PANDA 2000: CONSERVATION PRIORITIES FOR THE NEW MILLENNIUM

Proceedings of an International Conference
San Diego, California
October 15-18, 2000

Edited by
DONALD LINDBURG
And
KAREN BARAGONA

THE SHAPE OF ENRICHMENT, INC.
San Diego, California

The Phylogenetic Position of the Giant Panda *(Ailuropoda melanoleuca)*: A Historical Consensus Through Supertree Analysis

Olaf R. P. Bininda-Emonds

Lehrstuhl für Tierzucht, Technical University of Munich, Germany

Introduction

Perhaps no question in mammalian systematics has engendered such long-term controversy and uncertainty as the phylogenetic placement of the giant panda, *Ailuropoda melanoleuca*. Although its formal introduction to western science placed it as a member of the bear family (Ursidae) (David 1869), similarities to the lesser or red panda, *Ailurus fulgens*, and, by extension, raccoons and allies (Procyonidae) were quickly noted (Milne Edwards 1870). Since that time, a variety of evidence has been used to ally *Ailuropoda* with ursids, procyonids, or *Ailurus* (either within the previous two families or as the separate family Ailuridae), or to place it in a family by itself (Ailuropodidae). Fueled largely by molecular evidence, there is perhaps finally a growing consensus that *Ailuropoda* represents the sister group to the remaining ursids.

In this paper, I approach the question of panda phylogeny from a historical perspective to examine trends in the placement of *Ailuropoda* through time. My work follows on from that of O'Brien et al. (1991), although it differs in two key respects. First, I employ a phylogenetic rather than a taxonomic perspective. The taxonomic status of any species is highly subjective (e.g., is *Ailuropoda* "sufficiently distinct" to justify being placed in its own family?), whereas a study of its phylogenetic or sister-group relationships is much more objective and concrete. Second, through the use of supertree construction (sensu Sanderson et al. 1998), I am able to infer the consensus estimate of the affinity of *Ailuropoda* for any given time period. Thus, I can demonstrate how consensus opinion has shifted over time and by how much. This resembles work done previously with *Ailurus* and the pinnipeds (Bininda-Emonds 2000a). Because *Ailurus* has played a critical historical role in the controversy surrounding the origin of *Ailuropoda*, I also perform similar analyses for it here.

The Problem—Issues of Evidence and Convergence

The uncertainty surrounding the placement of *Ailuropoda* derives from the numerous similarities that it shows to each of ursids, procyonids, and especially to *Ailurus*. In fact, were it not for the existence of the procyonid-like *Ailurus*, the acceptance of *Ailuropoda* as an ursid would likely be considerably less, if at all, in dispute. The key lines of evidence used to infer the ancestry of *Ailuropoda* historically are given in Table 1. The majority of evidence, both morphological and molecular, allies *Ailuropoda* with ursids. Fossil evidence, particularly the inferred close relationship with the Pliocene fossil ursid *Hyaenarctos* (now included in *Agriotherium*, a member of the extinct sister group to ursids; McKenna & Bell 1997), also unanimously indicates an ursid origin.

In one of the most thorough and impressive comparative morphological investigations for any species, Davis (1964: 322) declared that "every morphological feature examined indicates that the giant panda is nothing more than a highly specialized bear." However, a few morphological features have been used to argue against such a relationship, even if they do not indicate a relationship with either procyonids or *Ailurus* ("negative evidence"; see below and Table 1). These include the greater than expected robustness of the skull, skeleton, and dentition of *Ailuropoda* for an animal of its size (Morris and Morris 1981).

Virtually all molecular evidence points to an ursid affinity for *Ailuropoda*. Only the karyotype is equivocal. In its diploid number, *Ailuropoda* (2N = 42) resembles procyonids (e.g., 2N = 42 for *Procyon lotor*) and *Ailurus* (2N = 44) more so than ursine bears (2N = 74). Although this observation is correctly attributed to Newnham & Davidson (1966), the attendant implication of procyonid ancestry is not. Newnham & Davidson (1966:161) explicitly pointed out that large differences in karyotypes and diploid

Table 1. Shared features between *Ailuropoda* and Ursids, Procyonids, and *Ailurus*.

Feature of *Ailuropoda*	**Ursidae**	**Procyonidae**	***Ailurus***
Morphology			
size and gross morphology	+		
skull robustness	–		
brain morphology	+		
auditory region and ossicles	+		
epipharyngeal bursa		+	
ridges on hard palate	+		
dentition (especially massive size)	–		+
skeletal robustness	–	+	
specialized sesamoid on forepaw			? (unique)
respiratory tract	+		
intestines (shorter and less complex)	–		
external (soft) morphology	? (unique)		
genitalia			+
coloration		+	+
hair structure	+		
Molecular			
karyotype	+	+	+
serology / immunology	+		
sequence data	+		
Behavioral			
vocalizations	–	+	+
life history traits	+		?
scent marking (and glands)	–		+
feeding behavior			+
mating behavior			+
Other			
fossil affinities	+		

A plus sign indicates that the feature is similar between the two taxa. A minus sign indicates that the feature has been used to argue against a relationship between the two taxa, even if *Ailuropoda* does not share the feature with another taxon.

numbers occur within families such as Canidae (dogs) and that the evidence merely indicates *Ailuropoda* to be a different species from ursine bears. They added that the number of chromosomal arms ("nombre fondemental") might be a more informative measure in this regard. Along these latter lines, O'Brien et al. (1985) discovered that although *Ailuropoda* possesses a procyonid-like diploid number, the banding patterns of its chromosomes are virtually identical to those of ursine bears. Together with other molecular evidence, they persuasively argued that *Ailuropoda* is related to ursids and that its reduced diploid number is a result of extensive chromosomal fusion in the past (also Nash et al. 1998). It is noteworthy that similar, albeit independent, fusions have been inferred to explain the karyotype of the spectacled bear, *Tremarctos ornatus* (2N = 52; Nash & O'Brien 1987; Nash et al. 1998).

Finally, behavioral characteristics strongly group the two panda species together. Only life history traits are similar between *Ailuropoda* and ursids. Otherwise, *Ailuropoda* resembles *Ailurus* in its unusual scent marking behavior, and in its mating and feeding behaviors. The latter is the most remarkable, with both pandas being renowned for the ability to precisely manipulate their herbivorous food items, although only *Ailuropoda* possesses an enlarged sesamoid that acts as an analog of an opposable thumb.

Researchers have sought to make sense of the conflicting signals within the phenotypic evidence (i.e., morphological and behavioral data) through one of two evolutionary scenarios. The first holds that *Ailuropoda* is an ursid that has shifted to an almost exclusively herbivorous diet (the so-called "bear school"). This scenario accounts for such features as the more robust dentition as being obvious (convergent) adaptations for herbivory. The second holds that *Ailuropoda* is instead derived from a small herbivore, typically with procyonid affinities, that has converged secondarily on a larger bear-like body plan (the "raccoon school"). The greater-than-expected robustness of the skull and skeleton has been used as evidence of rapid growth in the lineage leading to *Ailuropoda* (Morris & Morris 1981). The raccoon school in particular has relied on the "negative evidence" found in Table 1 in combination with behavioral information.

