CHAPTER 17

Molecular and Biochemical Evolution of the Carnivora

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The fissiped carnivores include eight distinct families that are traditionally grouped into two superfamilies: the Canoidea (or Arctoidea) and the Feloidea (or Aeluroidea). The Canoidea include the bear, dog, raccoon, and weasel families; and the Feloidea include the cat, hyena, mongoose, and civet families. Both groups are extremely heterogeneous with respect to the morphology and life history of their constituents. They include taxa that are entirely carnivorous, insectivorous, and omnivorous and that have cursorial, arboreal, fossorial, and aquatic habits. Such wide-ranging adaptations have led to several instances of parallel and convergent evolution of morphologic traits which have confounded the efforts of taxonomists to relate certain taxa.

Over the last few years a variety of molecular techniques has been applied to determine the evolutionary relationships within and among several carnivore families (Sarich 1969a, 1969b, 1973; Collier and O'Brien 1985; O'Brien et al. 1985, 1987; Goldman et al. 1987; Wayne and O'Brien 1987; Wayne et al. 1987a, 1987b). In this chapter we review the relationships of three carnivore families derived from these studies: the Canidae (dogs), the Ursidae (bears), and the Felidae (cats). We also present a phenogram of the Carnivora, including carnivore species from each of the eight families plus species from two pinniped families, the Otariidae (sea lions) and the Phocidae (earless seals).

The trees we present were derived from evolutionary distance estimates obtained from several molecular techniques, including (1) DNA hybridization, (2) protein electrophoresis, (3) measurement of albumin immunological distance (AID), and (4) high-resolution G-banding of karyotypes. Evolutionary trees were constructed using published phenetic algorithms designed to analyze distance matrices (Fitch and Margoliash 1967; Sneath and Sokal 1973; Dayhoff 1976; Fitch 1981). In this chapter we present the deduced phylogenies, an assessment of the various aspects of confidence and ambiguity for each topology, and an interpretive review of the implications of the molecular results in the context of morphologic and fossil data.

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Molecular Procedures

In 1962 Zuckerkandl and Pauling suggested that mutations in genomic DNA accumulated in a stochastic but steady fashion that was roughly related to elapsed time. The genetic difference between individuals from different species would therefore be proportional to the amount of time that had passed since they last shared a common ancestor. By assuming that the "molecular clock hypothesis" is valid (Wilson et al. 1977; Nei 1978; Thorpe 1982), one can relate phenetic trees derived from molecular data to absolute time by calibration with a fossil date. For instance, the time of separation of Old and New World primates is approximately 30–50 millions years before present (M.Y.B.P.) (Radinsky 1978); thus, an absolute time scale can be placed on trees of the primate order based on this date, and the rate of molecular evolution can be calculated and used in trees of other groups. However, it is generally preferable to use a calibration date based on species from the group of interest since the rate of gene evolution of different taxonomic groups may vary (Benveniste et al. 1977; Brownell 1983; Britten 1986). The reader is referred to Wilson et al. (1977) and Thorpe (1982) for a technical discussion of the molecular clock hypothesis and to Gribbin and Cherfas (1982) for an excellent description of the contributions of molecular techniques to our understanding of human evolution.

One karyological and three molecular procedures have been utilized in the study of carnivores. We would encourage the use of several procedures because confirmation of evolutionary relationships with multiple, independent methods tends to reveal incorrect deductions and thereby minimizes error in phylogenetic inference (Gribbin and Cherfas 1982; O'Brien et al. 1985; Ayala 1986). For example, all of the methods described here were used to assess the relationships of the giant panda, and a consistent phylogeny was derived (O'Brien et al. 1985).

The first procedure we employ is DNA hybridization (Kohne et al. 1972; Benveniste 1976, 1985). This method involves the hybridization of radioactively labeled cellular DNA of one species to the cellular DNA of other species and measures the stability of DNA hybrids that are formed. Two measurements can be derived from these experiments: first, the percentage of hybridization between species A and B; and second, the difference between a melting profile of heterologous DNA hybrids and that of homologous DNAs. The latter measurement, termed ΔTm, is directly proportional to the extent of base pair mismatching. The ΔTm (or ΔTmR, which is ΔTm corrected for the normalized final percentage of hybridization) values are compiled in a table that is used to construct phenetic trees. DNA hybridization data are particularly powerful for species that diverged 10–60 M.Y.B.P. but less sensitive for comparisons of recently diverged taxa (Sibley and Ahlquist 1983; Benveniste 1985).

The second method involves the estimation of genetic distance (D) (Nei