Part I

Origins and evolution

2 Origins of the dog: The archaeological evidence

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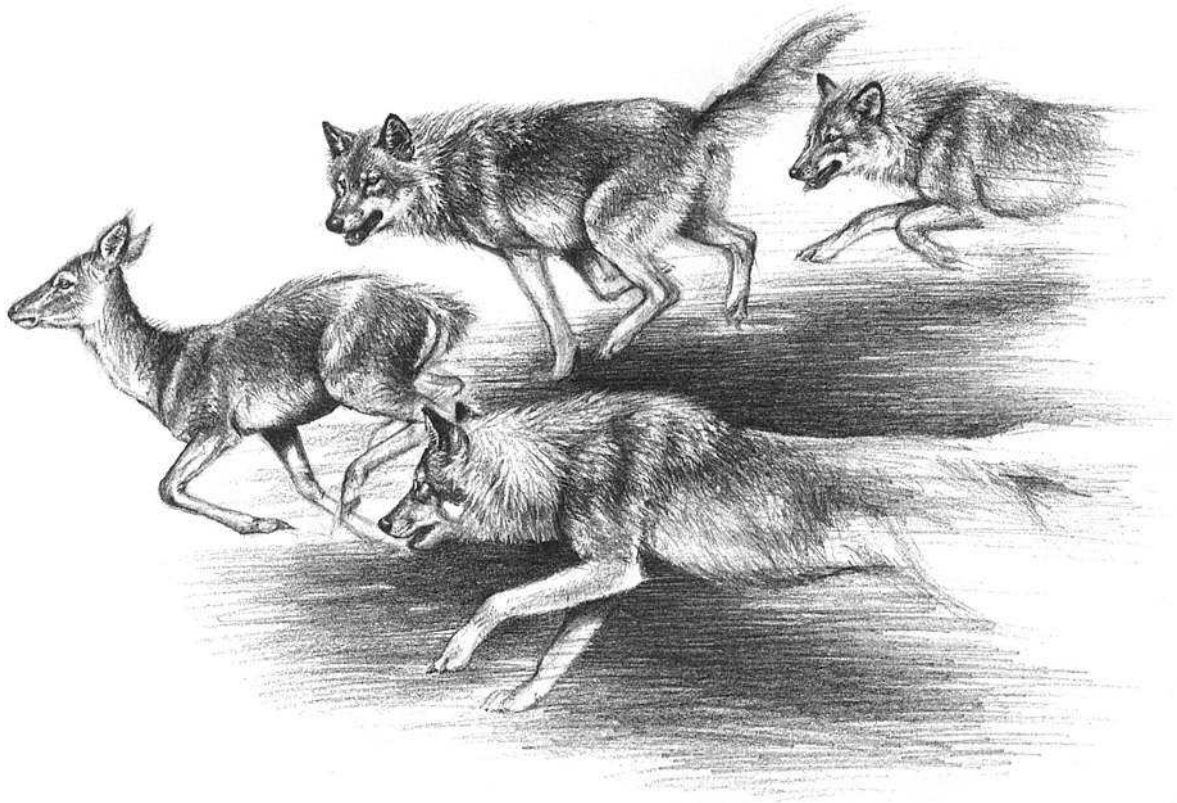

2.1 Introduction

After more than a century of argument and discussion, it is now generally agreed that the single progenitor of all domestic dogs, ancient and modern, was the grey wolf, *Canis lupus*, but when and where domestication first took place is still much argued about. Was the wolf domesticated in one part of the world or in many regions over its huge range covering the Northern Hemisphere, and what exactly constitutes a domestic dog? The word "domestic" means simply "of the home," so any tamed animal may be said to be domestic, but if the term is to be used as a scientific descriptive it must have a biological definition, and there must be a clear separation between a wild species and its domestic derivative. A domestic dog is not a tamed wolf but is it a separate species?

