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Phylogeny of the Procyonidae (Mammalia: Carnivora): Molecules, morphology and the Great American Interchange

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Abstract

The Procyonidae (Mammalia: Carnivora) have played a central role in resolving the controversial systematics of the giant and red pandas, but phylogenetic relationships of species within the family itself have received much less attention. Cladistic analyses of morphological characters conducted during the last two decades have resulted in topologies that group ecologically and morphologically similar taxa together. Specifically, the highly arboreal and frugivorous kinkajou (*Potos flavus*) and olingos (*Bassaricyon*) define one clade, whereas the more terrestrial and omnivorous coatis (*Nasua*), raccoons (*Procyon*), and ringtails (*Bassariscus*) define another clade, with the similar-sized *Nasua* and *Procyon* joined as sister taxa in this latter group. These relationships, however, have not been tested with molecular sequence data. We examined procyonid phylogenetics based on combined data from nine nuclear and two mitochondrial gene segments totaling 6534 bp. We were able to fully resolve relationships within the family with strongly supported and congruent results from maximum parsimony, maximum likelihood, minimum evolution, and Bayesian analyses. We identified three distinct lineages within the family: a (*Nasua, Bassaricyon*) clade, a (*Bassariscus*, *Procyon*) clade, and a *Potos* lineage, the last of which is sister to the other two clades. These findings, which are in strong disagreement with prior fossil and morphology-based assessments of procyonid relationships, reemphasize the morphological and ecological flexibility of these taxa. In particular, morphological similarities between unrelated genera possibly reflect convergence associated with similar lifestyles and diets rather than ancestry. Furthermore, incongruence between the molecular supermatrix and a morphological character matrix comprised mostly of dental characters [Baskin, J.A., 2004. *Bassariscus* and *Probassariscus* (Mammalia, Carnivora, Procyonidae) from the early Barstovian (Middle Miocene). J. Vert. Paleo. 24, 709–720] may be due to non-independence among atomized dental characters that does not take into account the high developmental genetic correlation of these characters. Finally, molecular divergence dating analyses using a relaxed molecular clock approach suggest that intergeneric and intrageneric splits in the Procyonidae mostly occurred in the Miocene. The inferred divergence times for intrageneric splits for several genera whose ranges are bisected by the Panamanian Isthmus is significant because they suggest diversification well precedes the Great American Interchange, which has long been considered a primary underlying mechanism for procyonid evolution.

Keywords: Procyonidae; Carnivora; Molecular phylogeny; Great American Interchange; Biogeography; Molecules versus morphology

1. Introduction

The Procyonidae is one of the 11 traditional families of the mammalian order Carnivora. The family consists of 14 extant species in six genera (Wozencraft, 2005) that are geographically distributed across the Americas and includes

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highly arboreal tropical frugivores (olingos [*Bassaricyon* spp.] and the prehensile-tailed kinkajou [*Potos flavus*]) and terrestrial to arboreal omnivores found across a diversity of habitats (ringtail and cacomistle [*Bassariscus* spp.]; coatis [*Nasua* spp. and *Nasuella olivacea*]; and raccoons [*Procyon* spp.]) (Zeveloff, 2002; Nowak, 2005). As a result of their diets and in contrast to many other species in the Carnivora, most procyonids are characterized by having hypocarnivorous dentitions. Coat patterns among the species are diverse, with *Nasua, Procyon* and *Bassariscus* having striking tail annulations and masks, while in *Bassaricyon* and *Potos* such markings are either reduced or lacking altogether.

Systematic relationships of the extant Procyonidae have received a great deal of indirect study. As pivotal subjects in the long-running controversy over placement of giant and red pandas (*Ailuropoda* and *Ailurus*), procyonids became the perennial outgroup or ingroup (O'Brien et al., 1985, 1991; Mayr, 1986; Tagle et al., 1986; Goldman et al., 1989; Zhang and Shi, 1991; Hashimoto et al., 1993; Pecon Slattery and O'Brien, 1995). Yet these studies did not directly examine relationships within the Procyonidae and earlier direct studies of procyonid interrelationships, based on overall similarity of various anatomical features, yielded conflicting results. For example, Gill (1872) and Hollister (1916) excluded ringtails (*Bassariscus* spp.) from the family, whereas McGrew (1938) adamantly included them. Pocock (1921) concluded that procyonid genera probably shared a common ancestor, but placed each genus in its own subfamily because of their morphological dissimilarites. Davis (1941) and Segall (1943) both questioned the placement of *Potos* within procyonids. Story (1951) examined the pattern of the carotid arteries and their branches in *Procyon lotor* and other procyonid taxa and used these patterns to infer relationships among genera, with *Procyon* and *Nasua* being most similar.

Recent cladistic analyses using morphological characters have been more congruent and suggest that the family is composed of two primary clades, one containing *Bassariscus*, *Nasua* and *Procyon*, with *Nasua* (plus *Nasuella*) and *Procyon* joined as sister taxa, and the other clade containing *Bassaricyon* and *Potos* (Baskin, 1982, 1989, 1998, 2004; Decker and Wozencraft, 1991) (Fig. 1). These two major clades have been classified either as subfamilies (Procyoninae and Potosinae; Decker and Wozencraft, 1991) or tribes (Procyonini and Potosini; Baskin, 2004). Relying primarily on dental characters, Baskin (1982, 1989, 1998, 2004) investigated the relationships among fossil and extant genera within the family. The classification of procyonids into the Potosini and Procyonini (Fig. 1A) stems from Baskin's (1998, 2004) recognition of three subfamilies as comprising the Procyonidae: Procyoninae (which includes the extant genera and their fossil relatives), Ailurinae (*Ailurus* and its fossil relatives), and the extinct Simocyoninae. This arrangement suggests that these three subfamilies descended from a common ancestor, a conclusion supported by other paleontological studies, except that the subfamilies are elevated to familial rank (Ginsberg et al., 1997; Wang, 1997). However, other neontological and paleontological evidence (e.g., Wolsan, 1993; but see Wang, 1997) suggests that Ailurinae and Simocyoninae are not part of the monophyletic Procyonidae, a conclusion that is firmly supported, at least for the Ailurinae (as represented by *Ailurus*) by molecular data (Flynn et al., 2000, 2005). Decker and Wozencraft (1991) used 129 craniodental, postcranial and soft anatomical characters to infer relationships among the extant genera only (Fig. 1B). Despite differences in the composition of the respective character matrices, the congruence of relationships among extant genera in the Baskin (2004) and Decker and Wozencraft studies (Fig. 1) suggest that morphology is a reliable indicator of procyonid phylogeny.

These morphology-based phylogenetic hypotheses have not, however, been tested with molecular data, although several studies have hinted at potential disagreement between molecular and morphologic data for these taxa (Sarich, 1973; Couturier and Dutrillaux, 1986). While various DNA sequence data have been generated for several procyonid genera, these have usually been employed to assess higher level relationships among carnivoran families, especially those included in the Arctoidea (Zhang and Ryder, 1993, 1994; Vrana et al., 1994; Ledje and Arnason, 1996a,b; Dragoo and Honeycutt, 1997; Flynn and Nedbal, 1998; Flynn et al., 2000, 2005; Yu et al., 2004; Delisle and Strobeck, 2005; Sato et al., 2006). Therefore, a direct assessment of relationships among procyonid genera using DNA sequences has, until now, been lacking.

Despite being presently restricted to the Americas, procyonids first appear in Late Eocene or Late Oligocene deposits of Western Europe, represented by fossils of the genus *Pseudobassaris* (Pohle, 1917; Wolsan, 1993; Wolsan and Lange-Badré, 1996; McKenna and Bell, 1997). Other fossil taxa from European localities assigned to the Procyonidae are also known (see McKenna and Bell, 1997), but paleontologists differ considerably over the taxonomic affinities of these taxa (e.g., Wolsan, 1993; Baskin, 2004). Procyonids first appear in the North American fossil record in the Early Miocene (Hunt, 1996; Baskin, 1998, 2004). Phylogenetic analyses based on morphological characters suggest a shared ancestry between North American genera and the Early Miocene taxon *Broiliana* of Europe (Baskin, 1998, 2004). Once in North America, procyonids diversified and gave rise to a number of genera, including the extant lineages. The lineage leading to *Bassaricyon* and *Potos* (which both lack a fossil record) is believed to have diverged in the Early Miocene, based on their presumed relationship to the stem fossil genera *Bassaricyonoides* and *Parapotos* (Baskin, 2003) (Fig. 1A). This is consistent with Simpson's (1945) earlier supposition of a Miocene ancestry of the kinkajou based on its highly derived morphology. Fossils of *Bassariscus* first appear in the early Middle Miocene, and *Nasua* and *Procyon* first appear in the Early Pliocene and Late Miocene, respectively (Baskin, 1982, 1998, 2004). Therefore, fossil evidence suggests that most intergeneric divergences among extant genera occurred during the Miocene epoch, most likely in southern North American and/or Central American

