study is now required to address several open questions. Most pertinently: how do ants encode skyline information? And, how do ants derive a movement direction from the comparison of their current skyline view and their remembered view? Recent experiments, also with *M. bagoti* [10], have addressed the first question. By masking different portions of the visual panorama, it was possible to show that being able to view prominent skyline features at high retinal elevations was neither necessary nor sufficient for successful orientation. This suggests that *M. bagoti* derive information from a broad range of azimuthal directions rather than a small set of the most prominent features.

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01585-1

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Evolutionary history of the Falklands wolf

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After visiting the Falkland Islands during the voyage of the Beagle, Charles Darwin remarked on the surprising presence of a wolf-like canid unique to the islands [1]. One hundred and forty years after its extinction [2], the evolutionary relationships of this unusual canid remain unresolved. Here, we present a phylogenetic analysis based on nuclear and mtDNA sequence data from the extinct Falklands wolf and find that its closest extant relative is the South American maned wolf. Molecular dating analyses suggest that the Falklands wolf and several extant South American canid lineages likely evolved in North America, prior to the Great American Interchange. The Falklands wolf was the sole representative of a distinct South American canid lineage that survived the end-Pleistocene extinctions on an island refuge.

The Falklands wolf (*Dusicyon australis*) was the only endemic terrestrial mammal inhabiting the Falkland Islands until its extinction in 1876 [1,2]. Since its description by Darwin, the occurrence of this large, wolf-like canid on a pair of islands 480 km from the eastern coast of Argentina has remained a mystery [1–4]. Although formerly abundant on the islands [1,4], few museum specimens of the species have been preserved. The Falklands wolf presents a puzzling combination of craniodental characteristics, resulting in controversial taxonomic alliances with domestic dogs (*Canis familiaris*) [2], the North American coyote (*Canis latrans*) [5], and South American foxes (*Pseudalopex* and *Cerdocyon*) [5,6]. Hypotheses for its presence on the islands, which have never been connected to the South American mainland [7], have ranged from dispersal by ice or logs [3,7], to domestication and subsequent transport by Native Americans [2].

We sequenced the complete *cytochrome oxidase II* mitochondrial gene and part of the *cytochrome b* gene from five museum specimens of Falklands wolf, including one specimen collected by Darwin himself (see Supplemental data published with this article online for details). We also sequenced four nuclear loci containing phylogenetically informative polymorphisms. Phylogenetic analyses of these datasets using neighbour joining, maximum likelihood and Bayesian inference do not recover a close relationship between the Falklands wolf and South American foxes (*Cerdocyon* and *Pseudalopex*) or *Canis* species, as suggested by morphological data [2,5,6]. In contrast, we found a surprising and well-supported sister group relationship to the South American maned wolf (*Chrysocyon brachyurus*) (Figure 1). Given our limited sequence data, we were unable to recover a monophyletic South American canid clade, or a clade comprising the maned wolf and bush dog (*Speothos venaticus*) in our unconstrained analyses. However, a topology constrained to include these well-documented relationships is not significantly less likely than the tree produced by unconstrained analyses (see Supplemental data). Furthermore, the monophyly of both the South American canids and the maned wolf/Falklands wolf/bush dog clade are independently supported by nuclear polymorphisms (Figure 1). Although the maned wolf is the closest extant relative of the Falklands wolf, a morphologically similar species, *Dusicyon avus*, survived in South America until the mid-Holocene [7]. This species may have an even closer relationship with the Falklands wolf and warrants further investigation.

Both Darwin [1] and Fitzroy [3] were surprised by the striking differences between the Falklands wolf and the canids of the South American mainland. We estimated the divergence time between the Falklands wolf and maned wolf as 6.7 million years ago (mya) (Figure 1; 95% highest probability density (HPD) = 4.2–8.9 mya). Such a long divergence time, coupled with subsequent ecological isolation on the Falkland Islands may account for the pronounced morphological

