Ailurid Evolution: From Late Paleocene to Holocene

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ABSTRACT

The red panda *(Ailurus fulgens)* is the only extant member of the family Ailuridae. These species evolved in Order Carnivora but presently are obligate bamboo eaters. Red pandas have several adaptations to assist them in their current environmental roles but still retain many Carnivora characteristics. Some of these adaptations have been present since the Miocene.

Ailurids began in Eurasia and spread into North America. Once on both continents, members of the Ailurid family evolved simultaneously in both the New and Old World. Eventually, all New World species went extinct, leaving only the Ailuridae in Asia.

INTRODUCTION

Presently, there are two species that make up the family Ailuridae, the Chinese red panda *(Ailurus fulgens refulgens)* and the Himalayan red panda *(Ailurus fulgens fulgens*). This makes Ailuridae one of the smallest extant mammalian families. However, this family was once widespread and successful, with traces seen as early as the Late Oligocene to Early Miocene (18-20 million years ago). Though today's red pandas are only found in Nepal, Bhutan, China, Myanmar, and India (Thapa et al., 2018) their ancestors once lived in Europe and North America as well (Wallace, 2011). Broadly, Ailuridae is part of Order Carnivora, which is distinguished from other orders in part by the presence of a carnassial blade formed by the upper fourth premolar and lower first molar and fusion of the scaphoid/lunar carpals (Cope, 1879). However, the extant species of red pandas rarely eat meat and instead rely on bamboo to make up the bulk of their diet (Pradhan, 2001). They are also arboreal, spending the majority of their time in the trees as opposed to being more terrestrial like their ancestors (Salesa et al., 2011). These lifestyle changes have caused red pandas to develop attributes to help them adapt to their new diet and habitat. However, red pandas still retain many traits linking it to its carnivorous past.

MIACIDS

Approximately 65.5 million years ago during the Paleocene lived a small carnivoramorph who would give rise to modern carnivorans (Wesley-Hunt and Flynn 2005). Unfortunately, due to a sparse fossil record from this time, and rapid diversification of modern carnivoran lineages during the Oligocene, the exact earliest carnivoran fossil is unknown (Wesley-Hunt and Flynn, 2005). One early relative of early carnivorous mammals was the miacid, which belonged to the clade Carnivoramorpha (Miacoidea + Carnivora) and the paraphyletic group Miacoidea (Wesley-Hunt and Flynn, 2005). Miacids were found across North America and Europe (Wang, 2000). They had binocular vision and larger brains than the Credonts who were the other family of carnivorous mammals which lived at the same time. The Credonts were a dog-like mammal with a long skull (Macdonald, 1992). Miacids are thought to have been omnivores and as carnivoramorphs, they possessed Carnivora type carnassials, both molars as well as premolars, and a total number of 44 teeth (Wang, 2000). It was these premolars that likely allowed Carnivoramorpha to dominate the Creodonts, also referred to as *Pseudocreodi*, or “archaic carnivores”. The Creodonts lacked premolars, forcing them to be obligate carnivores while premolars allowed Carnivoramorphs to grind up objects like grasses and fruits when meat was scarce (see Figure 1), thus giving them a better chance of survival with a wider range of diet (Macdonald, 1992). One basal example of a Carnivoramorph is the genus *Miacis*, which was only about the size of today's ferret (see Figure 1.1).

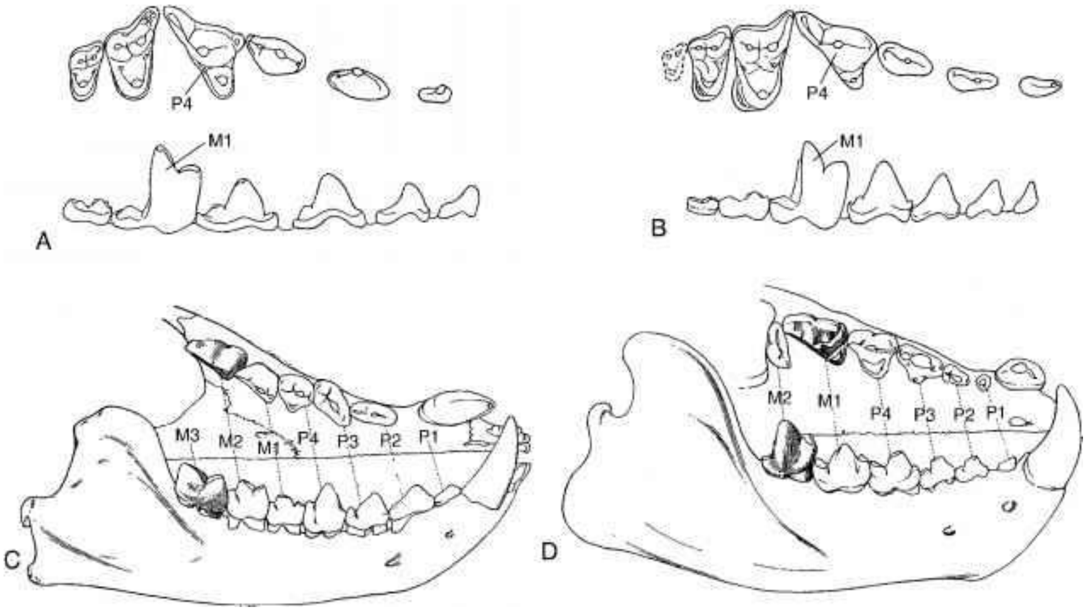

Figure 1 A, B show molar and carnassial placement in carnivorans. C, D show molar and carnassial placement in Credonts (Fossil Hunter, 2020).