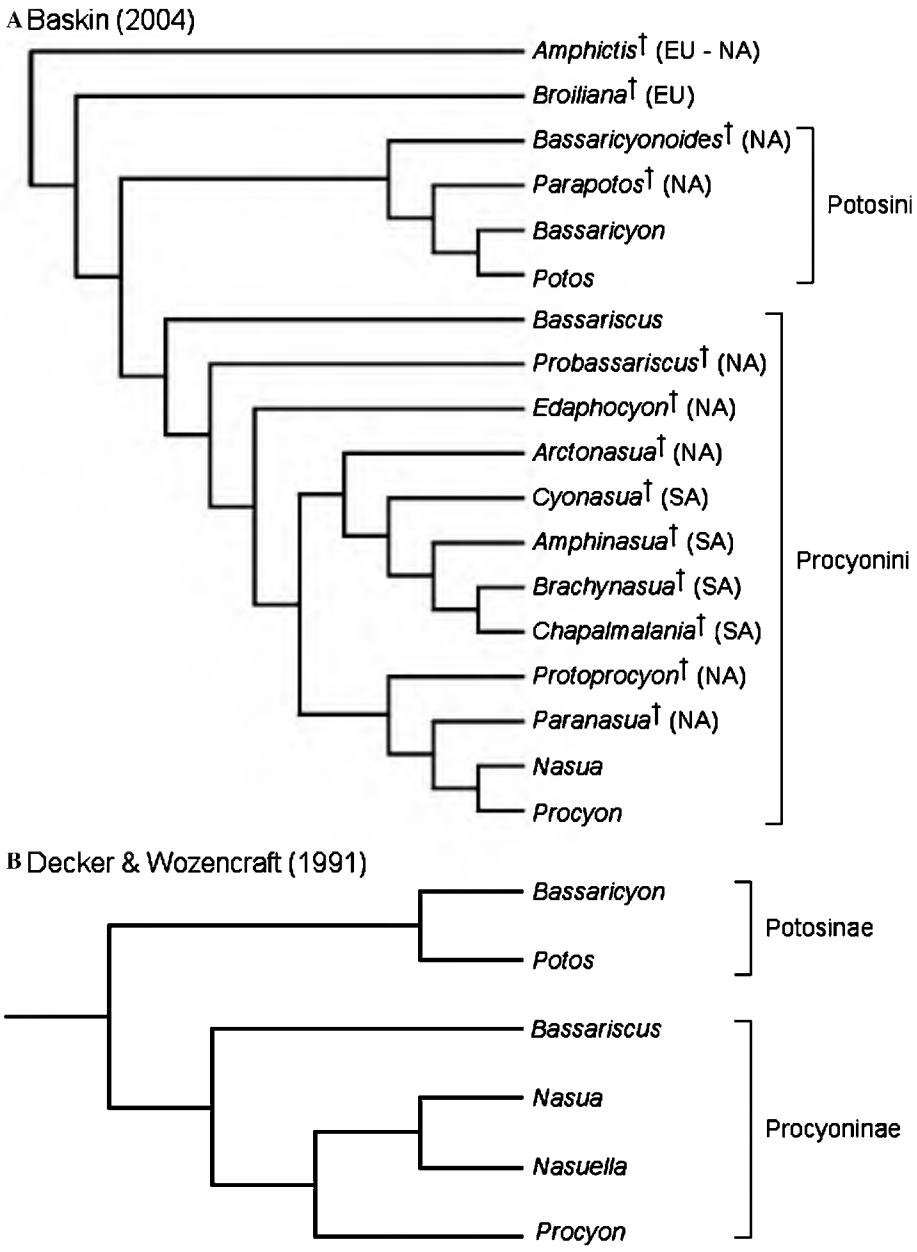

Fig. 1. Phylogenetic hypotheses of Procyonidae derived from morphologic cladistic analyses. (A) Phylogeny of fossil and extant genera from Baskin, 2004. *Amphictis* is the outgroup. Extinct genera are denoted by a cross (†). Geographical origins of fossil taxa are indicated in parentheses. EU, Europe; NA, North America; SA, South America. (B) Phylogeny of extant genera only from Decker and Wozencraft, 1991. Proposed tribal (A) or subfamilial (B) affiliations are shown at right.

subtropical and/or tropical forests (Simpson, 1945; Hershkovitz, 1972; Baskin, 1982, 1998; Webb, 1985). A well-resolved molecular phylogeny of the Procyonidae, combined with reliable estimates of divergence times, can be used to examine temporal patterns of diversification in this group, allowing comparisons with inferences based on the fossil record.

The timing of *intrageneric* divergences is less well understood, particularly with regard to species distributed in South America. This is primarily due to either the complete lack of a fossil record for some species [e.g., five species of *Bassaricyon*, although these may represent just one species (Poglayen-Neuwall and Poglayen-Neuwall, 1965; Nowak, 2005)] or the fragmentary record for other species (e.g., *Nasua* spp. and *Procyon* spp.). Regarding the latter, fossils of *Nasua* and *Procyon* from South America are first recorded in Early to Late Pleistocene deposits (Berta et al., 1978; Marshall et al., 1984). Therefore, a large temporal and spatial gap exists between the time and place *Nasua* and *Procyon* first appear in North America (Late Miocene and Early Pliocene, respectively [*ca.* 5.3 mya for this boundary]) and the time they first appear in South America (Early to Late Pleistocene, 1.5–0.1 mya). Intriguingly, however, current geographic ranges of *Bassaricyon*, *Nasua*, *Procyon*, and *Potos* are bisected by the Isthmus of Panama. The Isthmus rose above sea level *ca.* 3–2.5 mya in the Late Pliocene, forming a landbridge between North and South America

that facilitated one of the major biological events of late Cenozoic history, the Great American Interchange (Marshall et al., 1979, 1982; Marshall, 1985; Webb, 1985, 1997; Marshall and Sempere, 1993; Coates and Obando, 1996). Ranges of putative sister species within *Nasua*, *Procyon*, and possibly *Bassaricyon* overlap on or meet near the Isthmus of Panama, suggesting that current procyonid diversity and biogeography may have been influenced by formation of the Panamanian landbridge. Whether the rise of the Isthmus of Panama played a role in intrageneric speciation events of procyonids can be tested by comparing molecular divergence times of the species involved with the well-defined geochronology of the formation and closure of the Panamanian landbridge (e.g., Marshall et al., 1979; Marshall, 1985; Marshall and Sempere, 1993).

Here, we present sequence data from two mitochondrial and nine nuclear gene segments to examine phylogenetics and divergence dating of the Procyonidae from a molecular perspective. Our primary aims are to: (1) critically evaluate relationships among genera within the family, (2) assess congruence between phylogenetic hypotheses generated from the present molecular study and previous cladistic morphological studies, and (3) estimate the relative divergence times of genera as well as sister species. The latter issue is particularly interesting in the context of better understanding the biogeographic history of the family and the potentially pivotal role that the rise of the Isthmus of Panama may have had on the radiation of procyonids.

2. Materials and methods

2.1. Taxonomic sampling

Our study includes nine species in the Procyonidae, representing all genera except *Nasuella* (Table 1). Numerous lines of evidence suggest that Mustelidae (badgers, martens, otters, and weasels) is sister group to Procyonidae (e.g., de Jong, 1986; Flynn et al., 1988, 2000, 2005; Sato et al., 2006). Therefore, we used five species from the Mustelidae as outgroups (Table 1). Our sampling of taxa does not include the red panda (*Ailurus fulgens*) because recent studies based on both mitochondrial and nuclear DNA sequences have shown that this taxon diverged prior to divergence of Procyonidae and Mustelidae (Flynn and Nedbal, 1998; Flynn et al., 2000, 2005; Yu et al., 2004) and most likely represents a monotypic lineage within the newly defined Musteloidea (Flynn et al., 2005; Sato et al., 2006).

2.2. Laboratory methods

Total genomic DNA was extracted from tissue samples using a commercial kit (QIAamp DNA Mini Kit). We used the polymerase chain reaction (PCR) to amplify segments containing exon sequences or exon plus intron sequences from nine nuclear loci and two coding regions from the mitochondrial genome (Table 2). Amplification reaction and cycling conditions for all loci, and purification of PCR products, followed Koepfli and Wayne (2003). PCR products were cycle sequenced using PCR primers and CEQ Dye Terminator Cycle Sequencing Quick Start Kit (Beckman Coulter). Sequencing reactions were precipitated following the manufacturer's protocol and products were sequenced on a CEQ2000XL automated capillary sequencer (Beckman Coulter). Electropherograms were checked for accuracy and edited using Sequencher 3.1 (Gene Codes Corporation). We were unable to amplify *RAG2* sequence from *Bassariscus sunichrasti*, and question marks were used to represent missing data for this taxon. Seven previously generated *CHRNA1* and two *CYTb* sequences were from Koepfli and Wayne (2003) and four *CYTb* sequences were from Koepfli and Wayne (1998) (Appendix A). Newly generated sequences were deposited

Table 1
Species, common name and origin of the tissue samples for the taxa used in this study

Species	Common name	Source locality	Voucher or collector information
Procyonidae			
Bassaricyon alleni	Allen's olingo	Amazonas, Peru	MVZ 155219
Bassaricyon gabbii	Bushy-tailed olingo	Limbo, Panama	R. Kays
Bassariscus astutus	Ringtail	Arizona, USA	S. Ratnayeke
Bassariscus sunichrasti	Cacomistle	Veracruz, Mexico	I. Poglayen
Nasua narica	White-nosed coati	Barro Colorado Island, Panama	M. Gompper
Nasua nasua	South American coati	Santa Cruz, Bolivia	MSB 12987
Potos flavus	Kinkajou	San Jose, Costa Rica	LSU-MNS 28393
Procyon cancrivorus	Crab-eating raccoon	Presidente Hayes, Paraguay	MSB 15018
Procyon lotor	North American raccoon	Montana, USA	UAM 33819
Mustelidae			
Eira barbara	Tayra	Santa Cruz, Bolivia	MSB 58756
Enhydra lutris	Sea otter	Mednyi Island, Russia	J. Bodkin
Martes americana	American marten	Wyoming, USA	H. Henry
Mustela vison	American mink	Texas, USA	TK 29694
Taxidea taxus	American badger	New Mexico, USA	MSB 64932

LSU-MNS, Louisiana State University, Museum of Natural Sciences; MSB, Museum of Southwestern Biology, University of New Mexico; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; TK, Museum of Texas Tech University; UAM, University of Alaska Museum, Fairbanks.

Table 2
Abbreviated gene symbol, type of sequence, and forward (F) and reverse (R) primer sequences for nine nuclear and two mitochondrial gene segments amplified and sequenced in this study

Gene	Type of sequence	Primer sequences (5′ → 3′)	Reference
ADORA3	Exon	F: ACC CCC ATG TTT GGC TGG AA R: GAT AGG GTT CAT CAT GGA GTT	Murphy et al. (2001)
APOB	Exon	F: GTG CCA GGT TCA ATC AGT ATA AGT R: CCA GCA AAA TTT TCT TTT ACT TCA A	Amrine-Madsen et al. (2003) Jiang et al. (1998)
BDNF	Exon	F: CAT CCT TTT CCT TAC TAT GGT T R: TTC CAG TGC CTT TTG TCT ATG	Murphy et al. (2001)
CHRNA1	Exon/intron	F: GAC CAT GAA GTC AGA CCA GGA G R: GGA GTA TGT GGT CCA TCA CCA T	Lyons et al. (1997)
COL10A1	Exon	F: ATT CTC TCC AAA GCT TAC CC R: GCC ACT AGG AAT CCT GAG AA	Venta et al. (1996)
PNOC	Exon	F: GCA TCC TTG AGT GTG AAG AGA A R: TGC CTC ATA AAC TCA CTG AAC C	Murphy et al. (2001)
RAG1	Exon	F: GCT TTG ATG GAC ATG GAA GAA GAC AT R: GAG CCA TCC CTC TCA ATA ATT TCA GG	Teeling et al. (2000)
RAG2	Exon	F: TCA TGG AGG GAA AAC ACC AAA R: TGC ACT GGA GAC AGA GAT TC	Murphy et al. (2001)
WT1	Exon/intron	F: GAG AAA CCA TAC CAG TGT GA R: GTT TTA CCT GTA TGA GTC CT	Venta et al. (1996)
CYTb	Mitochondrial coding	F: CGA AGC TTG ATA TGA AAA ACC ATC GTT G F: GCA AGC TTC TAC CAT GAG GAC AAA TAT C F: ATA GAC AAA ATC CCA TTC CA R: TAG TTG TCA GGG TCT CCT AG R: AAC TGC AGT CAT CTC CGG TTT ACA AGA C	L14724; Irwin et al. (1991) L15162; Irwin et al. (1991) L15408; Irwin et al. (1991) H15494; Koepfli and Wayne (1998) H15915; Irwin et al. (1991)
NADH5	Mitochondrial coding	F: GGT GCA ACT CCA AAT AAA AGT A R: AGA ATT CTA TGA TGG ATC ATG T	Waits et al. (1999)

Gene names are: *ADORA3*, A3 adenosine receptor; *APOB*, apolipoprotein B; *BDNF*, brain-derived neurotrophic factor; *CHRNA1*, cholinergic receptor, nicotinic, α polypeptide 1 precursor; *COL10A1*, collagen type X α I; *PNOC*, prepronociceptin; *RAG1*, recombination-activating protein 1; *RAG2*, recombination-activating protein 2; *WT1*, Wilms tumor 1; *CYTb*, cytochrome *b*; *NADH5*, NADH dehydrogenase subunit 5.

in GenBank under the following accession numbers: DQ660167–DQ660306 (Appendix A).