Proponents of the raccoon school concede that the majority of evidence places *Ailuropoda* with ursids (e.g., Ewer 1973; Morris & Morris 1981). In supporting a non-ursid origin, they instead argue that the fewer features that cluster *Ailuropoda* with either procyonids or *Ailurus* represent evolutionary novelties that are more difficult to envisage evolving on multiple occasions (Ewer 1973; Morris & Morris 1981). Similar reasons have been used to cluster megachiropteran bats with primates on the basis of a shared optic network and other neural features in spite of an overwhelming number of similarities, mostly related to flying, with microchiropteran bats (Pettigrew 1986, 1991). An extension of this general argument is that organisms with a similar body plan are more likely to develop convergently evolved features given similar selective regimes. This argument was used to explain why the two main groups of pinnipeds (true seals versus sea lions and walruses) were so similar morphologically, despite formerly being believed to have separate ancestors (McLaren 1960; Mitchell 1967; Repenning 1990). This conclusion is now held to be false (Wyss 1987; Vrana et al. 1994; Bininda-Emonds et al. 1999). With respect to *Ailuropoda*, the full argument is that its overall similarity with ursids applies only to features that are phenotypically plastic or that are expected to show a greater degree of convergence in response to similar selection pressures, possibly due to the inheritance of a common, primitive, arctoid body plan (Ewer 1973; Morris & Morris 1981).

The issue is not easily resolved. Molecular evidence has played a valuable role because convergence at this level is unlikely to mirror that at the morphological level. However, problems remain within a purely morphological domain. Character weighting continues to be a controversial area in phylogenetic systematics, with no clear guidelines. Presumably, the use of as much evidence as possible, both morphological and molecular ("total evidence", sensu Kluge 1989), is the key to resolving this issue. It is widely held that the best phylogenetic inference is the one supported by the most independent lines of evidence (Mickevich 1978; Farris 1983; Penny & Hendy 1986; Kluge 1989; Novacek 1992; de Jong 1998). So long as homoplasy, of which convergence is one form, remains relatively rare and randomly distributed both among features and the relationships it infers (see Sanderson & Hufford 1996), the true phylogenetic history will be reflected in the majority of features. Thus, surveying as many features as possible in a cladistic framework (to distinguish shared primitive and shared derived features; Hennig 1966) should be sufficient to overrule any instances of convergence, however improbable they might seem.

Methods

To examine the affinities of both panda species through time, I surveyed the systematic literature from the description of *Ailuropoda* by David (1869) to the present. In total, 105 studies presented evidence on the position of either *Ailuropoda* or *Ailurus*; this list is not exhaustive. A breakdown of the studies according to data source and whether they provided phylogenetic information about *Ailuropoda*, *Ailurus*, or both is provided in Tables 2 and 3.

The Data

Information from the literature was analyzed in one of two ways. These methods differ with respect to whether panda relationships were examined in isolation or not. The first method assessed simple statements of phylogenetic affinity of the form "*Ailuropoda* is most closely related to …". To summarize this information quantitatively, I derived a simple "affinity metric". Statements advocating an ursid origin were scored arbitrarily as 1, those advocating a procyonid origin as –1. If ursids or procyonids formed the sister group, but not the immediate sister group to either panda species (an "extended" relationship), scores of 0.5 and –0.5 were given, respectively. When neither ursids nor procyonids could be said to be more closely related than the other, a score of 0 was given, regardless of the identity of the inferred sister group. This includes when the pandas were held to be each other's closest relatives. For any set of studies, the average value of the metric varies between –1 and 1, with more positive values indicating increasing ursid affinity and more negative values indicating increasing procyonid affinity. Values tending to zero indicate a relationship to neither group, whether due to conflicting opinions and/or due to an inferred relationship to another carnivore taxon.

The second method used the supertree construction method of matrix representation with parsimony analysis (MRP; Baum 1992; Ragan 1992) to maintain the context of all other carnivore taxa men-

Table 2. Survey of the systematic literature since 1869 bearing on the phylogenetic placement of *Ailuropoda* and *Ailurus*.

Study	**Sister group** of *Ailuropoda*	**Sister group** of *Ailurus*	**Data** source	**Evidence**
David (1869)	Ursidae		(1)	morphology
Milne Edwards (1870)*	Procyonidae	Procyonidae	(1)	osteological characters and dentition similar to lesser panda
Gervais (1870)	Ursidae	Procyonidae	(1)	intracranial cast; skeletal morphology
Mivart (1885)*	Procyonidae	Procyonidae	(1)	overall morphology, but primarily skull architecture and dental morphology
Flower & Lydekker (1891)*	Ursidae	Procyonidae	(1)	review of mammals; similarity to fossil ursid, *Hyaenarctos*
Winge (1895; 1941)*	Ursidae	Procyonidae	(1)	skeletal morphology; similarity to fossil ursid, *Hyaenarctos*; dentition
Trouessart (1898; 1904)*	*Ailurus* (Ursidae)	*Ailuropoda* (Ursidae)	(1)	taxonomy of mammals
Schlosser (1899)*	Ursidae		(1)	similarity to fossil ursid, *Hyaenarctos*; dentition
Lankester (1901)*	Procyonidae	Procyonidae	(1)	skull, limb, and dental morphology
Lydekker (1901)	Procyonidae	Procyonidae	(1)	skull, limb, and dental morphology
Beddard (1902)*	Ursidae	Procyonidae	(1)	review of mammals
Kidd (1904)*	Felidae		(1)	arrangement of hair on nasal region
Weber (1904)	Ursidae	Procyonidae	(1)	similarity to fossil ursid, *Hyaenarctos*
Bardenfleth (1914)	Ursidae	Procyonidae	(1)	dental and osteological morphology
Pocock (1921)	Ailuropodidae	Ailuridae	(1)	external morphology (primarily feet, ears, rhinaria, and genetalia)
Matthew & Granger (1923)	Ursidae		(1)	morphology; similarity to fossil ursid, *Hyaenarctos*
Pocock (1928)	Ailuropodidae	Ailuridae	(1)	soft external features of head and foot
Weber (1928)*	Ursidae	Procyonidae	(1)	overall morphology; fossil affinities
Matthew (1929)	Ursidae		(1)	morphological review of ursids
de Carle Sowerby (1932)*	*Ailurus*	*Ailuropoda*	(1)	gross cranial morphology; dentition; coloration
Boule & Piveteau (1935)*	Ursidae	Procyonidae	(1)	dental and basicranial morphology; fossil affinities
Gregory (1936)*	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(1)	skull and dental morphology
Raven (1936)*	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(1)	visceral and vascular anatomy
Segall (1943)*	*Ailurus*	*Ailuropoda*	(1)	morphology of auditory region and ossicles
Kretzoi (1945)*	Ailuropdidae	Ailuridae	(1)	dentition; fossil affinites
Simpson (1945)	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(1)	review of mammals
Mettler & Goss (1946)	Ursidae		(1)	gross external brain morphology
Erdbrink (1953)	Ursidae		(1)	dentition
Colbert (1955)*	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(1)	review of vertebrates

Table 2. Continued.