To paraphrase the most frequently used definition (see e.g. Lawrence, 1995, p. 551): a species is a population of animals that breeds freely and produces fertile offspring. If the hybrid offspring are infertile then the parents are separate species, for example the horse and the donkey. However, many animals that are normally considered to be separate species will interbreed with fertile offspring, as will all the wild species of the genus *Canis*, these being the wolf, coyote, and the several species of jackal. A more useful definition is the biological species concept which states that, "species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1966, p. 19). Using this definition, all fully domesticated animals can be classified as separate species from their wild progenitors, from which they are reproductively isolated. The dog is no longer a tamed wolf but, as a result of selective breeding under human control, it has evolved into a new species, named by Linnaeus, *Canis familiaris*, which by further reproductive isolation and under the influence of both natural and artificial selection produces new breeds (Clutton-Brock, 2012).

2.2 Precursors of the dog

With the increasing care and advanced technology used in the excavation of archaeological sites during the second half of the twentieth century, the bones of wolves have been found in association with those of early hominins[1] from as early as the Middle Pleistocene period. Examples include the cave of Lazeret near Nice in the south of France, dated at 150 000 years bp[2] (de Lumley, 1969), Zhoukoudian in North China, dated at 300 000 years bp (Olsen, 1985), and the 400 000-year-old site of Boxgrove in Kent, England (Robert & Parfitt, 1999). As these associations demonstrate, the sites of occupation and hunting activities of humans and wolves must often have overlapped, but these finds are dated to before the appearance of anatomically modern humans (*Homo s. sapiens*), and there is no physical evidence of social interaction between the two species of hunters. During the 1990s, however, molecular studies were beginning to be applied to archaeozoology and, in 1997, Carles Vilà and his colleagues published their dramatic thesis suggesting that the wolf and the dog became separate breeding populations at least 135 000 years ago (Vilà *et al*., 1997). This conclusion was

[1] Hominin is the taxonomic term encompassing modern humans, extinct human species and all immediate ancestors, e.g. *Australopithecus*. The term hominid is now given a wider use and includes all modern and extinct great apes as well as modern humans and chimpanzees etc.

[2] bp denotes the radiocarbon date expressed as radiocarbon years before present (taken as AD 1950). When written in capitals, BP denotes that the radiocarbon date has been calibrated to provide the true or calendar age of the sample.

arrived at by comparing the number of genetic changes or substitutions in the control region of mitochondrial DNA derived from samples of wolves, dogs and coyotes. It was found that dog and wolf mtDNA differed by a maximum of 12 substitutions and an average of 5.3, whereas the DNA of wolves and coyotes (*Canis latrans*) differed by at least 20 substitutions. Wolves and coyotes are believed, on fossil evidence, to have diverged about one million years ago, so the scientists used this figure to calculate the rate of gene substitution assuming that such mutations occur at a steady rate over time. This led them to conclude that dogs and wolves could have diverged more than 100 000 years ago.

The assumptions from this molecular evidence are no longer considered to be valid and this extraordinarily early date for the emergence of the first "dogs" must be discounted (see vonHoldt & Driscoll, Chapter 3). But dating from about 100 000 years after this period, but before the peak of the Last Glacial Maximum (hereafter LGM), around 26 000 to 20 000 years ago, a tranche of canid remains has been identified from cave sites in Europe, the Ukraine and Siberia in which the skulls and teeth appear to show what are assumed to be the characteristics of incipient domestication. These characters include a reduction in overall size, a shortening of the jaws and widening of the snout, often without reduction in size of the teeth so that the cheek teeth are compacted. When a wild canid is found with these abnormalities it is sometimes an animal that has been kept in captivity under stress and fed on an improper diet. Based on the presence of these known characters, Mietje Germonpré and her colleagues have identified more than six skulls which they claim as Palaeolithic dogs from faunal assemblages that include large numbers of wolf remains together with the bones of their prey, particularly mammoth. The sites are the caves of Goyet in Belgium, Předmostí in the Czech Republic, and two sites in the Ukraine dating from before the LGM (Germonpré *et al*., 2009, 2012),