Figure 1.1 Artists depiction of *Miacis* from Wang (2000).

CARNIVORA

The most basal true carnivoran gave rise to the two main branches of order Carnivora about 55 million years ago during the Eocene (Wang, 2000). These two branches were the suborder Caniformia, or the "dog-like" carnivorans, and the suborder Feliformia, or cat-like" carnivorans (Wang, 2000). Caniformia eventually split into Amphicyonidae ("bear-dogs"), Canidae, and the infraorder Arctoidea (Ursidae+Pinnipedia+Musteloidea) (Flynn et al., 2005). Following Flynn et al. (2005) Arctoidea is comprised of three main clades: Ursoidea (Ursidae+Hemicyonidae), Pinnipedia (Enaliarctidae+Phocidae+[Otariidae+Odobenidae]), and Musteloidea (Ailuridae+Mephitidae+[Procyonidae+Mustelidae]) (see Figures 2, 2.1). Early musteloids first appeared during the late Eocene in North America, and during the early Oligocene in Europe (Salesa et al., 2011).

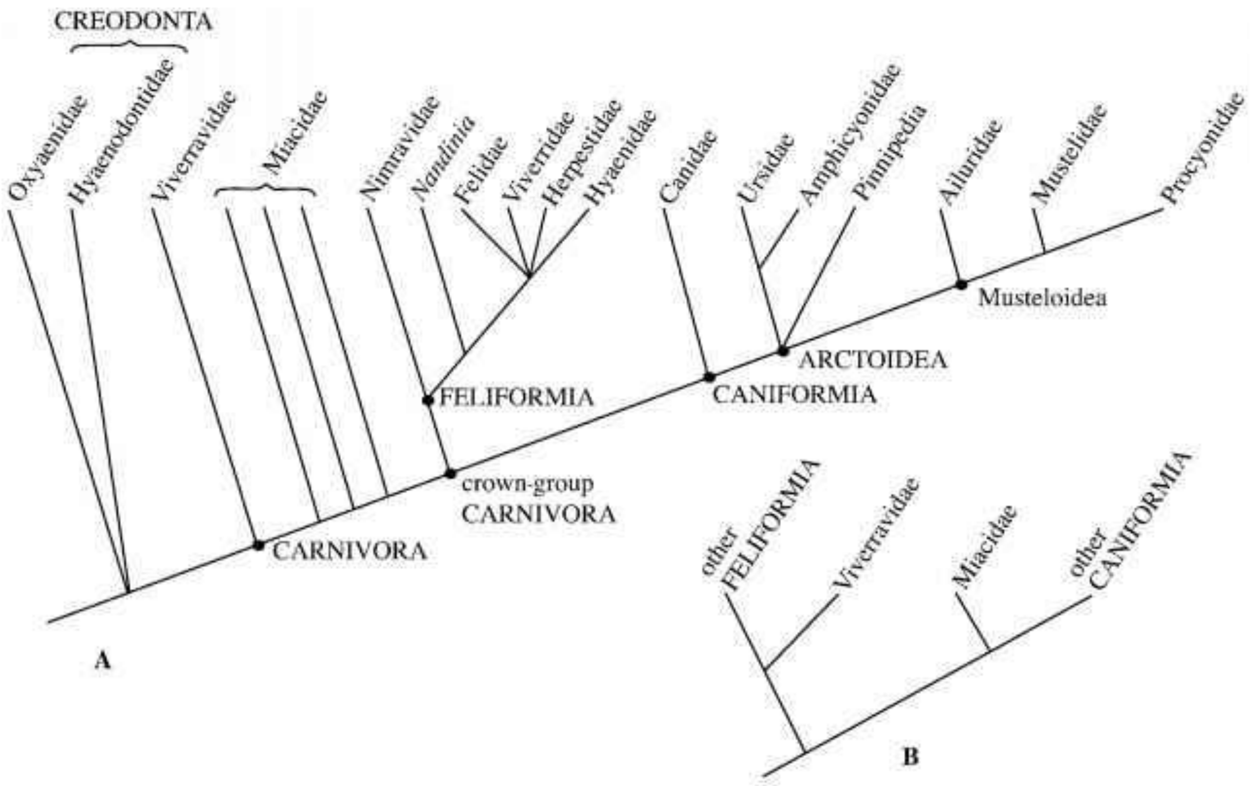

Figure 2 Early phylogenetic tree showing Credonta as well as Carnivora and Caniformia branches (Fossil Hunter, 2020).