2.3. Phylogenetic analyses

Mitochondrial and nuclear gene sequences were manually aligned and alignments for all loci were unambiguous. Three nuclear loci (*APOB*, *CHRNA1* and *WT1*) contained insertions and/or deletions (indels) 1–16 bp in length that necessitated introduction of gaps into alignments of these segments.

We reconstructed phylogenetic trees from three different partitions and concatenations of data: (1) nine combined nuclear gene segments; (2) two combined mitochondrial gene segments; and (3) combined nuclear and mitochondrial segments (hereafter referred to as the supermatrix). Maximum parsimony (MP), maximum likelihood (ML), and minimum evolution (ME) trees were estimated using PAUP* (Swofford, 2002), while Bayesian inference (BI) was conducted using MrBayes 3 (Ronquist and Huelsenbeck, 2003). Concatenations of mitochondrial and nuclear gene segments were analyzed with MP, ML, and ME methods only, whereas the supermatrix was analyzed with all four tree reconstruction methods. For MP analyses, all nucleotide sites were equally weighted and gaps were coded as present or absent (1 or 0), regardless of length, to utilize potential phylogenetic signal contained by indels (Barriel, 1994). For ME and ML analyses, gaps were coded as missing and we used Modeltest 3.7 (Posada and Crandall, 1998) to estimate the best-fitting model and parameters of DNA evolution (ML) or distance measure (ME) for each data partition. In both MP and ML analyses, we employed heuristic searches with 100 replicates of a random stepwise addition and tree bisection–reconnection branch swapping (TBR) algorithm. ME analyses utilized heuristic searches with starting trees obtained via neighbor-joining and TBR branch swapping. Nodal support was assessed by bootstrap resampling, with 1000 (MP and ME) or 500 (ML) pseudoreplicates using the same heuristic search conditions listed above (except that only five replicates of random stepwise addition were used in ML). For BI, gaps were treated as missing and the best-fitting model of DNA evolution selected by Modeltest 3.7 for the supermatrix was used for the likelihood function component of Bayes' rule. We used uniform default priors for model parameters, which were estimated as part of the Markov Chain Monte Carlo (MCMC) analyses. MCMC analyses were run for 3.0×10^6 generations, with each Markov chain started from

a random tree and from which trees were sampled every 100 generations, using one cold and three heated chains. We used the program Tracer v1.3 (Rambaut et al., 2003) to check that chains had mixed well and to verify that convergence of log-likelihood scores and model parameters had reached a stationary distribution, after discarding 300,000 generations as burn-in. Two separate MCMC runs were performed to ensure consistency of stationary distributions of likelihood values and parameter estimates between runs. Mean posterior estimates and 95% highest posterior densities of likelihood scores and model parameters for the two runs were calculated using Tracer v1.3. Clade credibility values were estimated after discarding the first 3000 trees (following a burn-in of 300,000 generations) from each run.

2.4. Assessing congruence between molecular and morphological phylogenies

We used several approaches to assess congruence between the phylogeny based on the molecular supermatrix and those estimated with morphological data matrices of Decker and Wozencraft (1991) and Baskin (2004). First, we compared the topology derived from MP analysis (as well as topologies derived from the model-based methods) of the molecular supermatrix with the original maximum parsimony topologies from the two morphological studies (Fig. 1).

Second, we evaluated levels of bootstrap support for nodes in the molecular and morphological phylogenetic hypotheses to assess whether congruence or incongruence was significant or insignificant among data sets. Bootstrap analyses of the most parsimonious trees were not performed in either the Decker and Wozencraft (1991) or Baskin (2004) studies. This test was conducted to rule out the possibility that any incongruence was caused by weakly supported nodes in one or both data sets, which would suggest an undersampling of characters as the cause of incongruence rather than any real character conflict *per se* (Hillis and Wiens, 2000). We were unable to obtain the original data matrix from the Decker and Wozencraft (1991) (D. Decker, pers. comm.) and could, therefore, not evaluate bootstrap support for nodes recovered in their reconstructed phylogeny. Congruence between the supermatrix phylogeny and the phylogeny from Decker and Wozencraft (1991) was, therefore, assessed by comparison to their published phylogeny alone (Fig. 2 in Decker and Wozencraft, 1991). For the 18 taxa (17 ingroup, 1 outgroup) in the Baskin (2004) data set, 39 of the 40 characters in the data matrix were coded as ordered as in the original study. Maximum parsimony bootstrap analysis of this matrix was performed using 1000 bootstrap pseudoreplicates with branch and bound search and the "farthest" taxon addition option in PAUP* (Swofford, 2002). We also adjusted the Baskin (2004) data matrix so that it matched our matrix with respect to generic representation by excluding all extinct genera except *Amphictis*, which was used to root the tree. We then used the abridged Baskin (2004) matrix to reconstruct maximum parsimony trees (with 39 ordered and one unordered characters) and to perform bootstrap analysis using the same search conditions and settings as those used with the unabridged data matrix.

Third, to exclude the possibility that any incongruence between the supermatrix topology and that derived from the abridged Baskin (2004) matrix was due to the use of different outgroups (e.g., Hillis and Wiens, 2000), we reconstructed unrooted maximum parsimony networks from the two data matrices. For these analyses, one representative species of each genus was chosen from the supermatrix to make taxon representation of the supermatrix equal to the abridged Baskin (2004) matrix (five taxa total). Exhaustive searches were performed with both data matrices separately *and* combined using PAUP*. We used 1000 bootstrap pseudoreplicates with branch and bound search and "farthest" taxon addition option to evaluate nodal support for unrooted trees. The combined analysis was used to infer the most parsimonious network that had the greatest congruence among molecular and morphological characters in the context of total evidence (Kluge, 1989). For the combined analyses, we quantified the Bremer support (Bremer, 1988) and partitioned Bremer support (PBS) of nodes in unrooted trees using TreeRot 2.0 (Sorenson, 1998).

Finally, MacClade 4.0 (Maddison et al., 2000) was used to map putative synapomorphies from the Decker and Wozencraft (1991) and Baskin (2004) studies onto the molecular supermatrix topology using the simple parsimony criterion with accelerated (ACCTRAN) and delayed (DELTRAN) transformation in order to evaluate ancestral character states and derivation based on the molecular topology. ACCTRAN maximizes character state reversals whereas DELTRAN maximizes parallelism of character states (Swofford and Maddison, 1987; Maddison et al., 2000).

2.5. Estimation of divergence times

Divergence time estimates were performed using the well-supported optimal topology obtained with the molecular supermatrix (see Section 3), using the Relaxed Molecular Clock approach developed by Thorne et al. (1998) and Kishino et al. (2001). This topology and the DNA supermatrix data set were used with the program *estbranches* to obtain estimates of branch lengths and a matrix of rate variance–covariance. The *estbranches* output was used to infer divergence dates with the program *divtime5b*, with 1.0×10^6 generations run after 100,000 generations of burn-in. Seventeen independent runs of *divtime5b* were performed to assess convergence of posterior distribution estimates with varying root age priors (see below) and fossil constraint combinations. Final runs used four conservative fossil calibrations drawn from McKenna and Bell (1997) to constrain node times: (i) 1.8 mya as a minimum age for the origin of *Procyon* (applied to node F in Fig. 3); (ii) 3.6 mya as a minimum age for the origin of *Nasua* (node E in Fig. 3); (iii) 11.2 mya as a minimum age of crown Procyonidae (node

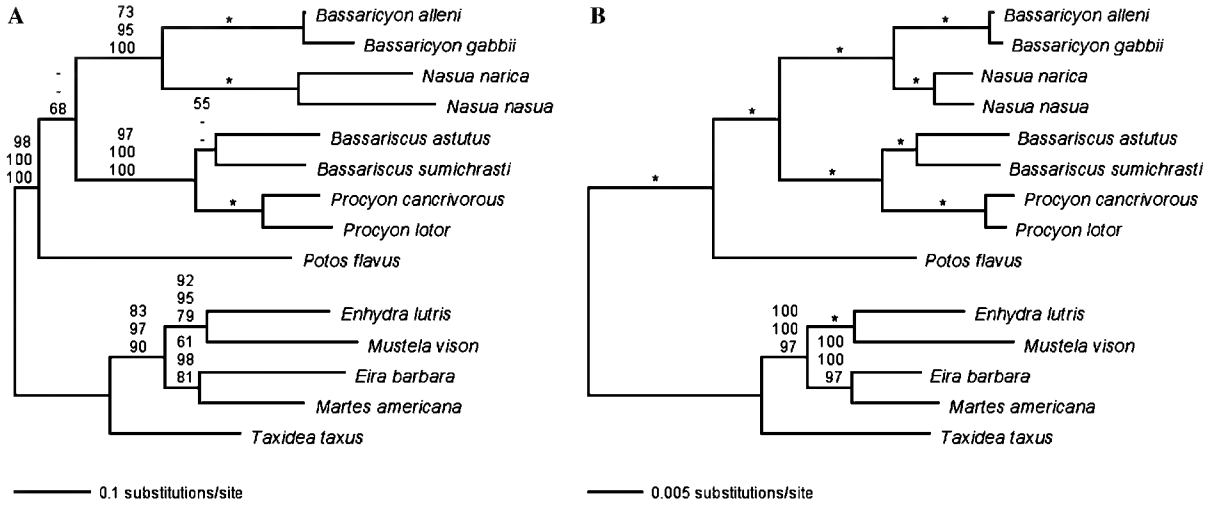

Fig. 2. (A) Maximum likelihood phylogram based on a combined analysis of mitochondrial *CYTb* and *NADH5* gene segments. (B) Maximum likelihood phylogram based on combined analysis of nine nuclear gene segments (*ADORA3*, *APOB*, *BDNF*, *CHRNA1*, *COL10A1*, *PNOC*, *RAG1*, *RAG2*, and *WT1*). Numbers above internodes, from top to bottom, are bootstrap support values from MP, ML, and ME analyses, respectively. Asterisks above internodes indicate that bootstrap support was 100% in all analyses while dashes indicate bootstrap support <50%. See Table 3 for MP tree statistics and ML model parameters and scores. Branch lengths are proportional to number of substitutions per site (scale bars).

H), based on a fossil assigned to *Bassariscus*, and allowed here to be a stem taxon in that lineage (see Section 4); and (iv) 37 mya as an upper bound for the age of crown Procyonidae (node H), based on the putative stem taxa *Pseudobassaris* and *Amphictis* occurring in the Late Eocene and Early Oligocene, respectively. We set the mean of the prior distribution for the ingroup root age at 24 mya (based on the Early Miocene taxon *Broiliana*, proposed to be the earliest fossil procyonine—McKenna and Bell (1997); Baskin (1982, 1989, 1998, 2004)) and tested the impact of this prior value on the posterior distribution of nodal ages by varying it in both directions in seven independent runs.

