked up and reared wolf pups. The taming process, different from the domestication process, is known by virtually all peoples of the world and would have known among the last of the hunter-gatherers. According to this rationale, one of the primary reasons for domesticating the wolf to produce a dog would have been for hunting. As the dog is, and has been, consumed by numerous peoples, we should not rule out the idea that it may have been kept at the outset as a supply of food. Among the Australian aborigines, dingoes were also a source of heat during the cold nights of the southern winter. The role of guard of the camp, village and herd, may well have emerged later. Although the notion of the pet dog is perhaps rather modern, that of 'dog companion' must have existed for quite a long time. In some regions and periods, the dog helped to carry or drag objects. Sleigh dogs are a good example of this.

In health terms, cohabitation with the dog has probably had a number of consequences. The human flea (*Pulex irritans*) could be a relic of this cohabitation, as humans are the only primate species to have a flea. Internal parasites, such as echinococcus tapeworms, have also become 'domesticated', that is to say, they live inside human homes, and sometimes inside humans themselves, having been hosted by the domestic dog from wild reservoirs. In the case of *Echinococcus granulosus* in Australia, the strains carried by European dogs and sheep differ from those of dingoes and marsupials. Parasite lifecycles do not merge easily, having evolved independently over several millennia (30). The last example of the health consequences of human/dog cohabitation is rabies, which has a rather complex epidemiology. Chiropterans are doubtless essential to understanding the history of lyssaviruses. However, rabies of wolves and dogs seems to be an age-old affliction. Descriptions in texts of ancient times appear to refer to the disease. The absence of rabies in Australian dingoes would imply that either the virus was not present in the founder populations when they left Asia, or that the journey had effectively filtered out contaminated individuals before they arrived in Australia. The discovery in 2009 of the first cases of canine rabies, and unfortunately human rabies, on the island of Bali, in Indonesia, is perhaps indicative of a process of anthropogenic spread of the rabies virus across the archipelago. In all likelihood, it was a fisherman travelling by boat, accompanied by a dog in the incubative stage, taken along as both a sailing companion and possible food supply, that triggered this outbreak. The huge populations of 'domestic' dogs (which are in fact more or less free-roaming) found in many of the world's tropical and Mediterranean regions, now represent the bulk of the rabies reservoir responsible for tens of thousands of human deaths every year (5) (Fig. 4).

Fig. 4
Free-ranging domestic dogs, Mafia Island, Tanzania
Depending on the environment, free-ranging domestic dogs, now present over much of the globe, can pose a threat to biodiversity and public health
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The goat

The goat may well have been domesticated a little earlier than other domestic ruminants. The ancestral wild stock, which still exists, is the wild goat (*Capra aegagrus*), which is found from Anatolia to Pakistan. The other representatives of the *Capra* genus, the ibex and the markhor (*C. falconeri*) have not been domesticated and do not seem to have contributed to the emergence of the domestic goat. It is interesting to study goat populations on the Mediterranean islands and some Atlantic islands (Canaries and Madeira), because even though they were introduced, this happened a very long time ago (22, 23). These goats are probably pre-Hispanic. They illustrate ancient phases in the domestication process and would be worth protecting and preserving as testimony to it. As these goats returned to a free-living state shortly after their arrival, they have remained in the stage at which domestication led them up to that point, well before the recent, more intensive breeding stages through which almost all the domestic breeds have passed in recent centuries.

Contemporary studies of ancient sites in Turkey and Jordan enhance our understanding of the initial processes of domestication. In central Anatolia, we see an evolution in practices from the Neolithic to the Bronze Age, from animals that were perhaps farmed but not really isolated genetically from wild herds, to herds whose composition and movements were controlled. We see the culling of young males and marked morphological differences between wild goats and domestic goats (smaller) (1). In Jordan, around 7,000 years ago, male and female goats were also managed differently. In this country, the hunting

of gazelles (*Gazella* spp.) was still widely practised. The bone remains are clear proof of this (21). This shows that the hunting and farming of different species may have persisted for quite some time and that the human populations concerned made extensive use of one activity to complement the other. These populations should be classed as 'hunter-cultivators practising livestock production' rather than as true 'cultivator-livestock producers'. In the cases of both Turkey and Jordan, the taphonomic study and analysis of subfossil remains also indicate that goats and sheep cohabited but under different production and management systems.