Leone & Wiens (1956)*	Ursidae		(2)	precipitin test; serum proteins
Piveteau (1961)*	Procyonidae	Procyonidae	(1)	dental morphology; affinity with fossil taxa
Davis (1964)	Ursidae	unresolved	(1)	comparative anatomy
Walker (1964)	Procyonidae	Procyonidae	(1)	review of mammals
Wurster & Benirschke (1968), and Wurster (1969)*	Ursidae	Procyonidae	(2)	karyology
Kretzoi (1971)	Ailuropodidae	Ailuridae	(1)	dentition
Hendey (1972; 1980)	Ursidae		(1)	morphology (primarily of dentition); fossil relationships
Sarich (1973; 1975; 1976)*	Ursidae	Ursidae	(2)	immunological distance
Ewer (1973)*	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(1)	review of carnivores
Cave (1974)*	Procyonidae		(1)	morphology of epipharyngeal bursa
Chu (1974)*	Ailuropodidae	Procyonidae	(1)	morphology; dentition; ethology; neonatal allometry
Pei (1974)	Ursidae		(1)	fossil evidence; dentition
Wang (1974)	Ursidae		(1)	fossil evidence; cranial and dental morphology
Bugge (1978)*		Procyonidae	(1)	morphology of cephalic arterial system
Starck (1978)*	Ursidae	unresolved	(1)	morphology, paleontology, and geography
de Ridder (1979)*	Ursidae	Procyonidae	(3)	review of all available evidence
Thenius (1979)*	Ursidae	Procyonidae	(3)	review of paleontological, morphological, serological, karyological, and ethological characters
Wurster-Hill & Bush (1980)*	Procyonidae (extended)	Procyonidae (extended)	(2)	banded karyology
Eisenberg (1981)	uncertain	uncertain	(3)	review of mammals
Morris & Morris (1981)*	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(3)	summary of available data (morphological, molecular, and ethological).
Pan et al. (1981)*	Ursidae		(2)	serology
Schmidt-Kittler (1981)*		Procyonidae	(1)	morphology of dentition and skull; fossil evidence
Ginsburg (1982)*	Ursidae	Ursidae	(1)	skull and dental morphology
Honacki et al. (1982)	Ursidae	Procyonidae	(3)	review of mammals
Peters (1982)*	Procyonidae	Procyonidae	(1)	vocalization structure
Nowak & Paradiso (1983)	Ursidae	Procyonidae	(3)	review of mammals
Wozencraft (1984)*		Ursidae	(1)	morphology
Braunitzer et al. (1985)	Ursidae		(2)	globin sequence
Couturier & Dutrillaux (1985)*		Procyonidae	(2)	karyology
Eisentraut (1985)*	Ursidae	Procyonidae	(1)	ridges on hard palate
Feng et al. (1985; 1991)*	*Ailurus*	*Ailuropoda*	(2)	protein electrophoresis

Table 2. Continued.

O'Brien et al. (1985)*	Ursidae	Procyonidae	(2)	DNA hybridization; isozyme genetic distance; immunological distance; karyological evidence
Pirlot & Jiao (1985)*	Procyonidae		(1)	relative brain size; external brain morphology
Schaller (1985)	Ursidae (extended)	Ursidae (extended)	(3)	review of fossil, morphological, and molecular data
Romer & Parsons (1986)*	Ursidae	Procyonidae	(1)	review of vertebrates
Tagle et al. (1986)*	Procyonidae (extended)	Procyonidae (extended)	(2)	globin sequence
Braunitzer & Hofmann (1987)*	*Ailurus* (Procyonidae)	*Ailuropoda* (Procyonidae)	(2)	globin sequence
Hofmann & Braunitzer (1987)*	Ursidae	Ursidae	(2)	globin sequence
Liang & Zhang (1987)*	Ailuropodidae		(2)	amino acid composition of LDH-M4 isozymes
Ramsay & Dunsbrack (1987)*	Ursidae		(1)	life history traits
Flynn et al. (1988)*	Ursidae	uncertain	(3)	review of carnivores
Kamiya & Pirlot (1988)*	Ursidae	unresolved	(1)	brain size and morphology
Goldman et al. (1989)*	Ursidae	Procyonidae	(2)	protein electrophoresis
Qiu & Qi (1989)*	Ursidae	Procyonidae	(1)	dental morphology of new fossil discovery
Wang et al. (1989)*	Ursidae		(2)	immunology
Wayne et al. (1989)*	Ursidae	Procyonidae	(2)	DNA hybridization
Wozencraft (1989)*	Ursidae	Ursidae	(1)	overall morphology
Czelusniak et al. (1990)*	Ursidae	Ursidae	(2)	globin sequences
Taylor (1990)*	*Ailurus* (Ursidae)	*Ailuropoda* (Ursidae)	(3)	review of fossil, morphological, and molecular data
Czelusniak et al. (1991)*	Ursidae	Ursidae	(2)	globin sequences
Dziurdzik & Nowogrodzka-Zagórska (1991)*	Ursidae	Procyonidae	(1)	histological structure of hairs
Nowak (1991)	Ursidae	Procyonidae	(3)	review of mammals
Zhang & Shi (1991)*	*Ailurus* (Ursidae)	*Ailuropoda* (Ursidae)	(2)	mtDNA restriction site analysis
Baryshnikov & Averianov (1992)*		Procyonidae	(1)	morphology of deciduous dentition
Hashimoto et al. (1993)*	Ursidae	Ursidae	(2)	globin sequence
Wolsan (1993)*		Procyonidae (extended)	(1)	skull and dental morphology
Wozencraft (1993)*	*Ailurus* (Ursidae)	*Ailuropoda* (Ursidae)	(3)	review of carnivores
Wyss & Flynn (1993)*		Ursidae (extended)	(1)	morphology
Zhang & Ryder (1993)*	Ursidae	unresolved	(2)	mtDNA sequence analysis
Vrana et al. (1994)*	Ursidae	Ursidae (extended)	(3)	total evidence of mtDNA and morphology
Zhang & Ryder (1994)*	Ursidae	Procyonidae	(2)	mtDNA sequence analysis
Lento et al. (1995)*		unresolved	(2)	spectral analysis of mtDNA sequence data

Table 2. Continued.