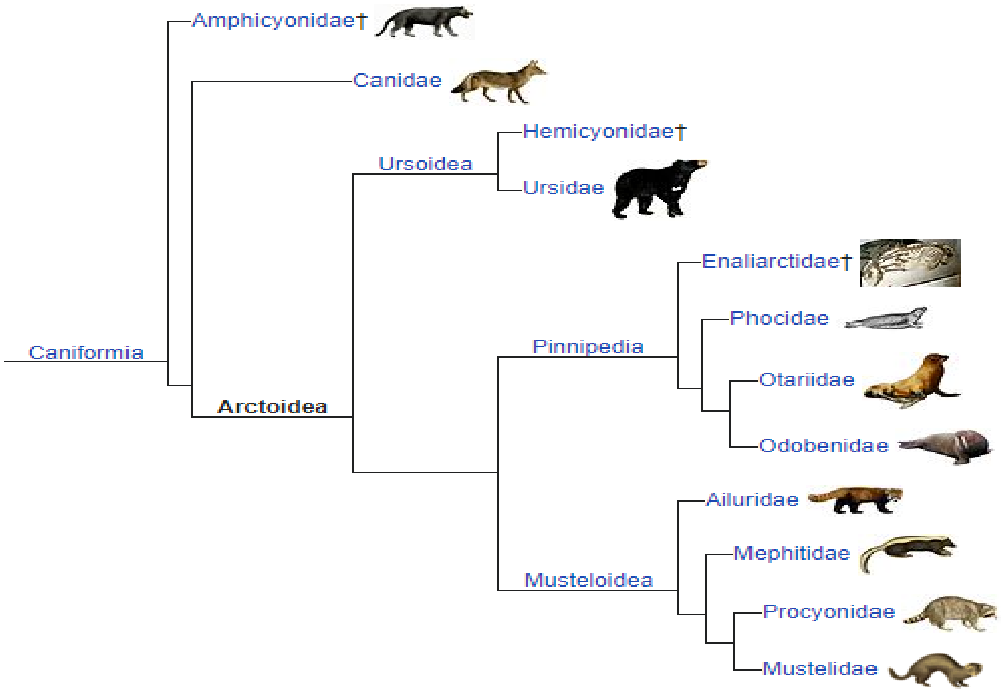

Figure 2.1 Caniformia cladogram (Lyon, 2017).

AILURIDAE

Ailurids most likely originated in Europe during the Late Oligocene to Early Miocene (25 to 18 million years ago), with the earliest known genus *Amphictis* (Salesa et al., 2011). This animal was approximately the size of extant red pandas *(Ailurus fulgens)* but had a more basal dentition resembling that of canids and mustelids (Salesa et al., 2011). *Amphictis* most likely had a diet of small invertebrates, fruits, bugs, and eggs (Salesa et al., 2011). Specimens from this genus have been found across the United Kingdom, Slovakia, Hungary, Germany, and France (Kundrat, 2011).

Other early ailurids were *Alopecocyon* and *Actiocyon* (possible junior synonym to *Alopecocyon*), which both lived during the Middle Miocene with the former occuring in Europe and Asia, and the latter in North America (Salesa et al., 2011). Both genera had dentition that leaned slightly closer to herbivory than *Amphictis*, though there hasn't been much found in regards to either genera. *Alopecocyon* and *Actiocyon* represent the first movement of Ailurids into North America most likely by way of the Beringia land bridge (Haag, 1962).

Members of the subfamily Simocyoninae, the genus *Simocyon* is known from the Miocene/Pliocene across the northern Hemisphere (Salesa et al., 2011; Wallace, 2011). More material has been found than with previously discussed taxa, giving researchers a much more extensive understanding of its lifestyle. *Simocyon* was about the size of the extant mountain lion, and was most likely a generalized carnivore due to it's dentition (Salesa et al., 2011). The most well known species and also the earliest fossil record of the genus, *Simocyon batalleri*, lived during the Late Miocene (11.1 to 8.7 million years ago) in Spain (Salesa et al., 2011). This taxon had relatively smaller canines compared to the more basal, or early ailurids, with four premolars, and two molars (Salesa et al., 2011). The younger species, *Simocyon primigenius*, lived during the Late Miocene (8.7 to 5.3 million years ago), and had just one premolar but the same number of molars as *Simocyon batalleri*, however, the general morphology of the teeth is still similar to basal ailurids. Unlike today's red pandas, *Simocyon* was a large hyper-carnivore. Due to the evolution of a pseudothumb, first seen in the Miocene and present in today's extant red pandas, *Simocyon* developed climbing abilities and was able to forage on the ground for carrion as well as in the trees for fruits and seeds (Wallace, 2011).