Anatolia and the Levant are very close to the goat's original area of domestication. Doubtless the history of the domestic goat's invasion of other lands and other continents is not yet fully known. A study published in 1996 makes a number of suggestions for understanding the domestic goat's conquest of Africa (2). As with cattle, there appear to have been two waves of colonisation at two different times in history. The first invasion probably commenced in the fifth millennium BC and continued until the domestic goat had occupied the entire continent. The second, more recent, wave probably dated from the third millennium BC. The animals that descended from them would have occupied mainly the hottest central zones of the continent. According to this scenario, the pygmy goats specific to certain regions of Africa would have formed part of the first wave of colonisation. However, this is an interpretation based chiefly on morphological data. Numerous additional data, especially genetic, probably need to be collected and analysed before this scenario can be confirmed or refuted.

Few data exist concerning Asia. In the case of goats, as with other domestic ruminants, we know that humans travelling from Asia to conquer the Americas departed before goats had been domesticated. There were no further over-land movements of people or animals between these two continents after the glaciations ended. The first navigators of ancient times to occupy the islands of the Pacific could not have been familiar with goats either. Contacts between Asia and the Americas continued via the Pacific, but it was the domestic pig (Fig. 5) that accompanied travellers subsequently, well after human movements first began (18, 33). Today, the mountains of central Asia are teaming with wild goats (35), but these wild herds are gradually being replaced by herds of domestic goats and sheep. As has been demonstrated in the Alps, domestic herds can be a source of microorganisms that are pathogenic to wild herds when the two herds mix or follow one another closely in mountain pastures.

During the voyages of the Age of Discovery travellers landed goats on many of the world's islands. The idea was simple: to guarantee fresh provisions for the navigators' future stopovers. Unfortunately, the goats had a dramatic impact on the vegetation of islands and islets with no existing predators and an abundance of flora unsuited to sustaining large herbivores. The cases of the Galapagos Islands (Ecuador), Round Island (Mauritius) and the island of Guadalupe (Mexico) have become textbook ecological examples (20, 36).

Fig. 5
Free-ranging domestic pig, Sulawesi, Indonesia
They can have a detrimental impact not only on biodiversity (predation on local species and crossbreeding with other swine species), but also on health (transmission of pathogens)
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While there is no doubt that one reason for producing goats was for meat, what about other reasons for domestication? What about the use of its other products? A long-standing source of debate has been the date when dairy farming first began (32). For many years, certain authors suggested that goats' milk and hair had begun to be produced several thousand years after the start of meat production. Modern biochemical, isotopic and paleogenetic results have failed to confirm this hypothesis. On the contrary, they suggest that goat milk and fibres must have been produced, consumed and used as from the Neolithic period. This would presuppose the existence of a suitable very ancient technology. In a slightly different field, the age-old practice of consuming milk and dairy products also suggests prolonged exposure of human populations to microbial agents such as bacteria of the *Brucella, Coxiella* or *Rickettsia* genera, perhaps as long ago as the Neolithic period.