3. Results

3.1. Phylogenetic estimates

The length of the supermatrix alignment was 6534 bp (including gaps). The 11 gene segments contributed the following number of nucleotide sites to the supermatrix: *ADORA3* (376), *APOB* (935), *BDNF* (548), *CHRNA1* (376), *COL10A1* (326), *PNOC* (287), *RAG1* (1071), *RAG2* (468), *WT1* (712), *CYTb* (1140), *NADH5* (295). When gaps were coded following Barriel (1994), the length of the alignment was reduced to 6491 bp. The concatenated mitochondrial data set (*CYTb* and *NADH5*) contained 677 variable characters, of which 525 were parsimony-informative, while the concatenated nuclear data set (with coded gaps) contained 743 variable characters, of which 426 were parsimony-informative (Table 3). Best-fitting models of DNA substitution were identified by Akaike Information Criteria (AIC) in Modeltest 3.7 (Posada and Crandall, 1998; Posada and Buckley, 2004) for the three data partitions (Table 3). The general time reversible model (Tavare, 1986; Yang, 1994), with among-site rate variation approximated via a gamma distribution and a proportion of invariable sites (GTR+G+I), was selected as the best-fitting model of DNA substitution for the supermatrix partition. This model was employed in the ML, ME (as the distance correction measure) and BI supermatrix analyses.

Topologies estimated from MP, ML, and ME analyses of concatenated nuclear data and from ML and ME analyses of the concatenated mitochondrial data were identical (Fig. 2). In the MP analysis of concatenated mitochondrial data, *Potos* was resolved as the sister lineage to the *Bassariscus* plus *Procyon* clade, but this relationship had <50% bootstrap support (results not shown). Otherwise, topology of the MP tree from the mitochondrial data was congruent with that based on the concatenated nuclear data. Relationships among procyonids received 100% bootstrap support by all three methods of analysis for the concatenated nuclear data (Fig. 2B). All but two nodes also had high bootstrap support in most analyses of the concatenated mitochondrial data, although MP bootstrap values tended to be lower than values from ML and ME (Fig. 2A). There were no significantly conflicting nodes between the concatenated mitochondrial and nuclear gene partitions, using a value of $\geqslant 70\%$ as the criterion for significant bootstrap conflict/support (e.g., Hillis and Bull, 1993; Flynn and Nedbal, 1998). Therefore, we combined these partitions into a single supermatrix.

Parsimony, likelihood, minimum evolution and Bayesian analyses of the supermatrix yielded phylogenies with identical well-resolved topologies (Fig. 3). This topology matched trees estimated from separate analyses of concatenated mitochondrial and nuclear gene partitions (Fig. 2). Rooting the tree using mustelid outgroups, the kinkajou (*Potos*) is resolved as the sister lineage to a clade that is divided into two subgroups: one containing olingos (*Bassaricyon*) and coatis (*Nasua*), and the other containing the ringtail-cacomistle (*Bassariscus*) and raccoons (*Procyon*). Nodal support for

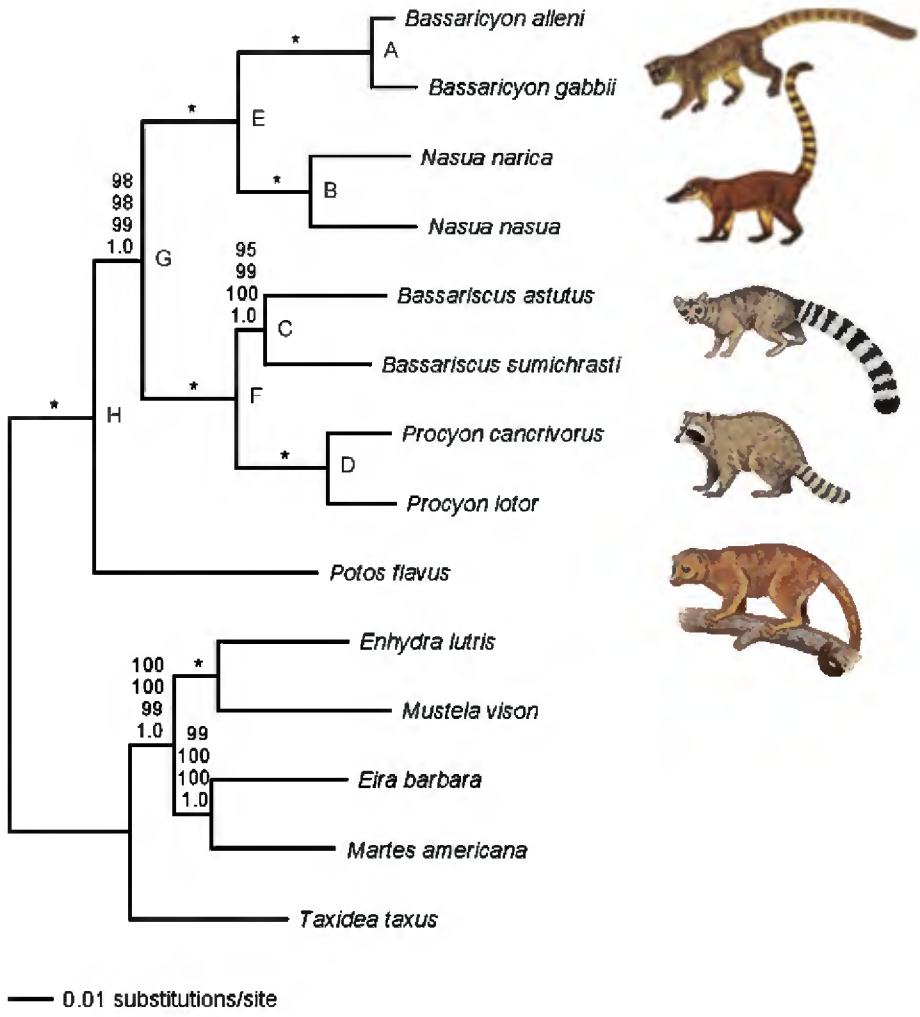

Fig. 3. Maximum likelihood phylogram of procyonids based on combined analysis of 11 gene segments (the supermatrix). Numbers above internodes are, from top to bottom, bootstrap support values from MP, ML, and ME analyses, and posterior probability values from BI, respectively. Asterisks above internodes indicate that bootstrap support and posterior probability were 100% or 1.0, respectively. Posterior probability values from BI based on 50% majority-rule consensus of 27,000 trees after discarding a burn-in of 3000 trees. Branch lengths are proportional to the number of substitutions per site (scale bar). Nodes used in molecular divergence dating analyses are lettered (A–H) and refer to Table 4. See Table 3 for MP tree statistics and ML model parameters and scores and Appendix A for estimated likelihood scores and parameter values from the two BI runs. Illustrations of representative species of procyonid genera (Eisenberg, 1989; Eisenberg and Redford, 1999; used with permission) are shown at right and are, from top to bottom: *Bassaricyon gabbii*, *Nasua nasua*, *Bassariscus sumichrasti*, *Procyon lotor*, and *Potos flavus* (not shown to scale).

relationships within the supermatrix tree is consistently high across all analyses with >95% MP, ML, and ME bootstrap values and 1.0 Bayesian clade credibility values (Fig. 3).

Several informative indels also support this pattern of relationships. Two deletions (of 1 and 11 bp, respectively) in the *CHRNA1* intron and a 1 bp insertion in the *WT1* intron define synapomorphies for the *Bassaricyon* plus *Nasua* clade, while a 2 bp deletion in the *WT1* intron is a synapomorphy for the *Bassariscus* plus *Procyon* clade. All other indels are either autapomorphic for a particular procyonid genus or species or represent synapomorphies that are found in the ingroup relative to the outgroup. Furthermore, a curious feature of the *CYTb* gene in *Bassaricyon* and *Nasua* also provides support for uniting these two genera. As first noted by Ledje and Arnason (1996a), the *CYTb* gene in nearly all Carnivora studied is terminated by an AGA stop codon at codon 380, but in *Bassaricyon*, this codon is occupied by GGG, which codes for a glycine residue. We confirmed this finding by sequencing multiple individuals of *Bassaricyon* (data not shown). In *Nasua*, we found that codon 380 codes for either a lysine residue (AAA in *N. narica* and AAG in *N. nasua*) or a stop codon (AGA) in some individuals of *N. narica*. For *Bassaricyon*, *Nasua nasua*, and some individuals of *Nasua narica*, the stop codon is instead TAA (based on the mammalian mitochondrial genetic code) at position 382, indicating that the *CYTb* gene is 6 bp longer in these two genera relative to other procyonids and Carnivora that have been sequenced for this gene.

3.2. Comparison of molecular and morphological phylogenies

Phylogenies based on parsimony analyses of two morphological data matrices (Decker and Wozencraft, 1991; Baskin, 2004) are largely congruent with one another, but

Table 3
Sequence characteristics, descriptive statistics from parsimony analyses, and models and substitution parameters selected by AIC in Modeltest 3.7 for the combined mitochondrial, nuclear, and supermatrix partitions

	Mitochondrial (2 gene segments)	Nuclear (9 gene segments)	Supermatrix (11 gene segments)
No. of nucleotides	1435	5099/5056	6534/6491
No. variable	677	743	1580
No. parsimony-informative	525	426	1056
No. of trees	1	1	1
Tree length	1814	956	2869
Retention index	0.434	0.878	0.623
Model	TrN+Γ+I	SYM+Γ	GTR+Γ+I
$-\ln L$	8949.1117	12853.5684	22697.1962
π_A	0.3444	0.2500	0.2690
π_C	0.3362	0.2500	0.2598
π_G	0.0826	0.2500	0.2234
π_T	0.2368	0.2500	0.2478
I	0.4379	—	0.5764
Γ	0.8903	0.1727	0.6139
r_{AC}	1.0000	1.3003	2.3962
r_{AG}	30.4364	5.2732	8.3456
r_{AT}	1.0000	0.5575	1.3060
r_{CG}	1.0000	1.3408	1.0253
r_{CT}	21.4421	6.5775	19.1958
r_{GT}	1.0000	1.0000	1.0000

No. of nucleotides, alignment length with gaps included in the alignment/alignment length with gaps coded according to Barriel (1994). π_A, π_C, π_G, and π_T, empirical base frequencies; I, proportion of invariable sites; Γ, gamma shape parameter; r_{AC}, r_{AG}, r_{AT}, r_{CG}, r_{CT}, and r_{GT}, rate of substitution for specified nucleotides. Model names: TrN, Tamura-Nei (Tamura and Nei, 1993); SYM, symmetrical model (Zharkikh, 1994); GTR, general time reversible model (Tavare, 1986).

are highly incongruent with phylogenies derived from three molecular data partitions (compare Fig. 1 with Figs. 2 and 3). In both morphological trees, *Nasua* is sister to *Procyon* and *Bassaricyon* is sister to *Potos*. *Bassariscus* is resolved as sister to the ((*Nasua*, *Nasuella*) *Procyon*) clade in the Decker and Wozencraft (1991) tree and in the original Baskin (2004) tree that includes both fossil and extant taxa. Bootstrap analysis of the MP tree using the unabridged Baskin (2004) matrix reveals that clades containing *Bassaricyon* + *Potos* and *Nasua* + *Procyon* are strongly supported (87 and 92% bootstrap values, respectively, Fig. 4A). However, sister-group relationships of these genera with respect to fossil genera within each clade are only weakly supported (Fig. 4A). In the analysis of the abridged Baskin (2004) matrix, *Bassariscus* is resolved as the sister lineage to the (*Bassaricyon*, *Potos*) and (*Nasua*, *Procyon*) clades (Fig. 4B). Thus, for the abridged matrix, placement of *Bassariscus* (and character states that define this taxon) is sensitive to whether fossil taxa are included (Baskin, 2004; Fig. 4A) or excluded (present study, Fig. 4B). Nonetheless, bootstrap support values for nodes from the abridged Baskin (2004) matrix are all relatively high, with 88 and 100% for the (*Bassaricyon*, *Potos*) clade and (*Nasua*, *Procyon*) clades, respectively (Fig. 4B).