AILURINAE

In Spain, the first probable member of Ailurinae, a subfamily of Ailuridae, was discovered, *Magerictis* (Wallace, 2011). This species lived during the Miocene approximately 16 to 17 million years ago but very little material has been found of *Magerictis*. However, the material that has been found has had enough diagnostic characters on the teeth to place it within this subfamily (Wallace, 2011). Due to the lack of physical findings for this species it is difficult to determine exactly where this taxon lies within Ailuridae, however the lower second molar (m2) has an elongated talonid base and well-defined cusps like other ailurines (Wallace, 2011).

During the early Pliocene, species belonging to the genus *Parailurus* were residing in Europe as well as in North America. Cranial fragments have been found from individuals belonging to *Parailurus* in England, Russia, Japan, Romania, and Slovakia as well as several different areas across Asia. The oldest of these fossil *Parailurus* was found in England. While not all the bone fragments have been assigned a species as of yet, *Parailurus* contained at least three separate species including the currently unnamed species found in Slovakia. The other two Old World species in this genus are *Parailurus anglicus*, the species found in England (and its junior synonym *Parailurus hungaricus*) and *Parailurus baikalicus*. The tooth found in Japan belonging to *Parailurus* comes from a species other than *Parailurus anglicus*. The species in Japan has a transverse width of the fourth premolar (p4) that is longer than the anteroposterior length. The opposite is true for *Parailurus anglicus* (Sasagawa et al., 2010).

In the New World, an Early Plilocene tooth surfaced in Washington State, proving to be the first New World *Parailurus* species. However, this species is currently unnamed and no other bone fragments have been found. Despite the lack of fossil evidence, researchers can confirm that this species was designed to grind vegetation (Wallace, 2001). A mandible was found in the Belgrade Formation in North Carolina as well. However this specimen is most closely related to specimens found in France and

Germany, *Amphictis ambiguus* and *Amphictis schlosseri* respectively (Baskin et al., 2020) than the *Parailurus* tooth found in Washington State.

One of the most well documented Ailurinae species is *Pristinailurus bristoli.* This species was found at Gray Fossil Site in northeast Tennessee in the United States. Multiple ailurid skeletons have been found at this Late Miocene site, allowing researchers to thoroughly study *P. bristoli* as well as compare its skeletal structure with that of extant red pandas. The distinctive cusp pattern on the molars and lateral grooves on the canines placed this specimen in the *Ailurid* family but it is a separate species from the others found in North America (see Figure 3, 3.1). *Pristinailurus bristoli* was larger than *A. fulgens* but smaller (see Figure 3.2, 3.3, 3.4) than the *Parailurus* found in Washington State. However, the teeth of *P. bristoli* are less advanced than those of the Washington State specimen (Wallace, 2011). *P. bristoli* also shows sexual dimorphism with males being larger than females, a trait not seen in *A. fulgens* (Fulwood, 2015).

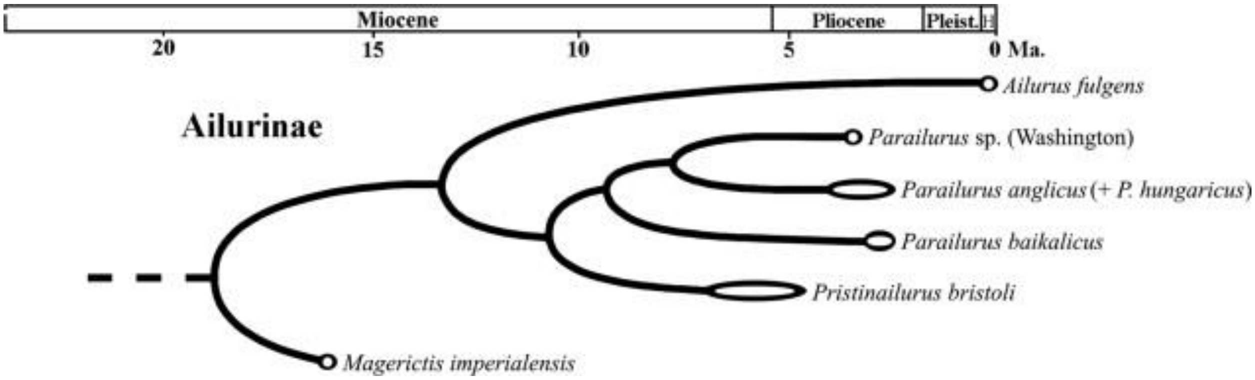

Figure 3 Phylogenetic relationships and temporal ranges of Ailuridae and other related families (Wallace, 2011).