The European rabbit

The European rabbit (*Oryctolagus cuniculus*) is not only a wild animal, but has also been used as a companion animal, laboratory animal and production animal (meat, pelt and hair) (Fig. 6). This makes it an animal familiar to everyone. However, it has an unusual history. A model

Fig. 6
European rabbit (*Oryctolagus cuniculus*), Tenerife, Canary Islands
A classic example of a species moved by humans all over the world
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invasive species, and the subject of one of the first documented cases of biological pest control in a natural environment, the rabbit is discussed at length elsewhere in this issue (26). This article examines the rabbit's origin and the process of its conquest of new territories. The chief source is a study for a PhD thesis in archaeozoology conducted around the Mediterranean Sea, the western shores of which represent the now-acknowledged native home of the species (3). Before that, the rabbit's natural place of origin had been disputed for many years. As it appeared on the Iberian Peninsula during the Pleistocene Epoch, this seems to be its native home, although North Africa cannot be ruled out totally. The pattern of Quaternary glaciations explains its subsequent population fluctuations south of the Pyrenees. Two breeding lines, A and B, then emerged, one in the east of the Iberian peninsula (A) and the other in the west (B). The expansion of Mediterranean vegetation subsequent to the glaciations enabled it to spread outside the Iberian peninsula (into southern France, Italy and as far as Sicily). While it was no longer present in Italy at the beginning of antiquity, the rabbit continued to spread alongside human movements, explaining its spread to places such as the Balearic Islands (Spain) and Zembra Island (Tunisia). However, in early time, it was not introduced into Corsica, Sardinia or Pantelleria Island, that is to say, into other islands in the western Mediterranean Sea (22). The Phoenicians, travelling from the eastern Mediterranean, discovered it when they landed on the Iberian Peninsula. They confused it with the rock hyrax (*Procavia capensis*), a small mammal of the order Hyracoidea, which is present in Africa as well as also in the Near East. The Phoenicians named this new land the 'country of the hyrax' (*I-Saphan-im*), which evolved as *Hispania* (and later *España* or Spain in English). Although this scenario is difficult to confirm once and for all, nothing discovered to date rules it out.

Having remained limited to the shores of the Mediterranean Sea for thousands of years, the rabbit went on to invade Europe in just a few centuries, but not just by itself. During the Middle Ages and until the late 13th Century it remained confined in enclosed rabbit warrens owned by nobles and the clergy. This explains its highly privileged status in those days. It was bred mainly for hunting. As from the 14th Century, rabbit breeding and distribution expanded, became democratised and spread virtually throughout Europe in less than five centuries. In so doing, it lost its symbolic value and prestige and became a source of food or income (sale of meat and pelts). The species can only be considered as truly domesticated as from the 18th and 19th centuries. In all that time, what we refer to as wild rabbits are in fact descended from captive rabbits that had escaped from private hunting grounds. There is therefore a very strong and ancient link between the distribution of the species and human activities. The European rabbit was only introduced onto numerous islands and other continents in more recent times, for a variety of economic, hunting and leisure purposes. The case of Australia is studied in depth in other articles in this issue, but the history of rabbit introductions on a host of tropical, temperate or sub-Antarctic islands illustrates the sometimes spectacular impact of invasive species on small areas (20, 36).

In the case of the rabbit, which was domesticated relatively recently, the reasons for domestication are numerous and have evolved over the centuries. Of the three animal species discussed here, it is the rabbit that has had the most varied relations with humans. Initially a game animal reserved for nobles and the clergy, it later became a highly prized small game animal in some regions. In more recent times, the rabbit was domesticated as a hutch animal, then later bred on farms for two types of production: meat and hair. The rabbit's role as a laboratory animal makes it rather original, as does the fact that some people view it solely as a companion animal, with the selective breeding of ever smaller animals, pygmy domestic rabbits.

Conclusion

Archaeozoology is a fast-expanding field of research. The International Council for Archaeozoology holds an international conference every four years, when numerous scientists come together to discuss a variety of subjects, one of the most important being the history and understanding of domestication. Its history can help to identify the developments that led to the current distribution and diversity of domestic species and to a clearer interpretation of their impacts on progressively invaded ecosystems. It is doubtless also a possible introduction to the epidemiology of the microorganisms associated with these species and their movements. ■

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