Pecon Slattery & O'Brien (1995)*	Ursidae	Procyonidae	(2)	mtDNA; protein electrophoresis
Ledje & Arnason (1996a)*	Ursidae	unresolved	(2)	cytochrome b sequence analysis
Ledje & Arnason (1996b)*	Ursidae	unresolved	(2)	12S rDNA sequence analysis
Talbot & Shields (1996)*	Ursidae		(2)	mtDNA sequence analysis
Lin et al. (1997)	Ursidae		(2)	RAPD DNA hybridization
Wang (1997)*		Procyonidae	(1)	skull and dental morphology
Flynn & Nedbal (1998)*	Ursidae	Procyonidae (extended)	(3)	total evidence of morphology and DNA sequences
Lan & Wang (1998)*	Ursidae	Procyonidae	(2)	RFLP analysis of rDNA
Schreiber et al. (1998)*		Ailuridae	(2)	comparative determinant analysis (immunology)
Waits et al. (1999)	Ursidae		(2)	mtDNA sequence analysis

A statement such as "*Ailurus* (Ursidae)" means that *Ailurus* was held to be the sister taxon to *Ailuropoda* with ursids forming a sister group to both. The term "extended" means that the group listed was the closest sister group between ursids and procyonids to the panda species; however, the panda species had an even closer sister group relationship with some other carnivore taxon. For data source, (1) = morphological, (2) = molecular, and (3) = both together ("total evidence"). Studies marked with an asterisk provided source trees for the supertree analyses.

Table 3. Number of studies providing statements of phylogenetic affinity for *Ailuropoda* and *Ailurus*, or providing source trees for the supertree analysis.

	Phylogenetic affinity	**Supertree analysis**
Ailuropoda	90	71
Ailurus	79	76
Either panda species	105	80
Both panda species	72	64
Total	105	116

Thirty-six additional source trees that do not mention either *Ailuropoda* or *Ailurus* were included in the supertree analysis give a better estimate of the family level relationships within Carnivora. These source trees were obtained from Gregory & Hellman (1939), Sarich (1969a; 1969b), Seal et al. (1970), Hunt (1974), Radinsky (1975), Tedford (1976), Arnason (1977), Hendey (1978), Ling (1978), Schmidt-Kittler (1981), Dutrillaux et al. (1982), Flynn & Galiano (1982), Goodman et al. (1982), de Jong (1986), Wyss (1987), Holmes (1988), Rodewald et al. (1988), Ahmed et al. (1990), Nojima (1990), McKenna (1991), Janczewski et al. (1992), Arnason & Ledje (1993), Garland et al. (1993), Hunt & Tedford (1993), Veron & Catzeflis (1993), Berta & Wyss (1994), Hunt & Barnes (1994), Masuda & Yoshida (1994), Slade et al. (1994), Arnason et al. (1995), Austin (1996), Bininda-Emonds & Russell (1996), Werdelin (1996), and Ortolani (1999).

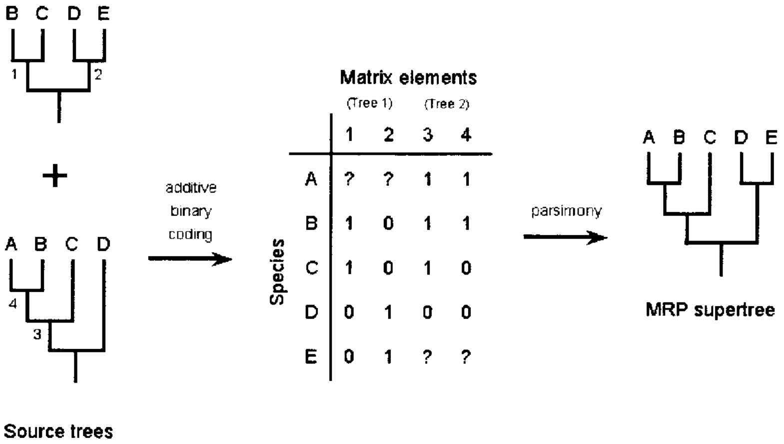

Figure 1. The basic procedure of supertree construction using matrix representation with parsimony (MRP). See text for details.

tioned in the source study. In this way, a consensus of carnivore phylogeny at any given time could be obtained, something that is possible only through supertree analysis. Combination of the primary data ("total evidence"; sensu Kluge 1989) requires that these data be available and compatible. For many studies, particularly the older ones, the primary data were either not provided or were given simply in the form of a statement of phylogenetic affinity. Data types were also incompatible, meaning that they could not be analyzed simultaneously using a common algorithm. Combination of the source tree topologies using various consensus techniques ("taxonomic congruence; sensu Mickevich 1978) was also impossible due to the requirement that all source trees possess the same set of species.

In contrast, MRP can combine phylogenetic information from any study, be it in the form of a tree or a simple statement, by coding it as a series of binary elements. These elements are then combined into a single matrix that is analyzed using parsimony to derive a tree that best summarizes the hierarchical information in the set of source trees. Briefly, each node from every source tree is coded in turn as follows: if a given species is descended from that node, it is scored as 1; if it is not, it is scored as 0. Species that are not present in a particular study, but are present in others, are scored as ? for that particular study (Fig. 1; Sanderson et al. 1998; Bininda-Emonds 2000b). In this way, supertree construction can combine studies examining different sets of species. Simulation studies show that MRP is as accurate as total evidence in cases where both methods can be applied (Bininda-Emonds & Sanderson 2001).

Matrix representations for all source trees were constructed by eye. Supertree analysis used PAUP* v.4.0b2 (Swofford 1999). Searches always used the exact branch-and-bound algorithm, thereby guaranteeing that all of the most parsimonious solutions for the data were found. The supertree was the strict consensus of all equally most parsimonious solutions. Differential support for the relationships within a supertree was quantified using the Bremer decay index (Bremer 1988; Källersjö et al. 1992) because the bootstrap is inappropriate due to character non-independence (Purvis 1995). The Bremer decay index measures the number of additional steps over the most optimal length before a node of interest is contradicted. Nodes that remain in the strict consensus solution of increasingly suboptimal trees are not readily contradicted and therefore inferred to have more support.

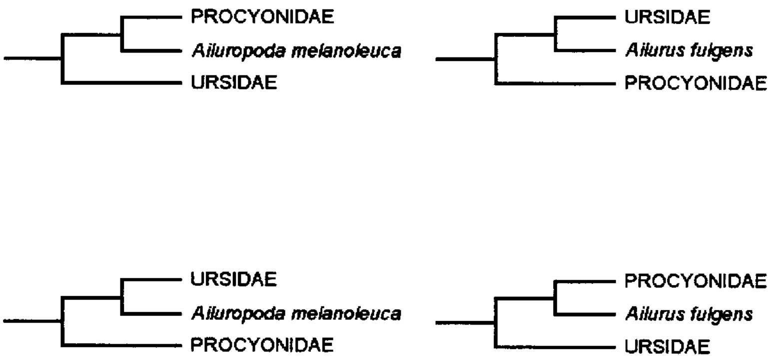

Figure 2. Backbone constraint trees used for the supertree analyses in PAUP*, forcing *Ailuropoda* or *Ailurus* into a sister group relationship with either ursids or procyonids.