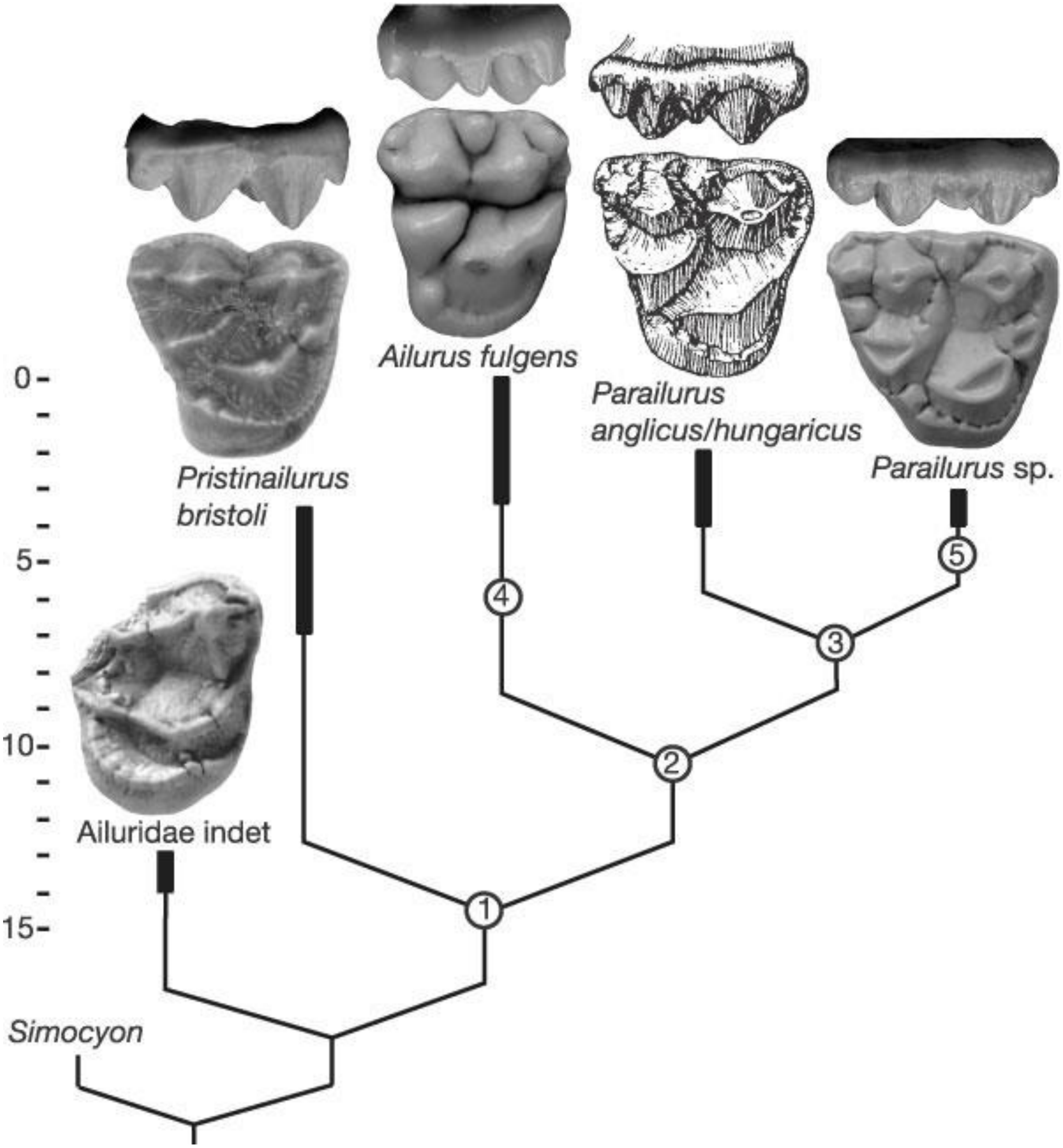

Figure 3.1 Evolutionary changes in ailurid teeth (Wallace and Wang, 2004).

Figure 3.2 Fossil *Pristinailurus bristoli* on the left, extant red panda, *Ailurus fulgens*, on the right. Note the longer snout and skull as well as the lack of a sagittal crest, all indicative of a less powerful bite than *Ailurus fulgens* (All About Gray Fossil Site's Red Panda, 2015).

Figure 3.3 *Pristinailurus bristoli* (All About Gray Fossil Site's Red Panda, 2015).

Figure 3.4 *Pristinailurus bristoli*, rear, and *Ailurus fulgens*, front (All About Gray Fossil Site's Red Panda, 2015).

DELINEATION OF SPECIES

There has been much debate about which family the red pandas should be placed with. Some researchers argue that they are closer to Procyonidae while others put them with Mustelidae or Mephitidae. Another hypothesis is that Ailuridae belongs in the larger Musteloid clade that includes both Procyonidae as well as Mustelidae. Despite the questions surrounding which family Ailuride is closest to, it has been definitively ruled out of the Ursid family (Wallace, 2011). However, most scientists tend to treat Ailuridae as a monotypic family in the Musteloida clade (Wallace, 2001). The most current Ailuridae lineage begins with Caniformia, which breaks into Arctoidea, and then superfamily Musteloidia which is sister to the monophyletic Pinnipedia (Sato et al., 2009). From the superfamily Musteloidia, there are four families. These families are Procyonidae, Mustelidae, Mephitidae, and Ailuridae. It is still being debated whether Mephitidae or Ailuridae is Musteloidiea’s basal most branch (Morlo and Peigne, 2010). However, study of the forelimbs muscular morphology in the extant red panda reveals basal muscle structuring, supporting ailurids role as a basal branch of Musteloidiea (Fisher et al., 2009).