Unrooted parsimony analyses, with taxon sampling restricted to representatives of five extant genera, also resulted in highly incongruent topologies between the molecular supermatrix and morphological matrix from Baskin (2004) (Figs. 5A and B). Discordance between unrooted networks was significant, with nearly 100% MP bootstrap support for completely different relationships. For example, while the molecular supermatrix joined *Nasua* with *Bassaricyon* with 100% bootstrap support, the Baskin (2004) matrix joined *Nasua* with *Procyon*, also with 100% bootstrap support. When we combined the two data sets into a single matrix, the unrooted parsimony network topology was identical to the one recovered by analysis of the supermatrix alone, also with high bootstrap support (Fig. 5C). Bremer support values for the two internal nodes were high (Fig. 5C). PBS analysis showed that the supermatrix contributed a substantial value to the total Bremer support at the two nodes, while the morphological matrix contributed either high negative support (*Bassaricyon*, *Nasua*) or minimal positive support (*Bassariscus*, *Procyon*). The combined unrooted analysis suggests that phylogenetic signal derived from morphological data either conflicts with or provides little support for relationships based upon the molecular supermatrix.

Putative synapomorphies that define the (*Bassaricyon*, *Potos*) and (*Nasua*, *Procyon*) clades in the two morphological studies are all resolved as convergences (homoplasies) when they are traced onto the molecular topology using MacClade 4.0 (Maddison et al., 2000) with both accelerated (ACCTRAN) and delayed (DELTRAN) transformation (Appendix A). The (*Bassaricyon*, *Potos*) clade is supported by nine and four putative synapomorphies in Decker and Wozencraft (1991) and Baskin (2004), respectively (Appendix A). The (*Nasua*, *Procyon*) clade is supported by five synapomorphies in Decker and Wozencraft (1991) (which also includes *Nasuella* as part of this clade) and 10 synapomorphies in Baskin (2004).

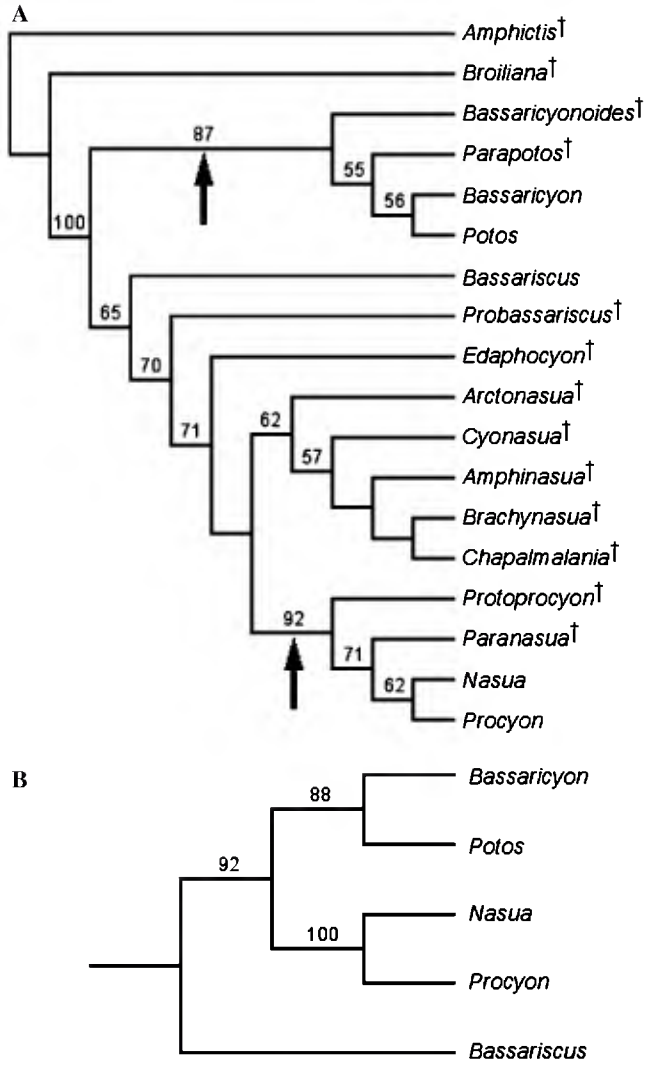

Fig. 4. (A) Single most-parsimonious cladogram of extant and fossil genera of procyonids reconstructed from analysis of 40 morphological characters from Baskin (2004). Tree length (TL) = 100, consistency index, excluding uninformative characters (CI) = 0.6022, and retention index (RI) = 0.7673. Arrows indicate nodes that are strongly conflicting with those of the supermatrix topology (Fig. 3). (B) Single most-parsimonious cladogram of extant genera only based on analysis of 40 morphological characters from Baskin (2004). TL = 68, CI, excluding uninformative characters = 0.8182, and RI = 0.7561. For both analyses, 39 characters were ordered and one was unordered, as in Baskin (2004) and both trees were rooted using *Amphictis* (not shown in B). Numbers above internodes are bootstrap support values, using 1000 pseudoreplicates for each analysis.

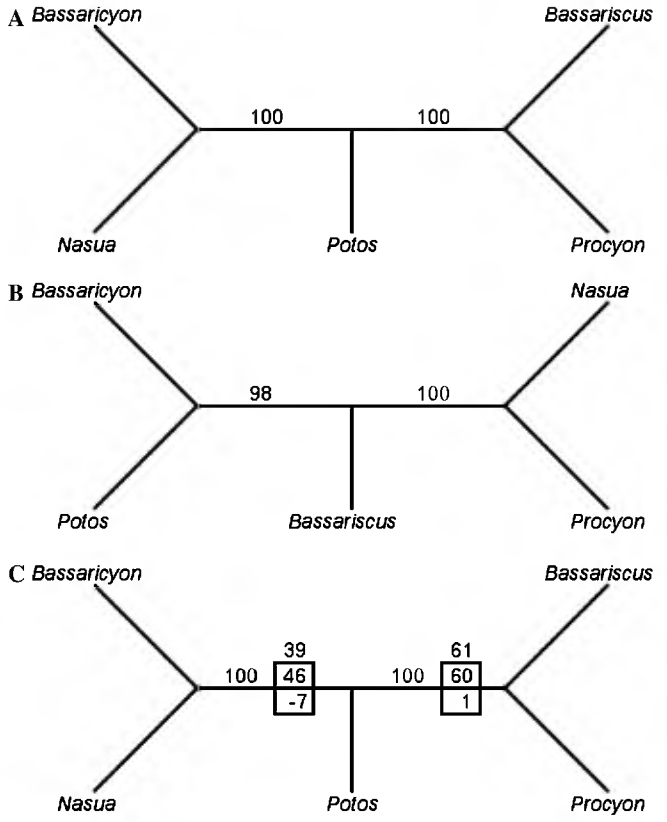

Fig. 5. Unrooted network of extant procyonid genera based on parsimony analysis of (A) the molecular supermatrix (6491 characters; Length (*L*) = 1135, CI, excluding uninformative characters = 0.7071, and RI = 0.5246), (B) 40 (39 ordered and one unordered) morphological characters from Baskin (2004) (*L* = 46, CI, excluding uninformative characters = 0.8611, and RI = 0.8000), and (C) combined molecular and morphological data (*L* = 1199, CI, excluding uninformative characters = 0.6883, and RI = 0.4909). In all three networks, numbers above internodes are bootstrap support percentages, using 1000 pseudoreplicates. In (C), numbers above boxes are Bremer support values and numbers inside of boxes are partition Bremer support values from the molecular supermatrix (above internode) and from the morphological matrix (below internode).

Original morphological trees (Fig. 1) also define the clade (*Bassariscus* (*Nasua*, *Procyon*)), although this clade is not recovered in our analysis of the abridged Baskin (2004) matrix (Fig. 4B). This clade is supported by nine and two putative synapomorphies in the Decker and Wozencraft (1991) and Baskin (2004) studies, respectively (Appendix A). When these synapomorphies are traced onto the molecular topology, their evolutionary transformations are differently resolved under ACCTRAN versus DELTRAN transformations. Under ACCTRAN, derived character states are resolved as symplesiomorphies among the three genera, with a secondary loss inferred for *Bassaricyon* (because *Bassaricyon* is grouped with *Potos* in morphological trees whereas it is grouped with *Nasua* in molecular trees). The same characters are resolved as convergences between *Nasua* versus the (*Bassariscus*, *Procyon*) clade with DELTRAN.

Because the original data matrix from Decker and Wozencraft (1991) was unavailable, we were unable to determine if other characters and their states in this matrix, under parsimony, were consistent with our molecular topology. We were able to explore this with Baskin (2004) matrix, however. Of the 40 characters included in his matrix, only one was consistent with our molecular topology: character 28, which defines relative placement of paraconid, protoconid and metaconid cusps on the m1 trigonid. There are four states for this character (see Appendix 1 in Baskin, 2004): 0 = paraconid, protoconid and metaconid more or less equally spaced; 1 = paraconid and metaconid close together; 2 = paraconid and metaconid adjacent; and

Table 4
Representative results of molecular divergence dating analyses using a Bayesian relaxed molecular clock method

Node	Age (mya)		
	Constraint set 1[a]	Constraint set 1[a]	Constraint set 2[b]
	Root prior = 24 mya	Root prior = 30 mya	Root prior = 24 mya
A	2.5 (1.2–4.7)	2.8 (1.3–5.0)	2.8 (1.5–4.8)
B	7.0 (3.7–12.1)	8.0 (4.1–12.9)	7.8 (4.8–12.3)
C	9.1 (4.9–15.4)	10.3 (5.4–16.1)	10.1 (6.5–15.7)
D	5.0 (2.6–8.7)	5.7 (2.8–9.2)	5.5 (3.3–8.9)
E	11.8 (6.4–19.7)	13.3 (7.0–20.6)	13.0 (8.5–19.9)
F	11.4 (6.2–19.0)	12.8 (6.8–19.8)	12.6 (8.2–19.3)
G	18.3 (10.3–29.7)	20.7 (11.1–30.9)	20.2 (14.0–30.1)
H	21.6 (12.1–34.8)	24.4 (13.3–36.0)	24.0 (16.7–35.2)

Point estimate of age is indicated for each node (labeled as in Fig. 3), with 95% credibility intervals (CI) shown in parentheses. Root priors indicate the mean of the prior distribution of root-to-tip age used in each run of the analysis.