Sliding Window Analysis

To view changes in phylogenetic opinion over time, I employed a sliding window approach to time series analysis. Specifically, the data sources were arranged in ascending chronological order and secondarily by author name in ascending alphabetical order. Contiguous, overlapping sets of data sources (e.g., sources 1–10, 2–11, 3–12, and so on) were then analyzed.

For statements of phylogenetic affinity, I calculated the average value of the affinity metric for windows that were either five or ten studies in size.

Table 4. Summary of statements of phylogenetic affinity for *Ailuropoda* and *Ailurus*.

Sister group	**Number of studies for:**	
	Ailuropoda	*Ailurus*
Ursidae	57	12
Other panda species within Ursidae	4	4
Total	61	16
Procyonidae	11	41
Other panda species within Procyonidae	7	7
Total	18	48
Other panda species	3	3
Other panda species within Ursidae or Procyonidae	11	11
Total	14	14
Unresolved or other	8	4

The overall consensus opinion at any given point in time was also obtained from the cumulative average of the affinity metric for all studies thus far added. For the supertree analyses, the window size was 15 studies. I used the affinity metric to summarize the placement of both *Ailuropoda* and *Ailurus* in the supertree of each window. I also examined the support for these inferred placements by using backbone constraint trees (see Swofford 1999) to force PAUP* to search only for solutions in which each panda species was more closely related to ursids than to procyonids and vice versa (Fig. 2).

Support for these alternative placements was quantified by how much less parsimonious they were than the optimal length for that window. Unlike the Bremer decay index, higher values in this case indicate decreasing support for the constrained placement.

Results

Types of Evidence

Unsurprisingly, morphological evidence dominates until the late 1970s (Table 2). Thereafter, molecular data come to bear increasingly on the question of panda relationships, either alone or in concert with morphological evidence (= "total evidence"). From the late 1980s, the phylogenetic placement of either *Ailuropoda* or *Ailurus* has been examined using molecular data almost exclusively. Behavioral information has only been used sporadically throughout the survey period.

Statements of Phylogenetic Affinity

Taken together, all statements of phylogenetic affinity strongly place *Ailuropoda* and *Ailurus* within separate carnivore families (Table 4). Roughly two-thirds of the 90 studies mentioning *Ailuropoda* cluster it with ursids, while a slightly lesser fraction of the 79 studies for *Ailurus* place it with procyonids. The two panda species were held to be each other's closest relative only 14 times, and usually within either Ursidae or Procyonidae. These observations are captured by the affinity metric. Over all studies, *Ailuropoda* possesses a value of 0.48, while *Ailurus* shows a value of –0.41.

The sliding window analysis demonstrates that these overall opinions are largely reflected in any time window since 1869 (Fig. 3). The trends are roughly identical for windows of either five or ten studies in size, although the former unsurprisingly displayed slightly greater fluctuations. Except for two occasions, *Ailuropoda* is always inferred to be more closely related to ursids on average. This is especially true from the late 1980s onwards, when all windows unequivocally indicate *Ailuropoda* to be a member of the Ursidae. Procyonid or uncertain affinities for *Ailuropoda* are only obtained sporadically across a relatively broad period from the 1940s to the mid-1970s, and a single instance around the mid-1980s. *Ailurus* is usually firmly held to have procyonid affinities, although the windows tend towards 0 (i.e., unresolved or "other" affinities) with time. In the 1990s, many windows indicate *Ailurus* to have ursid affinities. However, the most recent windows again cluster *Ailurus* more closely with procyonids.

These same trends are also evident when statements of phylogenetic affinity are viewed cumulatively (Fig. 4). Even during an initial period of uncertainty (marked by large fluctuations), the weight of all opinion up to a given time almost always has *Ailuropoda* more closely related to ursids than

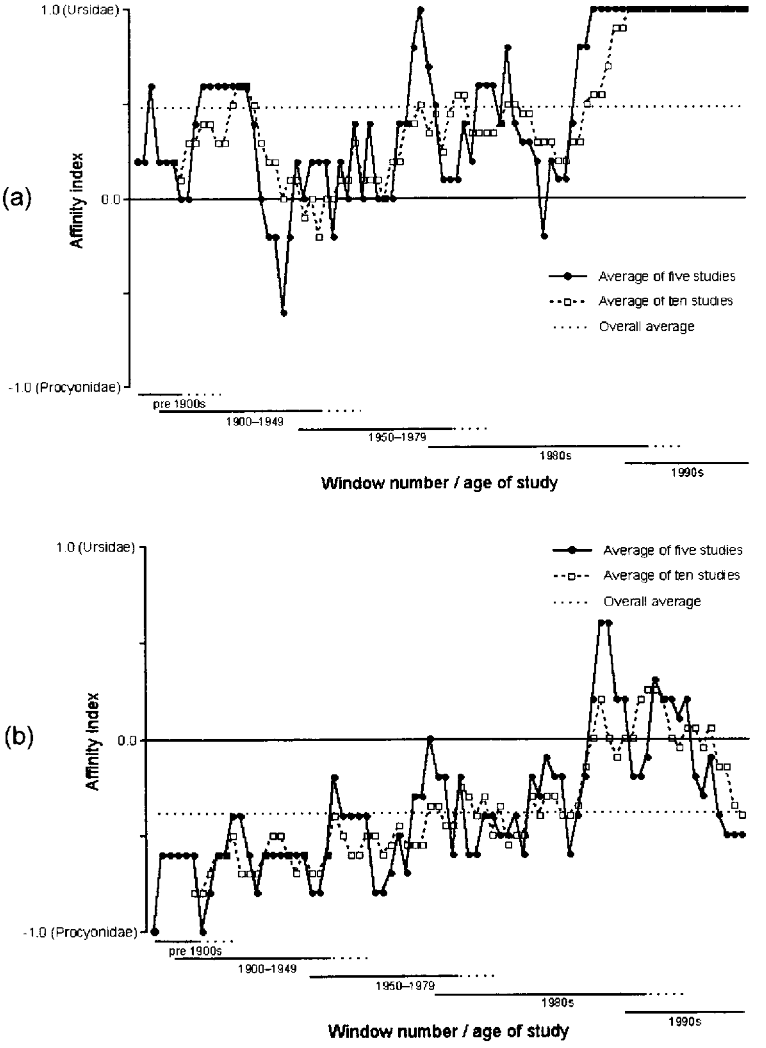

Figure 3. Sliding window analysis of statements of phylogenetic affinity for *Ailuropoda* (a) and *Ailurus* (b) using the affinity metric discussed in the text. Approximate time spans of the windows are given on the x-axis. The dotted extensions apply to windows of 10 studies only. The overall averages for all studies were 0.48 for *Ailuropoda* and –0.41 for *Ailurus*.

procyonids. Moreover, this opinion is generally strengthening with time, particularly from the mid-1980s, as the line moves to more positive values. In contrast, *Ailurus* is always held as being more closely related to procyonids. Again, this placement is becoming slightly more uncertain with time as the line tends towards less negative values.