From the Ice Age cave of Razboinichya in the Altai Mountains, Nikolai Ovodov and colleagues (2011) have identified another "incipient dog," which they suggest represents, "an early Holocene lineage of wolf domestication." All these canid remains that have been identified as "dog" have been dated to before the LGM; that is, to around 30 000 years ago. Interestingly, however, although more than 190 skulls of cave bears have been recorded from the 30 000 year-old cave of Chauvet in the Ardèche, and the walls are covered with a great many depictions of lions, there is not a single authentic record of a wolf, either as a skull or in the rock art. At this time, there is no published verification for the statement of Garcia (2005) and Germonpré *et al*. (2009, p. 481) that, "in the deepest part of the cave, a track of footprints from a large canid is associated with those of a child," or that torch wipes made by this child were dated at c. 26 000 bp, nor that, "based on the short length of medial fingers in the footprints the canid track was interpreted as being made by a large dog."

The early hypothesis that domestication originated from the practice of capturing and taming young wild individual animals was generally replaced in the second half of the twentieth century by the theory that wild animals became associated with human groups and were thereby habituated and tamed from their own volition (see e.g. Budiansky, 1992). Wolves would have scavenged around human settlements and would slowly have become enfolded into human societies; a process that could have occurred in any area where both wolves and humans lived, and in any period from the Middle Pleistocene up to the present (for a map see Larson *et al*., 2012). It is further predicted that young wolves, which no longer hunted megafauna but scavenged for food around human camps, would fail to develop the skulls and jaws of hunters and would exhibit the less powerful musculature and skull structure of domestic dogs, as was shown with measurements of the skulls of captive wolves as long ago as 1894 (Wolfgramm, 1894). This is the basis for the assumption by Germonpré and her colleagues that the canid skulls they identified from

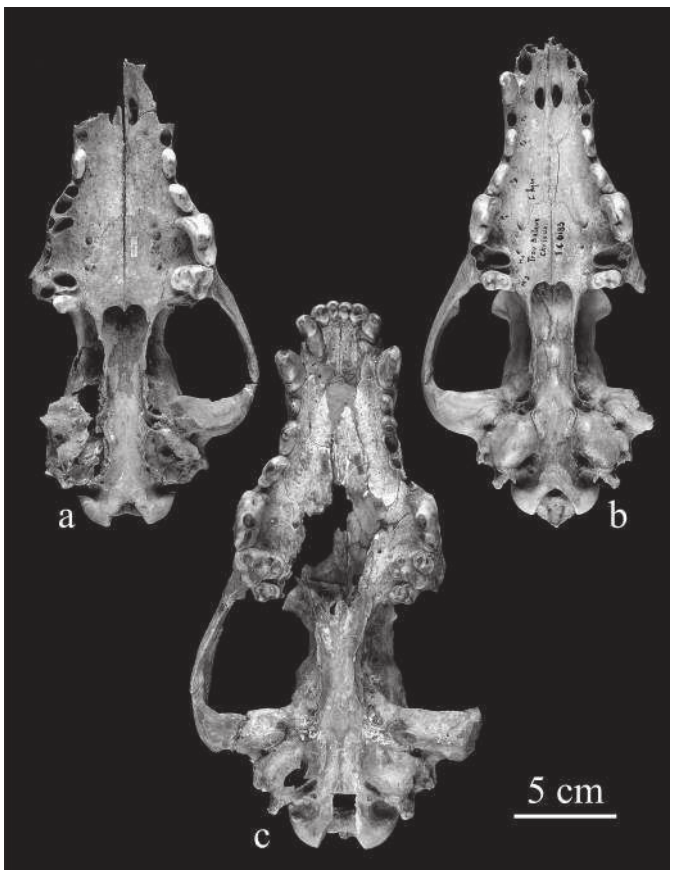

Figure 2.1 Ventral view of skulls identified as (a) "dog," and (b) and (c) wolves. (Reprinted from *Journal of Archaeological Science*, **36**, Germonpré M., Sablin, M.V., Rhiannon, E. *et al*., Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes, pp. 473–90 (2009), Elsevier and the Royal Belgian Institute of Natural Sciences, reprinted with permission.)