[a] Constraint set 1: conservative set of four fossil constraints (minima for nodes E, F and H, and maximum for node H), as described in Section 2.

[b] Constraint set 2: more restrictive set of five fossil constraints: (i–iii) minima for nodes E and F, and maximum for node H kept as in set 1; (iv) minimum of 11.2 mya based on the earliest putative *Bassariscus* fossil moved from node H to node G, thus making a less conservative assumption about its phylogenetic placement; and (v) new minimum (16.4 mya) added for node H, based on the young end of the Early Miocene interval, from which the fossil taxon *Broiliana* is used as a calibration for crown Procyonidae.

3 = paraconid blade-like, anteriorly placed. State 3 is inferred to be plesiomorphic, as this is the state coded for *Amphictis* (the outgroup). State 1 unites the (*Bassariscus*, *Procyon*) clade whereas state 2 unites the (*Bassaricyon*, *Nasua*) clade. However, character 28 is coded as a "?" for *Potos*, which renders interpretation of the state transformations for this character equivocal for the other two clades in the molecular tree.

3.3. Divergence time estimates

We estimated divergence times of eight nodes of the molecular topology of the ingroup using the Bayesian relaxed molecular clock method (Thorne et al., 1998; Kishino et al., 2001). Posterior distributions of nodal ages were very consistent among multiple runs, and were usually robust to changes in fossil constraint configurations and moderate alterations of prior root ages. Major changes (e.g., halving the value) in the root age prior had an impact on the posterior point estimates, although credibility intervals remained largely overlapping. Prior ages and nodal constraints that are consistent with conservative assumptions about the procyonid fossil record were used in the final runs, whose results are indicated in Table 4.

Divergence time estimates suggest that the genera originated and diversified during the Miocene epoch, 23.8–5.3 mya (Fig. 6). The split between *Potos* and the remaining procyonids (node H) is estimated to have occurred 21.6–24 mya (95% CI = 12.1–36.0 mya), depending on the constraint set and root prior used. Estimated divergence between the (*Bassaricyon*, *Nasua*) and (*Bassariscus*, *Procyon*) clades (node G) is 18.3–20.7 mya (CI = 10.3–30.9 mya). Interestingly, the split between *Bassaricyon* and *Nasua* (node E, 11.8–13.3 mya, CI = 6.4–20.6) and that between *Bassariscus* and *Procyon* (node F, 11.4–12.8 mya, CI = 6.2–19.8) occurred nearly simultaneously at the end of the Middle Miocene. The divergence between sister species within *Nasua*, *Bassariscus*, and *Procyon* (nodes B, C, and D, respectively) occurred in the Late Miocene (Table 4), whereas divergence between the two putative species of *Bassaricyon* (node A) is estimated at 2.5–2.8 mya (CI = 1.2–5.0 mya), which coincides with the Late Pliocene.

4. Discussion

4.1. Incongruence between molecular- and morphology-based procyonid phylogenies

Phylogenetic analyses of the supermatrix using four different methods of tree reconstruction (MP, ML, ME and BI) all strongly support the existence of three lineages: a (*Bassaricyon*, *Nasua*) clade, a (*Bassariscus*, *Procyon*) clade, and a *Potos* lineage (Figs. 2 and 3). This molecular phylogeny challenges recent views of the evolutionary relationships within the Procyonidae based on cladistic analyses of morphological data (Decker and Wozencraft, 1991; Baskin, 2004). In fact, molecular and morphological data sets recover strongly supported topologies that are incompatible with one another. For example, whereas our supermatrix shows that olingos (*Bassaricyon*) and coatis (*Nasua*) are each other's closest relative, the morphological matrices strongly support a grouping of olingos with kinkajous (*Potos*) and a grouping of coatis with raccoons (*Procyon*). *Bassariscus* is usually characterized as having a primitive dental morphology that distinguishes it from fossil and recent taxa with more derived hypocarnivorous dentitions (Baskin, 1982, 1989, 2004). Cladistic analyses of morphology lend support to this characterization, as *Bassariscus* has been suggested as the earliest diverging lineage within the Procyonini or Procyoninae (Fig. 1). Our molecular phylogeny, however, shows that *Bassariscus* is the sister group to *Procyon*, suggesting that the dentition of *Bassariscus* may not be so primitive after all.

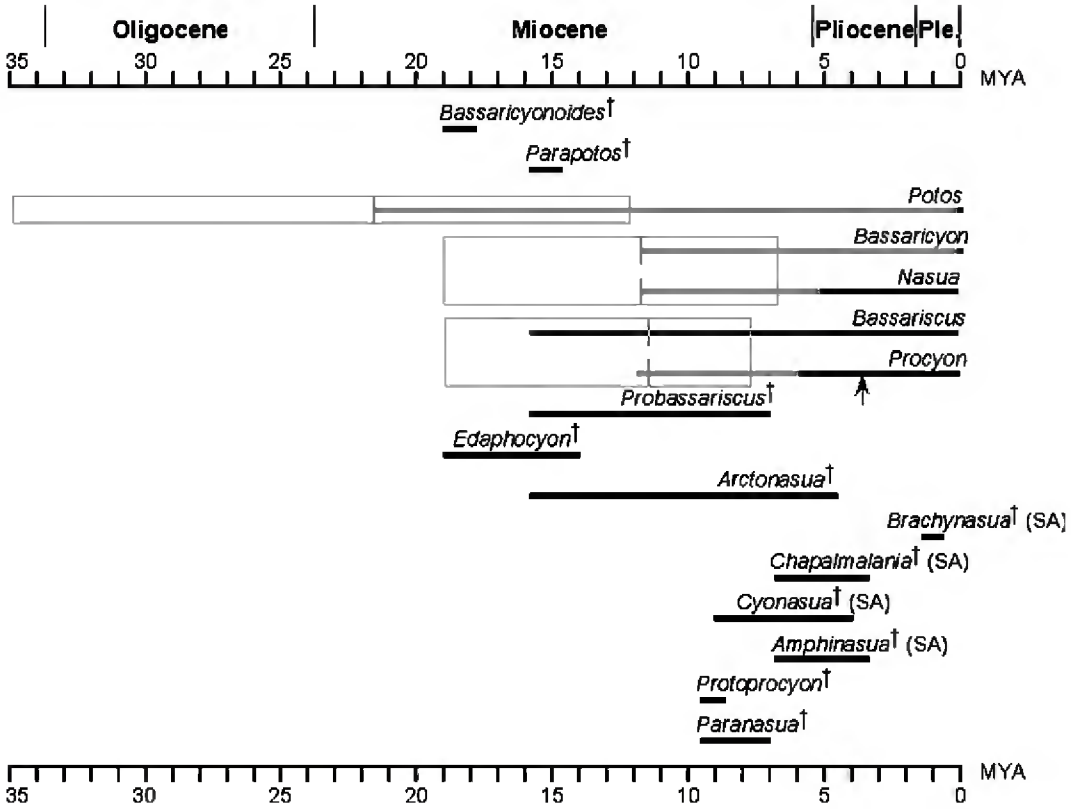

Fig. 6. Temporal ranges of extant and fossil New World procyonid genera. Extinct genera are denoted with a cross (†). Black lines indicate temporal range based on fossil evidence (McKenna and Bell, 1997; Baskin, 1982, 1998, 2003, 2004). Gray lines appended to extant genera indicate temporal range estimates based on analyses of the molecular supermatrix using a Bayesian relaxed molecular clock (see Table 4). *Bassaricyon* and *Potos* lack a fossil record and are, therefore, considered recent (McKenna and Bell, 1997). Arrow under temporal range of *Procyon* indicates earliest age based on McKenna and Bell (1997). Vertical gray lines represent mean Bayesian posterior divergence time estimates and red boxes are 95% credibility intervals for estimated divergence times. (SA) refers to genera endemic to South America. Ple., Pleistocene.

To assess which tree estimate is more likely to be correct, we first determined whether the incongruence between data sets is real (i.e., different biological and/or evolutionary processes have affected the data sets in ways such that they record different historic events) or is the result of an artifact related to sampling or methodology (Wendel and Doyle, 1998; Hillis and Wiens, 2000). In comparing our supermatrix with Baskin's (2004) matrix, we attempted to account for such possible sources of incongruence. First, incongruence is not due to weak support of relationships in one data set versus the other, which would suggest an undersampling of characters or high levels of homoplasy in one or the other data set. Bootstrap analyses of parsimony trees reconstructed from both data sets indicate that conflicting nodes are strongly supported by each data set (Figs. 3 and 4A). Furthermore, when all fossil taxa of the ingroup are removed from the Baskin (2004) matrix, bootstrap values increase and nodes remain significantly conflicting with those of the supermatrix tree (Fig. 4B). Second, both data sets were analyzed with the same optimality criterion (MP), and, therefore, incongruence is not a result of use of different methods of phylogeny reconstruction and thus different assumptions about character evolution. Third, incongruence could result from use of different outgroups or from use of different numbers of taxa in each data set. We accounted for these possible artifacts by performing unrooted MP and bootstrap analyses on the supermatrix and the abridged Baskin (2004) matrix. Relationships in unrooted trees from the two data sets, each recovered by exhaustive searches, remain significantly incongruent with one another (Figs. 5A and B). Thus, the cause of incongruence between molecular and morphological data sets does not arise from choice of phylogeny reconstruction method, use of different outgroups, or weak nodal support in one data set versus the other.

When putative synapomorphies from the morphological data sets are mapped onto the molecular topology, many are resolved as homoplasies due to convergence or reversals of character states. These results suggest that incongruence between molecular and morphological trees may partly arise from misleading effects of adaptive convergence in morphological characters. Wiens et al. (2003) proposed several criteria for detecting morphological convergence among unrelated taxa resulting in an inaccurate estimate of phylogeny relative to an independent (e.g., molecular) data set. Criteria include: (1) strong morphological support for clades containing taxa that share a similar selective environment; (2) characters that define clades in the morphology-based tree are associated with the shared selective environment and are thus likely adaptive for that

environment; and (3) a molecular topology based on a multilocus data set shows that species with similar selective environments are not monophyletic. Importantly in this context, the multilocus component of the molecular data set would support the notion that included segments are not subject to identical selective pressures, as they participate in a variety of cellular and metabolic processes assumed to be unrelated.