Supertree Analysis

The sliding window analysis of consensus supertrees, where the positions of the panda species were put into the context of higher level carnivore relationships, largely identified the same trends as above (Fig. 5). The only area of disagreement exists before 1950. During this period, both panda species show identical placements, either 1) not distinctly related to either ursids or procyonids or 2) as the sister taxon to procyonids plus some other carnivore taxon. While this mirrors the sliding window analysis of phylogenetic statements for *Ailuropoda*, it weakly contradicts the analogous findings during this time that held *Ailurus* to be more closely related to procyonids (see Fig. 3b; but see below). After the 1950s, supertrees in virtually every window place *Ailuropoda* as the sister group to ursids. *Ailurus* meanwhile is usually clustered with procyonids, except for periods in the 1980s and 1990s when it clusters distantly with ursids or its placement is equivocal between ursids and procyonids. On the whole, 81.0% of the windows in Fig. 5 placed *Ailuropoda* more closely with ursids, while 81.9% placed *Ailurus* more closely with procyonids.

Support for an ursid versus procyonid relationship for each panda species is given in Fig. 6. For *Ailuropoda*, an ursid affinity is usually the more parsimonious solution, particularly from the mid-1980s onwards. A sister group relationship with procyonids is more parsimonious only before 1950 and for a brief time during the mid-1980s. The reverse is true for *Ailurus*: a procyonid affinity is usually the more parsimonious. This includes the period before 1950, indicating that *Ailurus* also clusters equally parsimoniously with other non-ursid carnivore groups to produce the unresolved result seen in Fig. 5. It is only during the late 1980s to mid-1990s that an *Ailurus*-ursid pairing is the more parsimonious. The placement of *Ailurus* is also generally more uncertain than that of *Ailuropoda*. The difference in the length of the competing topologies for *Ailurus* (maximum = 7.9%) is typically much smaller than those for *Ailuropoda* (maximum = 14.8%), revealing that placements of *Ailurus* are not as strongly supported. Moreover, whereas the length difference is increasing for *Ailuropoda* with time (indicating increasing certainty), it is decreasing slightly for *Ailurus*.

The supertree obtained from all 116 source trees is completely resolved (Fig. 7). The high values for

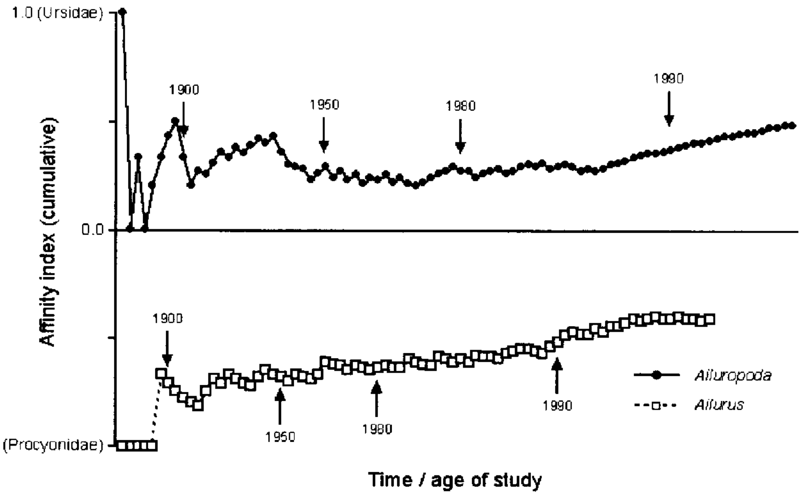

Figure 4. Cumulative values of statements of phylogenetic affinity for *Ailuropoda* or *Ailurus* using the affinity metric discussed in the text.

the goodness-of-fit measures CI, RI, and RC (see Farris 1989) indicate generally good agreement among the source trees. There is strong support for a sister group relationship between *Ailuropoda* and ursids. *Ailurus* clusters with procyonids, but this is comparatively weakly supported. Supertrees obtained for each of the major data sources used (morphological, molecular, and total evidence; Fig. 8) also place *Ailuropoda* with ursids. Again, support for this placement is strong, but comparatively higher for the molecular and total evidence supertrees. The different data sources indicate different affinities for *Ailurus*: as the sister group to procyonids (morphological) or musteloids (mustelids plus procyonids; molecular), or unresolved within arctoids (total evidence). Except for the morphological supertree, support for each placement is comparatively weak within each supertree.

Discussion

Despite being one of the most celebrated cases of controversy within mammalian systematics, virtually all lines of evidence hold *Ailuropoda* to be more closely related to ursids than it is to procyonids. Moreover, such a placement is favored relatively consistently through time and by each of morphological and behavioral (= phenotypic), molecular, and total evidence studies. This arrangement enjoys strong support at most times and has not been contradicted since the mid-1980s. Little doubt should now remain that *Ailuropoda* is the sister group to the true bears.

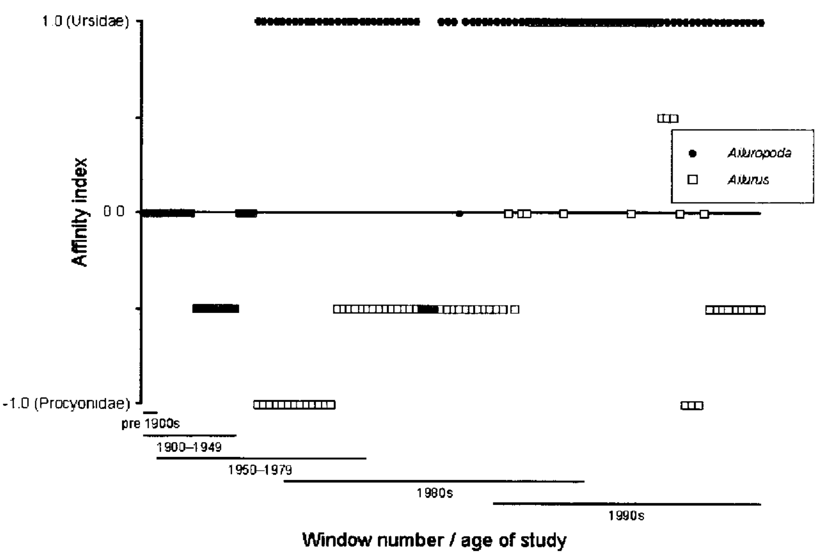

Figure 5. Sliding window analysis of supertrees to examine the inferred sister groups of *Ailuropoda* and *Ailurus* as quantified using the affinity metric discussed in the text.