Pleistocene caves were incipient dogs (see Figure 2.1). However, these "dog-like" characters do occur in wild canids as a result of ecological stress and inbreeding, as shown in the skulls of Arctic wolves (Clutton-Brock *et al*., 1994; Federoff, 1996) and sporadically in other wild canids as figured by Miles & Grigson (2003). It is quite unknown how often abnormalities of this type occur in the skulls of modern wolves, let alone their relative numbers in wolves of Pleistocene date. There is also the crucial point, noted by Crockford & Kuzmin (2012), that the caves in which Germonpré and colleagues' six putative dog skulls were found range over thousands of kilometres and at least 19 000 years in age.

It could well be that, from time to time, Palaeolithic hunters reared tame wolf cubs in their communities and it is possible that the skulls of these canids can be and have been identified as incipient "dogs." However, there is no evidence at present that these tamed wolves would have bred in reproductive isolation from the rest of their species and thereby produced future generations of domestic dogs (Crockford & Kuzmin, 2012; Larson *et al*., 2012). The latest potentially tamed wolf to be identified from the Pleistocene period, at present, is from the site of Avdeevo, an open air site on the Russian Plain near the city of Kursk, and dated between 20 000 and 21 000 years ago (Germonpré *et al*., 2012, p. 185). After this time the extreme climate of the Last Glacial Maximum may well have driven away all hunters and their prey from northern Europe and Asia for around 5000 years.

2.3 Morphology and domestication

After a few generations, the puppies of wolves living by scavenging as commensals in a human community would exhibit a general reduction in the size of the body and head, and this trend is marked in the remains of the earliest domestic dogs. Reduction in size is a characteristic feature of the early stages of domestication not only in canids but in many different species of mammal (Tchernov & Horwitz, 1991; Clutton-Brock, 1999). The small overall size of early domestic mammals would have been partly a result of progressive stunting caused by malnutrition from the time of conception. Stunted growth has been demonstrated in young animals kept on an inadequate diet, as in the experiments on pigs by McMeekan in the 1930s (see Hammond, 1940). There would also have been strong natural selection for diminution, since small animals would have survived better on little food. Tchernov & Horwitz (1991, p. 69) argued that diminution of size in the early dogs was also a response to the changed ecological regime of the domestic state and they suggested that:

> The relief of selective pressures associated with domestication set in motion a cyclical reaction of accelerated maturation, increased reproductive capacity with a tendency for litter sizes to be larger, and shortened generation time. This resulted in smaller sized, younger parents with smaller sized offspring.

During the process of domestication in the dog, the facial region (muzzle and snout) became shorter and wider with consequent crowding and displacement of the cheek teeth.[3] Tooth crowding occurred in the early stages because evolutionary reduction in the size of the teeth took place at a slower rate than the shortening of the maxillary and mandibular bones. However, the teeth did become smaller in time, and modern dogs have teeth that are very much smaller than those of wolves, even in giant breeds such as the Great Dane. The teeth may also be misplaced, or even increased in number over the normal for the canid dental formula (see Miles & Grigson, 2003, pp. 84–8). The shape of the mandible became more curved, and an angle developed between the facial region and the cranium, called the "stop" in modern breeds. The eyes became rounded and more forward-looking and the frontal sinuses became swollen, while the bones of the skull became thinner. The tympanic bullae were reduced in size and flattened.

It is probable that the colour of the coat would have changed from the tawny grey of the wolf to the yellow of the dingo quite early on in the first dogs, and maybe, before long, this will be established by molecular research, as it has been by Ludwig *et al*. (2009) for the first domestic horses. All these morphological changes are unlikely to have had much to do with intentional selection but occurred slowly as the result of physiological and hormonal changes associated with the transition to domestic existence (Crockford, 2006; Morey, 1992; Lord *et al*., Chapter 4).