Our results are consistent with an interpretation that ecological adaptation to similar habitats and diets in unrelated taxa has confounded cladistic analyses of cranial, dental and postcranial characters in the Procyonidae. For example, kinkajous and olingos are both arboreal frugivores and share many ecological and behavioral traits (Ford and Hoffmann, 1988; Kays, 1999, 2000). Adaptations to arboreality include a short rostrum and forwardly directed orbits for stereoscopic vision, short limbs with sharply curved claws, furred soles, and a long tail (prehensile in the kinkajou). Adaptations to frugivory in both taxa include bunodont dentition with a reduced number of cusps on molars and greater development of masticatory musculature in the mediolateral plane compared to the sagittal plane (Story, 1951; Decker and Wozencraft, 1991). Indeed, a reduced number of molar cusps is one character state that unites *Bassaricyon* + *Potos* in the Decker and Wozencraft (1991) phylogeny and the dental characters uniting these same taxa in Baskin (2004) reflect bunodonty. Ecological similarities between coatis and raccoons may have also resulted in convergent or parallel evolution of morphology in these taxa. Both genera are omnivorous, with highly tuberculate molars and longer rostra relative to kinkajous and olingos. Both coatis and raccoons inhabit forested habitats, forage on the ground and in the trees, and are good climbers and use their forepaws to manipulate prey (Lotze and Anderson, 1979; Gompper, 1995; Gompper and Decker, 1998). As with kinkajous and olingos, putative cranial and dental synapomorphies that group coatis and raccoons (Decker and Wozencraft, 1991; Baskin, 2004) are shown to be homoplasies when mapped onto the molecular phylogeny (under both ACCTRAN and DELTRAN transformation).

Arguments with regards to phylogenetically misleading effects of convergence assume, however, that morphological characters used in procyonid phylogeny reconstruction are *actually adaptive* for a particular habitat or lifestyle (criterion 2 in Wiens et al., 2003). This is difficult to demonstrate in general, but especially so for characters that have been established through the atomization of a trait for phylogenetic purposes. The dental characters in the Baskin (2004) matrix may indeed reflect adaptation to differing diets among procyonid genera, as tooth morphology is strongly correlated with diet in many mammals, including the Carnivora (e.g., Van Valkenburgh and Koepfli, 1993; Friscia et al., in press). Moreover, high bootstrap support for conflicting nodes in the Baskin (2004) tree do unite taxa that tend to share a similar diet, for example *Bassaricyon* and *Potos* (criterion 1 in Wiens et al., 2003), suggesting that the source of incongruence between the supermatrix phylogeny and the Baskin (2004) phylogeny is not due to randomly distributed phylogenetic signal in the Baskin (2004) matrix (Wenzel and Siddall, 1999; Wiens et al., 2003; Gaubert et al., 2006). This is also confirmed by the high CI and RI values of the unabridged and abridged analyses of the Baskin (2004) matrix (Fig. 4).

The adaptive value of some putative synapomorphies found in Decker and Wozencraft (1991) is somewhat more difficult to evaluate because they include cranial, dental, postcranial and soft anatomical characters. Nine characters unite *Bassaricyon* + *Potos*, and while some may be associated with adaptation to arboreality (e.g., sharply angled acromion process) and a particular diet (<3 cusps on molars), the functional significance is not clear for others (e.g., short and rounded external pinnae and short and stout malleus). Similarly, nine characters unite *Bassariscus* + *Nasua* + *Nasuella* + *Procyon* into the "Procyoninae" in the Decker and Wozencraft (1991) phylogeny (Fig. 1B). These are resolved as plesiomorphies or homoplasies depending on the method of character state optimization used. Three are dental characters, four are cranial, one is postcranial, and one is a soft anatomical character (presence of banded tail rings). Such coat patterns, however, although less distinct, are present in *Bassaricyon* (Nowak, 2005), suggesting that this character is plesiomorphic for all taxa except *Potos*. Nonetheless, comparative analyses suggest that tail rings, coupled with tail movement, may function in communication and thus be adaptive for species inhabiting forest habitats (Ortolani, 1999). Determining the adaptive value, if any, of the characters that define the "Procyoninae" is made more difficult by the fact that *Bassariscus*, *Nasua* and *Procyon* inhabit a diversity of environments and have extremely varied diets across their ranges.

Phylogenetically misleading effects of convergence may be exacerbated if morphological characters are not independent, especially if characters are developmentally, genetically, and/or functionally correlated (Felsenstein, 1988; Shaffer et al., 1991; Emerson and Hastings, 1998; Wiens et al., 2003). Non-independence of characters may apply to the Baskin (2004) data set in particular. Thirty of the 40 characters (75%) in the Baskin (2004) data matrix are dental characters, and 25 of these characters are based on just four teeth (P4, M1, m1, and m2) that have been atomized into four (m2), six (P4, m1) and nine (M1) separate characters. Moreover, in several cases, a particular dental character is subdivided into two separate characters (e.g., characters 24 and 25 deal with the presence or absence and the position, if present, of the M1 metaconule, respectively; Baskin, 2004). While such atomization of dental morphology increases the power of cladistic analyses (more characters = potentially more resolving power), such a strategy is problematic because empirical studies demonstrate that teeth are developmentally and functionally integrated structures (e.g., Gingerich and Winkler, 1979; Polly, 1998; Jernvall and Jung, 2000). For example, Kangas et al. (2004) have shown that small modifications in

the expression of a *single gene* in the enamel knot of developing mouse teeth can result in correlated state changes for multiple dental characters (number of teeth as well as cusp shape and position). Furthermore, cusp number and shape have been shown to be tightly integrated through a *shared* developmental genetic program (Jernvall et al., 2000; Jernvall and Jung, 2000). Individual molar cusps develop iteratively from secondary enamel knots through activation of the same set of genes (Jernvall et al., 2000), which can be deactivated and reactivated, causing character states to appear and disappear over evolutionary time (Jernvall and Jung, 2000). Moreover, this shared developmental information is likely propagated through both upper and lower jaws, thereby further limiting the independence of serially homologous structures such as teeth (e.g., Van Valen, 1994). Such pleiotropic effects on tooth morphology challenge the method of atomizing a tooth into separate characters and assuming that they are independently heritable and acted upon separately by natural selection.

An example of potentially correlated (and thus non-independent) characters in the Baskin (2004) matrix are the four characters that unite *Bassaricyon* + *Potos*: two from the P4 (absence of the metacone blade and presence of the parastyle) and two from the m1 molar: (a very reduced or absent paraconid and an unbasined talonid). Not only are individual cusps of these two teeth likely to be developmentally correlated (where no single gene codes for each individual cusp; Jernvall and Jung, 2000), but these two teeth and their associated cusps form a functionally correlated complex, the carnassial. Changes to one P4 cusp will probably result in a concomitant evolutionary change in morphology of the m1, to maintain functional occlusion between the two teeth and efficient food processing capability. Such atomization of non-independent characters has the potential to inflate homoplasy and result in incorrect yet well-supported phylogenies, especially if selection acts on an entire trait such as a molar.

Although nucleotide sites can also be affected by non-independence, particularly within genes (e.g., Cummings et al., 1995), our supermatrix topology is supported by multiple lines of independent evidence. First, the supermatrix topology is recovered in separate phylogenetic analyses of concatenated nuclear and mitochondrial sequence data (Fig. 2). Because loci are derived from different genomic compartments (nuclear versus mitochondrial) and the nuclear gene segments are derived from unlinked genes and, therefore, represent markers with presumably independent evolutionary histories, these results indicate that the gene trees derived from our sampled loci are tracing the same evolutionary history. Moreover, patterns of relationship are not due to phylogenetic signal arising from relatively few loci. For example, separate analyses of the 11 gene segments using MP and ME with bootstrapping shows that the (*Bassaricyon*, *Nasua*) and (*Bassariscus*, *Procyon*) clades are recovered by 10 and 9 of the gene segments, respectively, with high bootstrap support (Table 5). It is unlikely that all segments would be biased by natural selection in an identical or correlated fashion, as they participate in a variety of unrelated cellular and molecular processes.

Second, the (*Bassaricyon*, *Nasua*) and (*Bassariscus*, *Procyon*) clades are each supported by informative indels and the (*Bassaricyon*, *Nasua*) clade is further supported by sharing a *CYTb* gene structure that is two codons longer than in other procyonid taxa. Third, the finding that *Procyon* and *Bassariscus* are sister taxa is supported by immunological distance analyses (Sarich, 1973) and affinity of *Bassaricyon* and *Nasua* is supported by shared inversions on chromosomes 2 and 6 in these taxa (Couturier and Dutrillaux, 1986). Fourth, statistical tests (Kishino and Hasegawa, 1989) based on ML using PAUP* strongly favor the molecular topology of procyonid genera over the morphology-based topologies ($-\ln L$ molecular topology = 22697.196 versus $-\ln L$ morphological topologies = 22990.308; difference in $-\ln L = 293.112$, $P < 0.05$). Finally, even when the molecular supermatrix plus 40 morphological characters from Baskin (2004) are analyzed simultaneously, the unrooted network topology is identical to the one derived from analysis of the supermatrix alone (Fig. 5C), with high positive PBS values contributed by the supermatrix. This

Table 5
Bootstrap values derived from separate maximum parsimony (MP) and minimum evolution (ME) analyses of the 11 gene segments for three procyonid clades

	(*Bassaricyon*, *Nasua*)		(*Bassariscus*, *Procyon*)		((*Bassaricyon*, *Nasua*) (*Bassariscus*, *Procyon*))	
	MP	ME	MP	ME	MP	ME
ADORA3	87	75	88	90	98	99
APOB	72	87	91	88	90	92
BDNF	91	94	65	65	<50	<50
CHRNA1	100	99	87	78	69	55
COL10A1	96	94	70	75	83	79
PNOC	89	90	82	85	55	56
RAG1	99	99	97	98	<50	—[a]
RAG2	97	98	84	66	62	61
WT1	99	96	100	100	93	97
CYTb	69	99	99	100	<50	54
NADH5	<50	59	<50	<50	<50	<50

[a] In the ME analysis of *RAG1*, *Potos* was joined as the sister taxon to the (*Bassariscus*, *Procyon*) clade with a bootstrap value of 68%.

further suggests that the molecular supermatrix contains a greater number of independent characters and thus robust support for relationships relative to Baskin's (2004) morphological matrix (see Kluge, 1989).

Our results showing incongruence between molecular and morphological estimates of procyonid phylogeny are mirrored in phylogenetic studies of other families of the Carnivora. For example, in Viverridae (genets and civets), morphological similarity in craniodental features between African and Asian linsangs (*Poiana* and *Prionodon*, respectively) has traditionally led researchers to consider these genera to be closely related. These taxa share a similar spotted coat pattern, both are hypercarnivorous and adapted to an arboreal lifestyle in heavily forested habitats (Nowak, 2005). Initial molecular studies suggested that this morphological similarity actually represents convergent evolution, as Asian linsangs (*Prionodon*) form the sister group to the cat family (Felidae) while the African linsangs (*Poiana*) form the sister group to the genets (Gaubert and Veron, 2003). As with procyonids, morphological characters thought to be reliable indicators of phylogeny (e.g., dentition and basicranial characters) were found to be highly homoplasious (Gaubert and Veron, 2003). Subsequent study, however, suggested that incongruence between molecular and morphological estimates of viverrid phylogeny was caused by the overall lack of structuring phylogenetic signal in morphological data rather than adaptive convergence (Gaubert et al., 2006). These authors noted the importance of having an independent molecular phylogeny as a reference for deducing true phylogenetic signal from morphological data. This approach, using a multigene molecular phylogeny to evaluate the veracity of morphological characters, has also been implemented for other taxa, particularly primates (Fleagle and McGraw, 1999, 2002; Collard and Wood, 2000; Strait and Grine, 2004).