Recently, it was determined that there are actually two separate species of red panda, the Chinese and the Himalayan. The Chinese red panda *(Ailurus fulgens refulgens*, also referred to as *Ailurus fulgens styani)* is the larger and darker of the two species. The Himalayan *(Ailurus fulgens fulgens)* is smaller in size and lighter in color

(Hu et al., 2020). Researchers analyzed mitochondrial DNA as well as cytochrome b genes from 41 individuals in Sichuan, Yunnan, Tibet of China, and Burma. By analyzing haplotype and nucleotide diversity among the individuals, researchers were able to use mitochondrial phylogeography to determine that this development into two separate species was most likely due to habitat fragmentation and glacial refugia. The red panda population as a whole appears to have recently undergone several bottlenecks and expansions, resulting in the two separate species (Li et al., 2005).

BERINGIA LAND BRIDGE

The Bering Strait is currently 180' at its deepest point and it's floor is one of the flattest stretches of land in the world with a slope of only 3"-4" per mile (Haag, 1962). Scientists believe that this piece of land was not always submerged and served as a bridge between the Old and New Worlds. Geological records show that during the Tertiary, this piece of land, 1,300 miles wide at some points, was above water and connected Asia to North America (see Figure 4) (Haag, 1962). Glaciation periods tied up large amounts of the Earth's water in ice and subsequently lowered the sea levels. These lower sea levels would have exposed the land bridge and allowed for species to cross between continents (Haag, 1962).

Due to glacial periods, the land bridge was exposed intermittently from the Middle Eocene to the Middle Pliocene. Around the early Plesitocene, the land bridge was submerged due to warping continental crusts (Hopkins, 1959). Fossil evidence shows that *Alopcocyon* and *Actiocyon* crossed the land bridge into North America during the early Pliocene.