Instead, despite receiving much less attention due to a greater apparent consensus, it is the position of *Ailurus* within carnivores that is much more doubtful. Although it is usually held to have procyonid affinities at any given period since 1869, the strength of this inference is comparatively weak and perhaps decreasing with time. Only morphological studies provide reasonable support for this arrangement. Instead, several recent, mostly molecular studies propose an ursid affinity for *Ailurus* and many others are equivocal on the matter (see Table 2). As such, the position of *Ailurus* is perhaps less clear now than at any time in the past. Much of this may derive from other evidence that indicates *Ailurus* to be the last

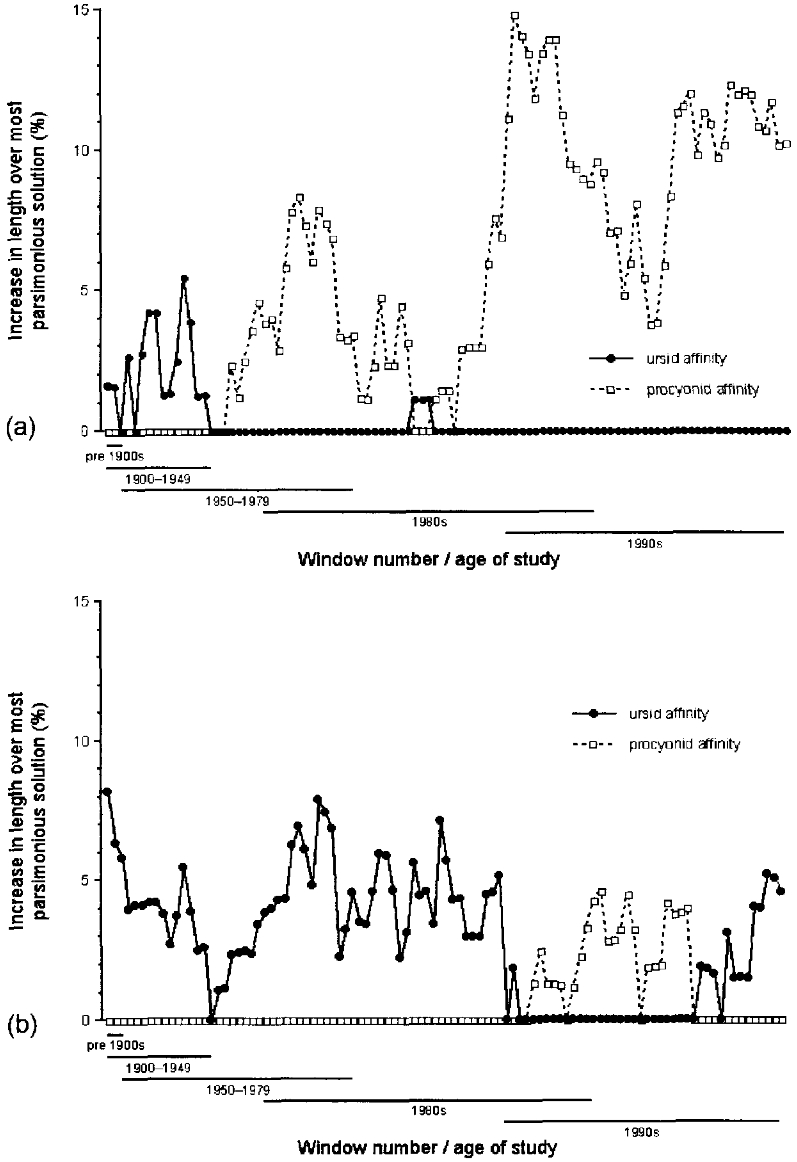

Figure 6. Sliding window analysis of the relative increase in length over the most parsimonious solution for that window when *Ailuropoda* (a) or *Ailurus* (b) are constrained to have either ursid or procyonid affinities in the supertree analysis (see Fig. 2). Higher values indicate decreasing support for the constrained placement.

surviving member of a relatively ancient lineage, one that may extend close to the origins of the major arctoid lineages (Sarich 1976; O'Brien et al. 1985; Bininda-Emonds et al. 1999). Compounded with evidence of a rapid adaptive radiation around this time (Bininda-Emonds et al. 1999), it has proved extremely difficult to resolve the position of *Ailurus* with any certainty or consistency. Much more research effort, using a wide variety of data types, is required.

Of the alternative evolutionary scenarios mentioned earlier, *Ailuropoda* should be viewed as a bear adapted to a herbivorous diet (as are *Helarctos, Tremarctos,* and *Ursus thibetanus*) rather than a small herbivore that has converged on a larger ursid body plan (cf. Davis 1964). Features shared with the herbivorous procyonids such as an enlarged dentition are therefore instances of convergence, possibly facilitated by both lineages being derived from the same arctoid body plan. Likewise, the apparent procyonid affinities of *Ailurus* mean that derived features shared by the two panda species (perhaps including the common name "panda"; see Mayr 1986) should be viewed as convergent. However, a definitive statement in this regard is not possible given the uncertain position of *Ailurus*. If *Ailurus* does have ursid affinities, as suggested by several recent studies, then its similarities with *Ailuropoda* would cease to be convergent, although they might still be primitive.

I actively refrain from making any taxonomic conclusions in this paper, even for *Ailuropoda* where the phylogenetic position seems reasonably secure. Although conservation decisions and priorities can be based on taxonomic information (e.g., Lockwood 1999; see also May 1990; Vane-Wright et al. 1991), such information is often only a crude approximation of the phylogenetic history of a group. Furthermore, taxonomic assessments are subjective and can frequently obscure or even misrepresent phylogenetic information. For instance, by placing *Ailuropoda* in its own family (Ailuropodidae), we gain the knowledge that it is (subjectively) "distinct" at the cost of realizing its close relationship and therefore similarity with ursids. While the former piece of information is an important factor in establishing conservation priorities, the latter is critical for conservation practice. In managing *Ailuropoda,* we will likely have greater success by adapting existing ursid conservation programs because of key similarities between all the species (e.g., the slow reproductive rate and associated life history traits). Instead, we would be better served by using the more resolved and

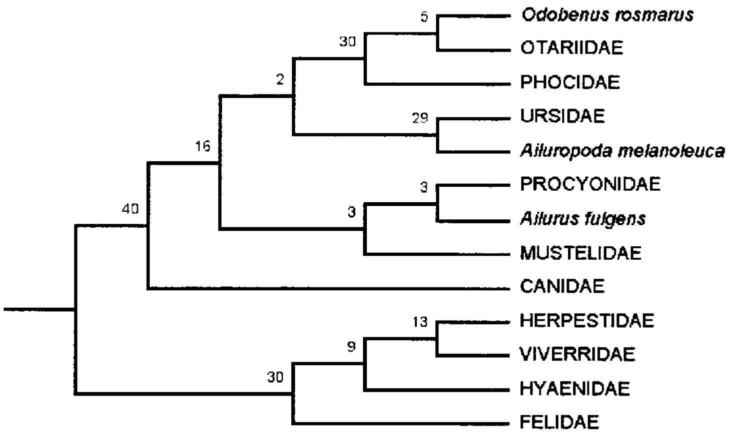

Figure 7. Overall supertree of family level relationships within Carnivora as determined from 116 source trees spanning the years 1870 to 1999 inclusive. The single most parsimonious solution had a length of 614 steps, CI = 0.681, RI = 0.749, and RC = 0.510. Support throughout the supertree is given above each branch in the form of Bremer decay indices. Higher values indicate increasing support.