In the well-known experiments on the domestication of silver foxes in Russia that were begun by D. K. Belyaev in the 1950s and continue to the present day, all the above changes occurred in a short time without a change of diet, but simply as a result of fox cubs being strictly selected for the physical and behavioral features of domestication. However, these remarkable results were achieved by intense artificial selection on animals that were the progeny of foxes that had been reared in small cages for the fur trade for about 50 years (Statham *et al*., 2011). Whereas, as recognized by Trut *et al*. (2004, p. 644), the domestication of wolves would have been determined by natural selection for

[3] Almost no whole skulls of the earliest domestic dogs have survived, so it is not possible to investigate relative changes in the different parts of the skull. The work of Wayne (1986) suggests that, while the muzzle may have widened, the length of the facial region, although shortened, would have remained in proportion to the reduced cranial length.

coexistence with human hunters who, "were only one factor that shifted the direction of selection to behavior and the ability to exist in the new, anthropogenic environment."

2.4 The first dogs

Apart from the possible precursors to the dog, dating from before the LGM, archaeological evidence indicates that the dog was the first species of animal to be domesticated with certainty. This occurred towards the end of the last Ice Age when all human subsistence still depended on hunting, gathering and foraging. The record for the earliest directly dated canid remains that can be identified as definite domestic dog, goes to a right maxillary fragment with cheek teeth from Kesslerloch Cave in Switzerland (Figure 2.2). This cave is one of the major Magdalenian sites in Central Europe and was first excavated in 1898/9. Recently, a reappraisal of the faunal remains from the cave was carried out by archaeozoologists, and a fragment of canid upper jaw was identified as dog and not wolf. This was confirmed from its small size and from the morphology of the upper carnassial and first molar. A sample of the dog maxilla was directly dated to 12 225 ± 45 bp (KIA-33350) or c.14 100–14 600 BP (Napierala & Uerpmann, 2012).

Until the identification of the maxilla from Kesserloch the earliest find of a dog was of a mandible from the late Palaeolithic grave of an old man and a young woman at Bonn-Oberkassel in Germany (Nobis, 1981). This dog is dated through closely associated material to around the same date as the Kesserloch maxilla, that is c.12 100 bp. After this period, the identification of the bones and teeth of dogs on prehistoric sites and their separation from those of wolves has become relatively straightforward, as it was, for example, with the skulls of a dog and a wolf from the Early Mesolithic site of Star Carr in Yorkshire, England.

The well-known site of Star Carr is the most important Mesolithic site in Britain. The site was occupied around a waterlogged lakeside for around 350 years from c.10 700–10 350 BP during the preboreal and boreal climatic periods. The Ice Age had ended and temperatures were close to those of recent times, although the sea levels had not yet risen enough to separate Britain from the

Figure 2.2 The right maxilla identified as domestic dog from the Magdalenian cave of Kesserloch, Switzerland. (From Napierala, H. & Uerpmann, H-P (2012), © 2010 John Wiley & Sons, Ltd, reprinted with permission.)

Continent. A huge number of organic artifacts were preserved in the peat, including nearly 200 harpoon points made of red deer antler. The site was first excavated by J. G. D. Clark in 1949–51, the faunal remains were studied by Fraser & King (1954), and the dog was described in detail by Magnus Degerbøl (1961), but work has continued on the site and on the artifacts and faunal remains ever since.

In 1985, during excavations at the nearby Mesolithic site of Seamer Carr, the neck vertebrae of a dog were retrieved that match in age and size the skull of the Star Carr dog (Clutton-Brock & Noe-Nygaard, 1990). A fragment of one of these vertebrae has provided a radiocarbon accelerator date of 9940 ± 110 bp [Oxa-1030]. It is conceivable that the skull and neck came from one individual dog, but they could also be from two dogs from the same litter or from unrelated dogs of the same size and age. These are the only remains of dogs that have so far been identified from Mesolithic Britain (of which there are a large number of sites), so it is probable that the number of dogs during this very early period was quite small. They were probably inbred and displayed little variation in size amongst individuals.