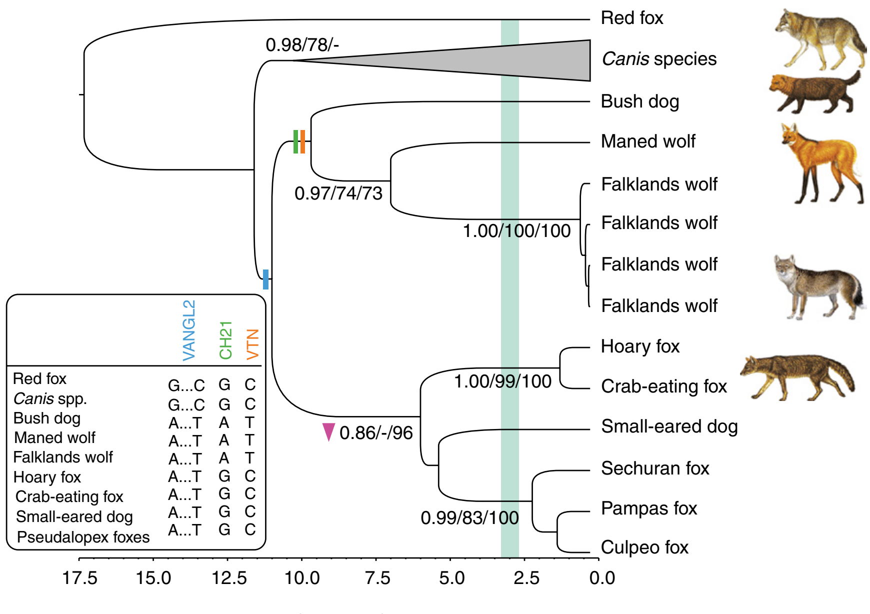

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Figure 1. Chronogram showing phylogenetic relationships of the Falklands wolf.

Colour bars indicate phylogenetically informative polymorphisms shared by the Falklands wolf. The Falklands wolf also lacks an insertion (purple arrowhead) specific to the South American foxes. The shaded green bar indicates formation of the Panamanian isthmus. Node support values are Bayesian inference/maximum likelihood/neighbour-joining. Values < 70% are indicated by a hyphen. Canid images with permission from D.W. MacDonald and P. Barrett (1999). Mammals of Europe (London: Harper Collins); J.F. Eisenberg and K.H. Redford (1999). Mammals of the Neotropics, Volume 3 The Central Neotropics: Ecuador, Peru, Bolivia, Brazil (Chicago: Chicago University Press); and St. G. Mivart (1890). A Monograph of the Canidae: Dogs, Jackals, Wolves, and Foxes (London: Porter).

divergence between these taxa. Furthermore, based on our dating analyses and fossil evidence, we suggest that most South American canid lineages originated in North America [7,8]. At least six exclusively South American canid lineages, including the Falklands wolf, originated prior to the formation of a Panamanian land bridge approximately 3 mya (Figure 1). Canids are not recorded in the South American fossil record until the late Pliocene (Uquian, 2.5–1.5 mya [7]), while three South American canid lineages are recorded in the North American fossil record before this time (*Cerdocyon,* 6–5 mya; *Chrysocyon,* 5–4 mya; *Theriodictis,* 5–4 mya; [9]). The South American canids probably evolved from the fossil taxon *Eucyon,* which was widespread in North America during the late Miocene [9]. The ultimate extinction of South American canid lineages in North America may have resulted from resource competition with *Canis*, which immigrated to the New World during the late Pliocene [7,9].

Based on mtDNA sequence analysis, we estimated the age of the most recent common ancestor of our Falklands wolf samples to be 330 thousand years ago (kya) (Figure 1; 95% HPD = 70–640 kya). Genetic and archaeological evidence suggests that humans first arrived in the New World no earlier than 20–15 kya [10], implying that a human-mediated origin of the Falklands wolf is unlikely [3,9]. The Falklands wolf may have reached the islands by rafting or dispersing over glacial ice [3,9] during the late Pleistocene and was probably able to survive into the recent past by subsisting on a rich diet of penguins, geese and pinnipeds [1,4]. Unfortunately, by the time Darwin described the species, its exploitation for the fur trade was well underway. Forty years later, the Falklands wolf was extinct, ending a long evolutionary process of the kind central to the development of Darwin's theories.

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01695-9.

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