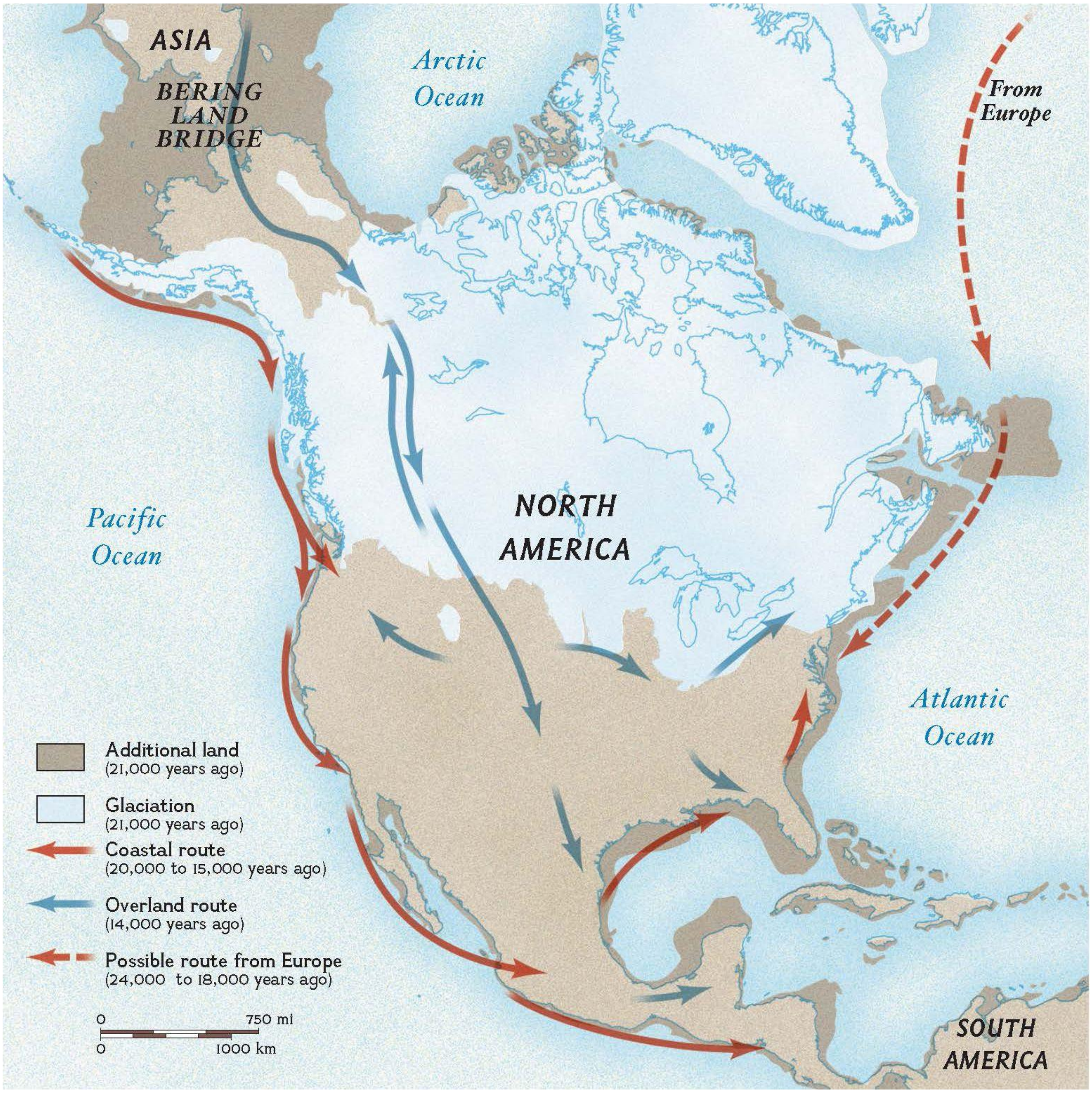

Figure 4 Beringia Land Bridge connecting Asia and North America (National Geographic, n.d.)

Another supporting factor for the Beringia Land Bridge theory is the fact that the land bridge, as well as other parts of the Northern Hemisphere, were dominated by the temperate forest biome. Overall, temperatures were warmer during the Middle Miocene than they are today, allowing for the higher elevations and more northern regions to have a cool, temperate forest (Pound et al., 2012). Today's ailurids still prefer to live in temperate forest biomes (Roberts and Gittleman, 1984). A land bridge and continent with areas full of temperate forests would have supported ailurids during their crossing and once they arrived in the New World.

SKELETAL AND PHYSICAL DIFFERENCES

Overall, the red panda still retains several of its carnivora characteristics. It has a simple stomach and short digestive tract, both uncommon in herbivores. In comparison to procyonids its size, the red panda has a larger head, but the increased skull depth may help increase bite pressure, allowing for better grinding of plant material. The extant red panda still contains the signature lateral groove on the canine tooth and molar cusps present in previous ailurid species. Each paw contains five semi-retractable claws, a sign of it's more arboreal lifestyle. The large postscapular fossa is also likely an adaptation to allow the red panda to climb easier and make the forelimbs more supportive than the hind limbs (Roberts and Gittleman, 1984). Current red pandas have smaller humerus/femur and humerus/tibia ratios than *Pristinailuris bristoli* indicating a more arboreal and less scansorial lifestyle. *P. bristoli* also had a smaller radial sesamoid bone in relation to its body size than Ailurus, which also supports *P. bristoli's* more terrestrial lifestyle (Wallace, 2011).

While most carnivores have their left lung separated into three lobes, ailurids have theirs separated into two. This is in line with Procyonidae, Mustelidae, and Ursidae. The right lung is divided into four lobes. It is believed the reduction in lobes in the left lung leads to a broadening of the thorax (Roberts and Gittleman, 1984). The functionality of this is unknown since not all carnivores have the same corresponding number of lobes per lung.

RADIAL SESAMOID BONE

As the Ailurid species moved from being mainly terrestrial to arboreal, they developed an enlarged radial sesamoid bone in the Miocene that assisted with climbing. The first species to show evidence of this was *S. batalleri*. This enlarged wrist bone gave Simocyons a functioning pseudothumb (see Figure 5). Since dentition shows that ailurids were still partaking in a mainly carnivorous diet at the emergence of the pseudothumb, researchers surmise that the enlarged radial sesamoid bone developed as a climbing aid. However, this pseudothumb was a preadaptation and also assists with grabbing fruits, stems, and leaves (Salesa et al., 2006).

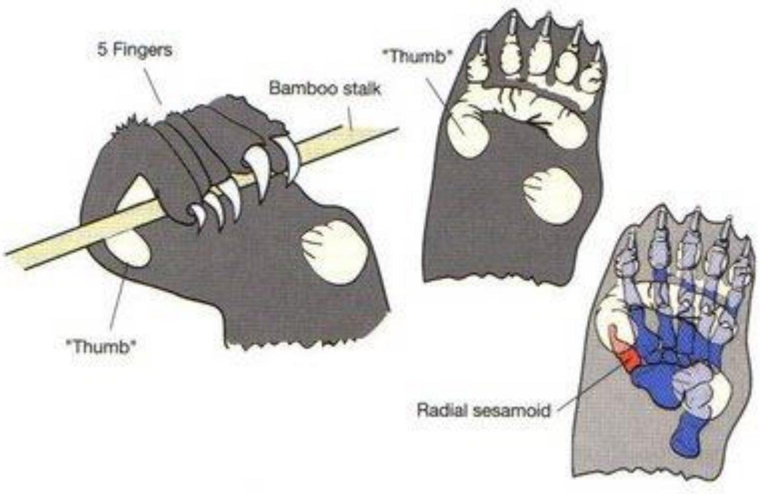

Figure 5 The radial sesamoid bone in a red panda's front paw and how the pseudothumb is used for holding branches (voltagegate, 2007).