Another remarkable feature of the dog vertebrae from Seamer Carr is that two samples of bone yielded stable carbon isotope ratios of –14.67% and –16.97%. These ratios reveal that the dog obtained a significant part of its food from marine fish. Clutton-Brock & Noe-Nygaard (1990) have therefore postulated that the sites of Star Carr and Seamer Carr were hunting camps that were visited by people who lived for much of the year nearer to the coast and obtained most of their food by fishing.

The skull of a fully adult dog very similar in size and proportions to the Star Carr skull has been excavated from another Mesolithic wetland site at Bedburg-Königshoven in Germany (Street, 1989). Similar remains of dogs have also been found from the numerous waterlogged Mesolithic sites in Denmark where the period is known as the Maglemosian. The similarity in size and osteological characteristics of the remains of these first domestic dogs found on prehistoric sites in northern Europe may indicate that all these early dogs were the result of dispersal from a single founder population. The skull of the dog from Bedburg-Königshoven, for example, is closer in size and morphology to the remains of the earliest dogs from western Asia than it is to the very large European wolves, as exemplified by the Mesolithic wolf skull from Star Carr. However, wolves must have lived close to human settlements in many parts of the world, and a single litter of puppies from any one of these could have provided the founders for an independent domestication event that subsequently became very widespread.

The dogs that have been identified from these Mesolithic sites in northern Europe come from a similar time period to the sites in western Asia from where a cluster of canid remains has been identified as belonging to *Canis familiaris*. These sites belong to the cultural period known as the Epipaleolithic or Natufian and they are associated with a dramatic change in human hunting strategies. During the Paleolithic period, animals were killed by direct impact from heavy stone axes and spears. During the Natufian, and the corresponding Mesolithic period of Europe, arrows armed with tiny stone blades called microliths came into widespread use (Mithen, 2003). The success of these long-distance projectiles would have been enhanced by the new partnership with dogs that could help to track down and bring to bay wounded animals. This cooperative hunting technique would thus have resulted in greater hunting efficiency, as it does among some contemporary hunting societies (Koster, 2008; Lee, 1979).

During the 1930s, a small number of canid skulls from Natufian sites in Palestine were identified as those of dogs by Dorothea Bate; the most notable of these being a nearly complete skull from the cave of Wady el-Mughara at Mount Carmel (Bate, 1937). Thirty years later, in the 1960s, I re-examined the skulls from Mount Carmel, Shukbah, Zuttiyeh, and Kebarah that are held in the

Natural History Museum, London, and questioned their domestic status. Measurements showed that they were very similar to the skulls of living Arabian wolves, except that they were slightly smaller and rather wider in the palate (Clutton-Brock, 1962). In western Asia the wild wolf, *Canis lupus arabs*, is, at the present day, the smallest of the subspecies that range over the northern hemisphere. This makes the identification of fragments of canid bone from later archaeological sites difficult because there is very little reduction in size from the wolf to the dog (Harrison, 1973). However, as described by Dayan (1994) and Tchernov & Valla (1997), the fossil remains of wolf from Natufian and earlier sites are from very large individuals, while the canids that have been identified from sites of this period as dogs are as small as the Mesolithic dogs from Europe. The realization that the early Holocene wolves of western Asia were as large as those in Europe has made a crucial difference to the acceptance of the small canids from sites of equivalent date as dogs, and it is now generally agreed that Bate's identification of the canids from her early sites as dogs was correct. But were they descended from the large wolves that inhabited the region at that time or had these dogs been imported from somewhere else?