4.2. Dating procyonid divergence and implications for the Great American Interchange

The molecular divergence times and fossil data, taken together, suggest that the Procyonidae is a product of a Miocene radiation. Divergence time estimates suggest that extant genera all originated and diversified during the Miocene epoch, which coincides with the first appearance of nearly all extinct procyonid genera (Fig. 6). Furthermore, these estimates are remarkably consistent with certain aspects of the procyonid fossil record, such as that for *Bassariscus*. Although our molecular estimate suggests a younger age for the origination of *Bassariscus*, compared to the minimum age of the earliest fossil for this taxon (*ca.* 15.9 mya, McKenna and Bell, 1997; Baskin, 2004), the 95% CI overlaps with the earlier age suggested by the fossil record (Fig. 6). For other taxa, our results support suggested gaps in the procyonid fossil record (*Bassaricyon* and *Potos* lack a fossil record altogether), with mean divergence times and 95% CIs indicating much earlier times of origin. In particular, the genetic distances separating *Potos* from the other taxa are consistently large for both mitochondrial and nuclear gene segments, indicating that *Potos* represents an ancient lineage that has been separated from other procyonid genera since the Early Miocene, and perhaps the Oligocene.

Molecular dating results also show that *Bassaricyon* vs. *Nasua* and *Bassariscus* vs. *Procyon* diverged contemporaneously near the end of the Middle Miocene, 11–12 mya (Fig. 6). Such correlated patterns of divergence between independent lineages is suggestive of the influence of major regional environmental processes on diversification (e.g., Delsuc et al., 2004). The poor fossil record of procyonids in general, and in the Neotropics in particular, precludes our ability to make meaningful inferences from intergeneric divergence times because the geographic location in North or Central America where diversification took place is uncertain. Also, although we were unable to sample *Nasuella*, a taxon found at high elevations in the Andes Mountains of northern South America, this taxon may be important in further understanding the context of procyonid diversification, particularly the influence of northern Andean uplift, which has been associated with the diversification of lineages within the Xenarthra (Delsuc et al., 2004). However, the mean divergence time estimate of 11–12 mya for the two pairs of genera coincides with a period of major global cooling, along with formation of the Antarctic ice sheet and a short-term but significant drop in global sea level (Haq et al., 1987; Zachos et al., 2001; Miller et al., 2005). The change in climate is associated with major vegetational changes across the globe, including the Neotropics, as forested environments were reduced and became mixed with expanding savanna-like environments (Potts and Behrensmeyer, 1992). These environmental events likely played a role in diversification of other clades of mammals (e.g., Mercer and Roth, 2003; Delsuc et al., 2004; Johnson et al., 2006), and, in this case, could have influenced connectivity of ancestral procyonid taxa among suitable areas in the New World prior to the formation of the Panamanian land bridge. Indeed, fossils of mammalian herbivores collected from the Panama Canal region with affinities to taxa in North America suggest that there was a broad connection between Central and North America during the Miocene (Whitmore and Stewart, 1965).

Timings of intrageneric splits range from Late Miocene to Late Pliocene (Table 4). Among these, the divergence time between the two putative species of *Bassaricyon* is the youngest, dated at *ca.* 2.5–2.8 mya (95% CI = 1.2–5.0 mya). This result should be treated with caution, however, given the uncertainty about the actual number of species included in *Bassaricyon* (see Section 5). The oldest intrageneric divergence occurs between *Bassariscus astutus* and *B. sumichrasti*, with a mean divergence time of *ca.* 9.1–10.3 mya in the Late Miocene (95% CI = 4.9–16.1 mya). This result lends additional support to earlier behavioral research that has shown that these two species display large differences in morphology, reproductive physiology and behavior, modes of communication, and ecology (Poglayen-Neuwall and Toweill, 1988; Poglayen-Neuwall and Poglayen-Neuwall, 1995). With regards to ecology, for example, *B. astutus*

inhabits dry tropical to semi-arid and montane woodland environments, is mainly terrestrial, and tends towards carnivory, whereas *B. sunichrasti* inhabits lowland tropical forests, is almost completely arboreal, and has a diet high in fruit and insects (Coates-Estrada and Estrada, 1986; Poglayen-Neuwall and Toweill, 1988 Poglayen-Neuwall and Poglayen-Neuwall, 1995).

Even more interesting are the divergence times within *Nasua* and *Procyon* because of their possible relevance to understanding faunal dynamics of the Great American Interchange (GAI). Procyonids figure prominently in the GAI, which involved reciprocal exchange of different lineages of formerly endemic mammals between North and South America due to formation of the Panamanian land bridge, *ca.* 3–2.5 mya (Marshall et al., 1979; Marshall, 1985, 1988; Webb, 1997). Fossil evidence suggests that procyonids dispersed from North America into South America on two different occasions, once before and once after the completion of the Panamanian land bridge (Webb, 1985). Procyonids are first recorded in South America in Late Miocene deposits from Argentina, represented by the fossil genus *Cyonasua*, which is morphologically similar and closely related to the North American extinct *Arctonasua* (Simpson, 1980; Baskin, 1982, 2004; Fig. 1A). *Cyonasua* is thought to have dispersed into South America via island hopping or rafting during the Late Miocene (Simpson's waif dispersal), when the inter-American seaway consisted of a large archipelago during a time when global sea level was relatively low (Haq et al., 1987; Coates and Obando, 1996; Coates, 1997; Miller et al., 2005). *Cyonasua* gave rise to a number of descendants, including the bear-sized *Chapalmalania*, but these South American endemic procyonids are thought to have gone extinct by the end of the Pliocene (Marshall, 1985). Procyonids, represented by the extant genera, are believed to have entered South America for a second time with other mammalian taxa as part of the "legions of the north" during the GAI *ca.* 2–3 mya, after the land bridge was completed (Simpson, 1980; Marshall, 1988; Marshall et al., 1979, 1982; Webb, 1985). Fossils of *Nasua nasua* and *Procyon cancrivorus* from South America are first recorded in Late Pleistocene deposits (Berta et al., 1978). Therefore, *Cyonasua* and its descendants are not considered to be progenitors to modern procyonid taxa that now inhabit South America, based on the temporal gap between occurrence of the two lineages in South America (Marshall, 1985; Webb, 1985) and on phylogenetic considerations (Baskin, 2004).

However, divergence times within *Nasua* and *Procyon*, coupled with consideration of present day configuration of the geographic ranges of sister species within these genera, suggest that these taxa may have entered South America at the same time as *Cyonasua* also via island hopping (as divergence time estimates suggest that the temporal gap separating these genera is now removed—Fig. 6). Estimates indicate that *N. narica* and *N. nasua* diverged *ca.* 7–8 mya, during the Late Miocene, whereas *P. cancrivorus* and *P. lotor* diverged *ca.* 5–5.7 mya, during the Early Pliocene. These divergence times well predate the final emplacement of the Panamanian land bridge, *ca.* 3–2.5 mya (Marshall et al., 1979; Marshall, 1985; Coates and Obando, 1996). The modern presence of North and South American sister taxa of *Procyon* and *Nasua* may be accounted for by pre-land bridge dispersal to South America (>3 mya), followed by isolation, drift and then secondary contact once the land bridge was completed. Inferring the mode of speciation or other historical processes from the configuration of modern day geographic ranges is obviously fraught with many problems (e.g., Losos and Glor, 2003). However, this hypothesis might eventually be tested through discovery of older fossils of *Nasua* and *Procyon* in Neotropical fossil localities (MacFadden, 2006).

5. Conclusions

The molecular phylogeny of the Procyonidae presented here highlights the morphological and ecological flexibility of these taxa. The available fossil record suggests that most procyonid genera, including extant genera, originated in southern North America and/or Central America (Simpson, 1945; Hershkovitz, 1972; Baskin, 1982, 1998; Webb, 1985). Although there is no evidence regarding the exact mode of speciation, diversification within such a limited geographic area would likely be driven by competition for resources, leading to ecological and morphological divergence of taxa (Darwin, 1859; Schluter, 2000), and may help explain why multiple procyonid genera can coexist within the same neotropical community (e.g., Bisbal, 1986; Kays, 2000; Márquez and Fariña, 2003).

Our findings suggest that procyonid phylogenetic relationships based on morphological evidence are problematic, and further, that phylogenetic hypotheses relating fossil and living taxa based primarily on dental evidence are also open to question because of extensive homoplasy associated with this type of evidence. This should not be taken as an indictment of *all* morphological characters, or even all those used in previous procyonid studies. Rather, careful study of dental and skeletal anatomy has shown that morphological features can accord with molecular estimates of phylogeny for a group (e.g., papionine primates; Fleagle and McGraw, 2002). Therefore, a thorough reevaluation of the morphology of procyonids in light of our molecular results would seem to be a fruitful avenue of research. Furthermore, understanding genetic bases of morphogenesis and ontogeny of cranial and dental characters can help to elucidate correlation or independence among morphological features and perhaps lead to better justifications for the atomization of characters or suites of characters (Lovejoy et al., 1999; Hlusko, 2004). For example, the study by Popwics (1998) on ontogeny of carnassial and postcarnassial teeth in ferrets (*Mustela putorius*) showed that while early stages of tooth ontogeny were similar to other carnivores, later stages of ontogeny resulted in species-specific dental morphologies. Such elegant studies, combined with an understanding of developmental genetics of

morphogenesis, provide a way to possibly differentiate homology from homoplasy (Lieberman, 2000) and thereby enhance the phylogenetic signal obtained from morphological traits. Understanding the genetic basis of phenotypic traits offers the best hope for deducing the historical forces that have influenced morphological evolution as well as improving our ability to reconstruct phylogenies that relate both fossil and living taxa.

Our results also suggest that earlier classifications of the Procyonidae (Decker and Wozencraft, 1991; McKenna and Bell, 1997; Baskin, 2004) need to be revised. The molecular phylogeny indicates that subfamilies or tribes defined on the basis of cladistic morphological analyses do not accurately reflect genealogical history of the family. The molecular phylogeny is consistent with the classification proposed by Trouessart (1904), in which *Potos* is placed as the sole member of the Potosinae and all other genera are placed within Procyoninae.

However, beyond these issues is the greater concern over uncertainty surrounding the exact number of species that comprise the Procyonidae (Glatston, 1994). First, it is still unknown how many species of olingo exist. Some consider the five described species to represent only one or two species at most. Second, multiple populations of *Procyon*, and one *Nasua*, are endemic to Caribbean islands. While most of these may be recent introductions, others have a long history of isolation (Pons et al., 1999; Cuarón et al., 2002; Helgen and Wilson, 2002, 2003, 2005; McFadden, 2004). Such examples highlight how little we actually know about the Procyonidae, and call for the need for further molecular systematic studies to not only help us close these gaps in knowledge, but also to help establish a solid foundation for the conservation of procyonid biodiversity (e.g., Avise, 1989).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2006.10.003.

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