The giant panda, a member of the Ursidae family, also developed an enlarged radial sesamoid bone, however, it did so independently from the red panda, a member of the Ailuridae family. In relation to the other bones in the wrist, the giant pandas radial sesamoid is larger than the red pandas. Since the giant pandas don't do as much climbing and have been strict herbivores longer than the red panda, researchers theorized that this enlarged bone evolved to assist the giant pandas with grabbing and holding, which was a preadaptation in the red panda (Salesa et al., 2006).

The genes responsible for this enlarged radial sesamoid bone in both the red and giant pandas are believed to be the *DYNC2H1* and *PCNT.* Both of these genes contribute to limb development and have undergone adaptive convergence in both of these species who diverged 43 million years ago (Hu et al., 2017).

UMAMI TASTE RECEPTOR

Red pandas are the only species aside from humans and Old World apes and monkeys who are known to be able to taste artificial sweetener (Goldman, 2014). In exchange for this taste, red pandas lost what is known as the umami taste. Umami is also referred to as “savory” and detects tastes in substances such as monosodium glutamate, 5′-monophosphates, L-amino acids, and 5′-ribonucleotides (Yamaguchi, 1979; Sato et al., 2012). The gene responsible for the umami taste is known as the *TAS1R1* gene (Hu, 2017). *TAS1R1* encodes for the T1R1 protein, which is one of three type-1 taste receptors and the one used by carnivores to detect the best tasting meat (Sato et al., 2012; Li, 2009; Yarmolinksky, 2014). As red pandas began to adapt more of a herbivorous diet, they pseduogenized the *TAS1R1* gene. Instead of the “umami” heterodimer T1R1/T1R3, red pandas possess the heterodimer for “sweet”, T1R2/T1R3. The protein for the “sweet” heterodimer is encoded by the gene *TAS1R2* (Li, 2009). Herbivores utilize the ability to taste “sweet” to detect carbohydrates in the plants they ingest. This ability to taste aspartame is a recent evolutionary development.

Besides the red panda, there are other non-primate species who inactivated their *TAS1R1* genes. These include the western clawed frog *(Xenopus tropicalis)*, some species of bats, the giant panda *(Ailuropoda melanoleuca)*, the bottlenose dolphin *(Tursiops)*, and the California sea lion *(Zalophus californianus)* as well as four other seal species. The carnivorous marine mammals are believed to have pseudogenized their *TAS1R1* gene due to a shift in their diet. Pinnipeds are moving away from tetrapods and eating more cephalopods and fish, prey that can be swallowed whole (Sato et al., 2012). The giant panda has a diet very similar to that of the red panda and may have evolved their “sweet” taste receptors in a response to their high carbohydrate diet as well.

A similar inactivation of the umami taste gene has occurred in hummingbirds *(Trochilidae).* The hummingbird's closest relative is the swift *(Apodidae).* Swifts mainly eat bugs and have maintained the *TAS1R1* gene for the umami taste. As hummingbirds moved to a nectar based diet, their protein receptors, which were used for the umami taste, were converted to carbohydrate receptors until eventually the hummingbird completely lost its ability to taste protein (Baldwin et al., 2014).

GUT MICROBIOMES

There are three species of obligate bamboo eaters: the red panda, the giant panda *(Ailuropoda melanoleuca),* and the bamboo lemur *(Hapalemur griseus).* Each are members of a different phylogenetic family (Hu, 2017). These three species share 48 low-abundance operational taxonomic units (OTUs). The bamboo lemur and it's sister species, the ring tailed lemur *(Lemur catta)* only share eight OTUs (McKenney et al., 2017). OTUs are sequences of similar genomic data on a DNA sequence and are used to determine relatedness among species (Galimberti et al., 2012).

Each of these species also has an increase in cyanide degradation enzymes, something that is found in herbivores but not carnivores. These enzymes help to break down the cyanide in the bamboo leaves (Zhu, 2018). Since each species developed independently of the others but yet all share similar characteristics, researchers believe that their diet of bamboo may drive some of the phenotypic evolution.

CONCLUSION

Despite the fact that there are only two living species left, Ailuridae is a complex and old phylogenetic family. Ailurid species were once widespread across North America, Asia, and Europe. Despite the fact that these animals once lived in so many areas, there is very little fossil evidence available to explain their evolutionary changes, or extinctions, over the millenia. One species that is very well represented so far, *Pristinailurus bristoli*, is unlike any of the other extinct and extant species of ailurids that are currently known. There are still many “missing pieces" needed to connect the various species of ailurids that have been discovered. Even with continuing advances in genetics and phylogeny, researchers still debate over where Ailuridae fits in the hierarchical tree. This family is unique and currently doesn't fit in neatly anywhere along the Carnivora tree.

Many of Ailuridae's genetic adaptations are also seen in species who are members of other phylogeny families. This is evidence of convergent evolution and provides researchers with new evolutionary information to analyze. This is also one of the few families that has transformed from a carnivorous diet to that of an obligate herbivore. That alone begets various evolutionary conundrums for researchers to study. Evolutionarily, red pandas are a genetic wild card. They have no close relatives who are still living and contain many genetic quandaries that continue to puzzle scientists and researchers.

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