In the 1970s the discovery of a Natufian site with the burial of a human skeleton with its hand on the remains of a puppy became the best-known early evidence for the domestication of the dog in the Near East (Davis & Valla, 1978). The site is near the Huleh Lake in the upper Jordan valley in Israel, and is dated at 12 000 years ago. Its inhabitants were hunter-gatherers who were on the verge of becoming agriculturalists. They lived in round stone dwellings, used basalt pestles and mortars for grinding cereals, and buried their dead in stone-covered tombs. In one of these, at the entrance to a dwelling, the skeleton of an elderly human was found together with that of a puppy of between four and five months of age. The human skeleton lay on its right side, in a flexed position, with its hand on the thorax of the puppy (Figure 2.3). Since the finding of this human and canid burial at Ein Mallaha, another Natufian burial with canid skeletons was excavated at the cave of Hayonim Terrace, Israel. This burial is late Natufian in date and held the remains of three humans and two dogs (Tchernov & Valla, 1997).

The canid remains in these graves have been widely accepted as those of the earliest dogs on cultural grounds, that is, their close association with the human skeletons must imply that in life they were highly valued animal companions and that therefore they must be domestic dogs. However, the remarkable discovery of a fox skeleton buried with a human in a pre-Natufian grave throws the identification of these "dogs" based on the cultural evidence alone in doubt and reopens the question of whether these canid skeletons are really those of domestic dogs. The skulls are not morphologically similar to those of jackals (*Canis aureus*) but what else could they be?

'Uyun al-Hammam is a pre-Natufian site in northern Jordan, with elaborate human burials associated with animal remains. Eleven human skeletons had been buried in at least eight graves, as described in the excavation report by Lisa Maher and her colleagues (2011). It is clear from the careful interpretation of the burials that one of these humans had been buried with the body of a fox (*Vulpes vulpes*), and later when this grave was opened again and the partly decomposed human skeleton was moved to a bed of red ochre in another area nearby, the head of the fox was moved with it. Maher *et al*. describe the association thus:

> It is possible that the link between fox and human was such that when the human died the fox was killed and buried alongside. Later, when the graves were re-opened, these links were remembered and bones moved so that the dead person would continue to have the fox with him or her in the afterlife.

The burial of the fox in close association with a human, as well as the burials of "dogs" in Natufian graves in Israel, supports the view that, throughout their evolution, humans have possessed a unique instinct for nurturing members other species of animals, irrespective of their potential "uses." Thus,

Figure 2.3 Burial of a human with a puppy from the Natufian site of Ein Mallaha, Israel. (© Simon Davis, reprinted with permission.)

the biological and semantic divisions between the wild and the domestic, as we view them today, may have taken thousands of years to become established.

Contemporary and later sites in other countries of western Asia have also yielded canid remains that have been identified as dogs (see, for example, Clutton-Brock, 1969 and Stanley Olsen's *Origins of the Domestic Dog*, 1985, pp. 71–9). Notable amongst these is a small mandible with compacted teeth from the site of Palegawra in Iraq, dated at around 12 000 years ago (Turnbull & Reed, 1974). From the following Neolithic period, between 9000 and 7000 years ago, remains of dogs become ubiquitous in archaeological sites from many parts of the world, and in these, the dog-like features of the skull and teeth are fully developed. One hundred and thirteen fragments of skulls, teeth and skeletal bones have been identified as those of large domestic dogs from the early Neolithic site of Jarmo in Iraq (9250–7750 bp) by Lawrence & Reed (1983). In China there are Neolithic dogs from 7000 years ago (Olsen, 1985).

Remains of dogs have been found with those of the extinct Japanese wolf, *Canis lupus hodophilax*, from the rock shelter site of Tocibara in Japan, dating at around 8000 bp (Miyao *et al*., 1984). Olsen (1977, 1985) considered that the small Chinese wolf, *Canis lupus chanco*, was the ancestor, not only of early Chinese dogs, but also of those that moved with the early human immigrants across the Bering Straits into North America. However, molecular analysis has now provided two conflicting theses for the origin of all dogs, worldwide: first, that of Leonard *et al*. (2002) and