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Cytogenetics and fossil record: confluent evidence for speciation without chromosomal change in South American canids

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South American wild dogs and foxes are the most diversified canids of any other continent, including seven genera and 11 species distributed in a wide range of habitats of the Neotropics (BERTA 1987). However, this group is the least known of the Canidae in many aspects of its general biology. The South American fox, *Dusicyon* (HONACKI et al. 1982) or *Pseudalopex* (BERTA 1987), is the most polytypic genus encompassing five living species among which the chromosomes have only been reported for *D. vetulus* from Brazil (WURSTER and BENIRSCHKE 1968). In this note we describe the karyotypes of two other species of *Dusicyon*, the Patagonian red fox, *D. culpaeus*, and the Pampean gray fox, *D. gymnocercus*. Moreover, we discuss the trends in chromosomal evolution of South American Canidae in conjunction with available information on fossil records.

Cytogenetic analysis was performed in four *D. culpaeus* from the breeding stock of PIROS SA, Argentina (1 male and 1 female) and from the Zoo of Buenos Aires City (2 females), and in three *D. gymnocercus* (1 male and 2 females) maintained at the Zoo of Buenos Aires City. Chromosomes were obtained from blood culture. In brief, blood samples were aseptically taken with heparanized syringes from the cephalic vein of the foreleg. One ml of whole blood was cultured in Eagle Minimum Essential medium supplemented with 20 % fetal calf serum, 2× glutamine, antibiotics (penicillin-streptomycin), and phytohemagglutinin. After 68 h at 37°C, cultures were arrested with colchicine (1 µg/ml of culture) for 1.5 h. Colchicine-treated cultures were centrifuged at 1,000 rpm, resuspended in 0.075 M KCl for 15 min at 37°C, and then fixed in cold 3:1, methanol:acetic acid. Chromosome spreads were air-dried and stained with Giemsa.

Both *D. culpaeus* and *D. gymnocercus* showed a $2n = 74$ (NF = 76) karyotype, with an all-telocentric autosomal complement decreasing gradually in size, a large submetacentric X, and a small subtelocentric Y chromosome (see Figure). This karyotype is identical to that previously reported for the hoary fox, *D. vetulus* (WURSTER and BENIRSCHKE 1968).

The South American canids evolved along two different lines (LANGGUTH 1975): invading forest habitats and producing specialist forms such as *Atelocynus* and *Speothos*; or, colonizing the open plains as generalized species, e.g. of the genus *Dusicyon*. Both evolutionary lines have maintained the same $2n = 74-76$ all-telocentric karyotype (Table).

Cerdocyon thous and *Urocyon cinereoargenteus* are exceptions to the chromosomal homomorphism which characterizes the South American canids. *C. thous* also shows a $2n = 74$ karyotype, but 36 metacentric and submetacentric autosomes which increase the number of arms up to 110 (WURSTER-HILL 1973). The origin of this karyotype may be deduced by the accumulation of pericentric inversions in the all-telocentric karyotype. However, the required extent of such repatterning and the lack of known intermediate



Giemsa stained karyotype of the Patagonian red fox, *Dusicyon culpaues* ($2n = 74$, $FN = 76$). The same karyotype is also found in the Pampean gray fox, *D. gymnocercus*

states between the all-telocentric condition and *C. thous*-karyotype weaken this assumption. The karyotype of *U. cinereoargenteus* ($2n = 66$; $NF = 70$) departs from the all-telocentric one, and may be derived by means of tandem fusions which reduce the diploid number without altering the number of arms, plus one pericentric inversion giving rise to the only metacentric autosome which characterizes this karyotype. Nevertheless, *U. cinereoargenteus* is mainly distributed in North and Central America, reaching Colombia and Venezuela, and there are no fossil records in South America. This species probably represents a North American canid which reached the north of South America (BERTA 1987).

Available chromosomal data in living species of South American Canidae

Species	$2n$	NF	Reference
<i>Atelocynus microtis</i>	74/76	76	WURSTER and BENIRSCHKE (1968)
<i>Cerdocyon thous</i>	74	110	WURSTER-HILL (1973)
<i>Chrysocyon brachiurus</i>	76	78	NEWHAM and DAVIDSON (1966)
<i>Dusicyon culpaues</i>	74	76	This study
<i>D. griseus</i>	?	?	
<i>D. gymnocercus</i>	74	76	This study
<i>D. sechurae</i>	?	?	
<i>D. vetulus</i>	74	76	WURSTER and BENIRSCHKE (1968)
<i>Speothos venaticus</i>	74	76	WURSTER and BENIRSCHKE (1968)
<i>Urocyon cinereoargenteus</i>	66	70	WURSTER and BENIRSCHKE (1968)

Fossil records indicate that the open plains of North America seem to have been the center of evolution of canids that later dispersed to South America (BERTA 1987). A species or group of generalized canids entered South America after the emergence of the Panamanian Land Bridge during the late Pliocene and early Pleistocene, and spread over the grasslands along the Andes reaching the southern pampas, the Patagonian grasslands, and the Brazilian highlands (BERTA 1987; LANGGUTH 1975). It is of interest to note that discrepancies in karyotype homomorphism mentioned above, are found in those genera for which earlier North American fossils are recorded – *Cerdocyon* and *Urocyon* – (BERTA 1987). The

remaining canid species that radiated in South America – *Atelocynus*, *Dusicyon* and *Speothos* – display a high chromosomal conservatism. In addition, the all-telocentric karyotype of 74 chromosomes is also found in *Chrysocyon*, a form early recorded for North America and now restricted to a South American distribution.

Chromosomal information, in conjunction with fossil records seems to indicate that:

1. the species recorded early in North America which later attained South America, show a low karyological affinity with the other South American canids and are more closely related to the North American ones; this is the case for *C. thous* and *U. cinereoargenteus*,
2. the $2n = 74$ all-telocentric karyotype is most likely the primitive condition for South American Canidae, retained without change during diversification which resulted mainly from an opportunistic feeding strategy (BERTA 1987), and
3. a North American origin may be suspected for this primitive karyotype which is also found in the early North American recorded genus *Chrysocyon*.

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