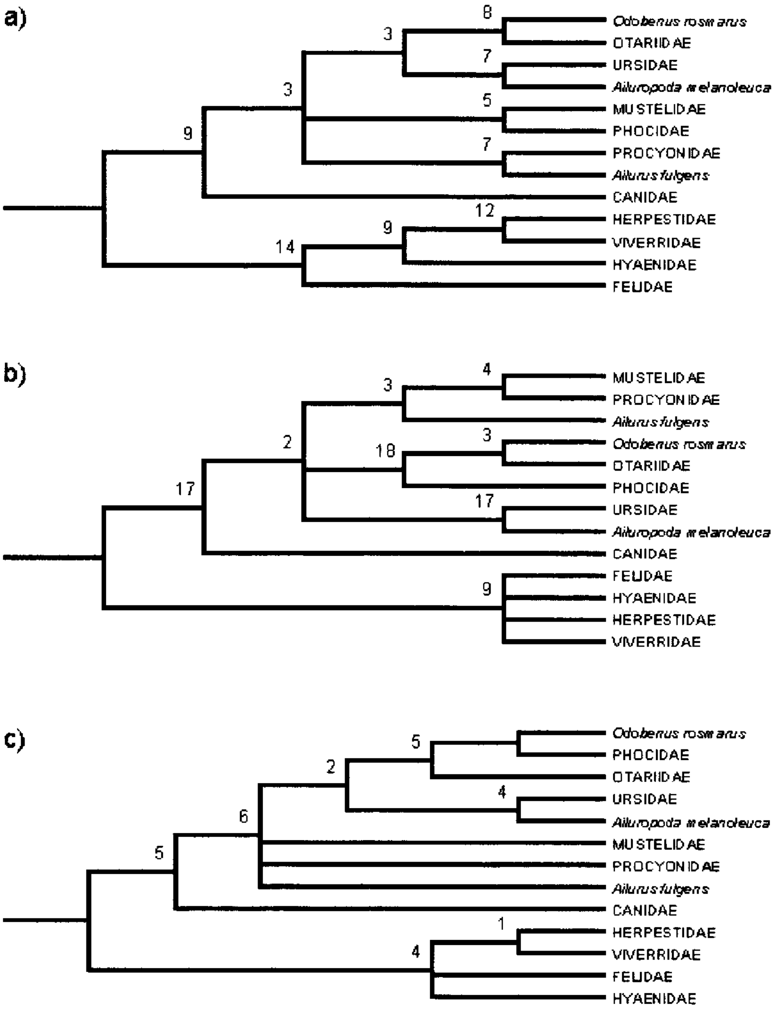

Figure 8. Supertrees of family level relationships within Carnivora as determined from source trees derived from morphological (a; $n = 2$, length = 287, CI = 0.662, RI = 0.734; RC = 0.486), molecular (b; $n = 6$, length = 241, CI = 0.718, RI = 0.764; RC = 0.548), or total evidence (c; $n = 4$, length = 74, CI = 0.757, RI = 0.861; RC = 0.651) data. Support throughout each supertree is given above each branch in the form of Bremer decay indices.

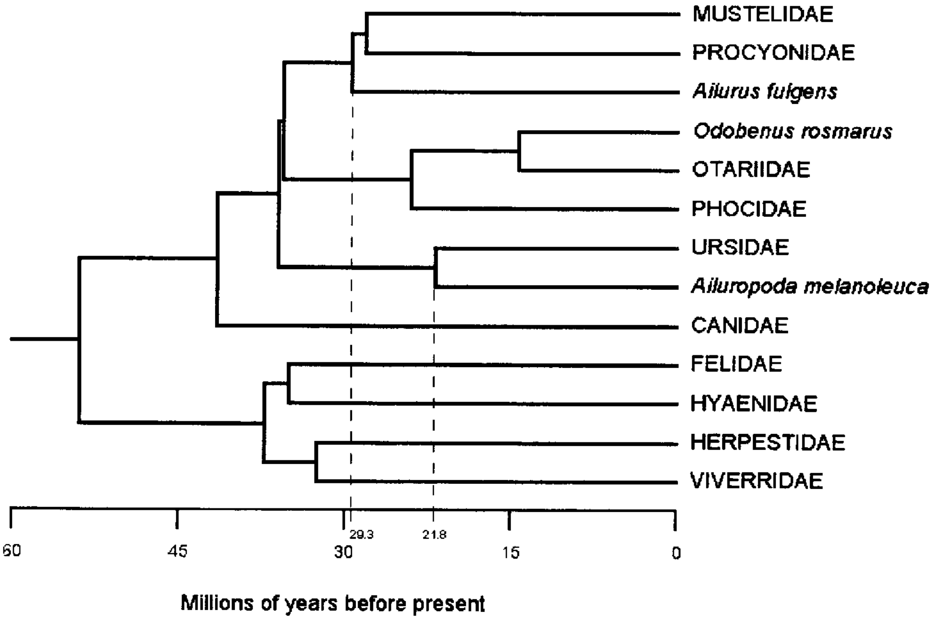

Figure 9. The best estimate of the relationships the *Ailuropoda* and *Ailurus*, together with times of divergence (adapted from Bininda-Emonds et al. 1999).

accurate phylogenetic information whenever possible (Crozier 1997; Nee & May 1997; Vázquez & Gittleman 1998). Conservation priorities can be set using metrics that quantify phylogenetic diversity or distinctiveness from phylogenies with branch length information (e.g., Faith 1994; Crozier 1997). In this regard, both *Ailuropoda* and *Ailurus* would be regarded as worthy of conservation because they represent the sole surviving members of relatively ancient lineages. This can be clearly seen from Fig. 9, which contains what I feel to be the best current estimate of higher level relationships and divergence times within carnivores. Based on both fossil and molecular data, the lineage giving rise to *Ailurus* probably diverged from the common ancestor of mustelids and procyonids about 29.3 million years before present, while the lineage for *Ailuropoda* separated from that leading to the true ursids about 21.8 million years before present (Bininda-Emonds et al. 1999).

Acknowledgments

I thank Lee Hagey and Don Lindburg for the opportunity to speak at the Phylogeny and Conservation session of the Giant Panda symposium of Panda 2000, and John Gittleman for his support and encouragement. Steve O'Brien kindly supplied copies of some otherwise difficult to obtain source studies. Financial support for this study was provided both by Panda 2000 and an NSERC of Canada postdoctoral fellowship.

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