Review of Amphicyonidae (Mammalia, Carnivora) from the Barstow Formation of California

Donald Lofgren[1], Maya Fassler[2], and Stephanie Aldaz[2]
[1] *Raymond M. Alf Museum of Paleontology, Claremont, California, 91711*
[2] *The Webb Schools, Claremont, California, 91711*

Introduction

The first major report describing Miocene vertebrate fossils from the Barstow Formation was by Merriam (1919). Shortly thereafter in 1923, C. Frick and his field crews began a long-term project to recover fossils, mainly mammals, from the abundant outcrops of the Barstow Formation in the Mud Hills north of the city of Barstow (Figure 1), efforts that continued into the early 1950's (Woodburne et al., 1990). Later, Frick's massive collection was donated to the American Museum of Natural History (AMNH) in New York.

The amphicyonids, *Amphicyon*, *Pliocyon*, and *Ischyrocyon* have been reported from the Barstow Formation based on the Frick collections at the AMNH (Woodburne et al., 1990; Hunt, 1998; Pagnac, 2005, 2009). *Pliocyon* was originally described by Matthew (1918) and the genotypic species was designated as *P. medius*. There are two additional species of *Pliocyon*, *P. robustus* (Berta and Galiano, 1984) and *P. ossifragus* (Douglass, 1903; Tabrum et al., 2001). The AMNH sample of *Pliocyon* from the Barstow Formation is small and was briefly described by Pagnac (2005), but the species represented was not determined. However, Berta and Galiano (1984) had already noted that undescribed lower jaws housed at the AMNH from the Barstow Formation represented *P. medius*.

The remaining sample of amphicyonid specimens from the Barstow Formation at the AMNH represent two taxa that differ in size. The larger taxon is *A. ingens* (Hunt, 1998, 2003; Pagnac, 2005). The smaller taxon was referred to both *Amphicyon* sp. indeterminate (Pagnac, 2005) and *Ischyrocyon gidleyi* (Hunt 1998, 2003), but these specimens now appear to represent *I. gidleyi* (Pagnac, 2009).

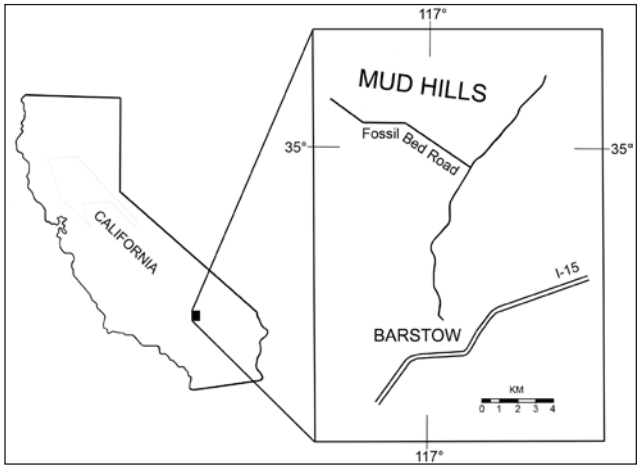

Figure 1: Location of the Barstow Formation within the Mud Hills, Mojave Desert, California (adapted from Steinen, 1966).

Here we describe the large AMNH collection of Barstow Formation amphicyonids, as well as the small collection of Barstow amphicyonids housed at the Raymond M. Alf Museum of Paleontology (RAM). A revised biostratigraphy of amphicyonids from the Barstow Formation is presented based on Pagnac (2009) and our study of AMNH and RAM specimens.

Materials and methods

Specimens housed at the AMNH were photographed and studied by D. Lofgren in 2015-2016. For each FAM or AMNH specimen a brief description of the material, as well as the locality and collection date are provided, if available. Frick collection specimens that are not cataloged are listed by their box number (BAR for Barstow) followed by a field number (example, BAR 95-51). Measurements of amphicyonid teeth were taken in mm using a Mitutoyo digital caliper. A cm tape measure was used to measure limb elements. *Hemicyon* Quarry is also commonly referred to as the *Hemicyon* Stratum, so AMNH specimens listed as either are considered the same locality. The unnamed middle member and unnamed upper member of the Barstow Formation are not formal stratigraphic units, but are referred to as middle member and upper member in the text to avoid the repetitive use of unnamed.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **FM**, Field Museum of Natural History, Chicago, Illinois; **FAM**, Frick Collection, American Museum of Natural History, New York, New York; **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts; **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California; **FSGS**, Florida State Geological Survey, Florida; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UF**, University of Florida, Gainesville, Florida.

Other Abbreviations: **Ba1** and **Ba2**, biochrons of the Barstovian NALMA; **NALMA**, North American Land Mammal Age.

Systematic paleontology

FAMILY AMPHICYONIDAE

Pliocyon Matthew, 1918

Pliocyon medius Matthew, 1918

Pliocyon medius was described by Matthew (1918) who designated AMNH 17207, a nearly complete skull from the Olcott ("Snake Creek") Formation in Nebraska, as the genotype. Based on AMNH 17207, *Pliocyon* was differentiated from *Amphicyon* based on its smaller molars, canines, and incisors (Matthew, 1918).

Currently, there are three known species of *Pliocyon*: *P. robustus*, *P. ossifragus*, and *P. medius*. The holotype and only known specimen of *P. robustus* is a partial left mandible (UF 24013) from the Upper Bone Valley Formation in Florida (Berta and Galiano, 1984).

Table 1: Measurements in mm of the p2-m3 of *Pliocyon robustus* from the Bone Valley Formation (UF 24013), *P. medius* from the Barstow Formation (FAM 27316, FAM 27504, FAM 27503), and *P. medius* from the Olcott Formation (AMNH 54323, AMNH 54348, AMNH 54344, AMNH 54319, AMNH 54342, AMNH 54330, AMNH 54339, AMNH 13849).

Tooth	UF 24013	FAM 27316	FAM 27504	FAM 27503	AMNH (various)
p2					
Length	11.0	10.2	10.7	10.4	9.6-12.0
Width	7.7	6.5	7.0	6.9	5.1-7.4
p3					
Length	10.7	--	--	12.2	11.4-13.7
Width	7.4	--	--	6.8	5.5-7.2
p4					
Length	19.5	18.1	16.9	18.2	12.1-24.2
Width	8.1	9.7	8.3	10.2	6.9-16.3
m1					
Length	33.2	29.3	28.3	30.4	19.3-31.2
Width	14.8	15.8	14.6	15.0	12.5-25.5
m2					
Length	21.5	20.0	17.4	--	15.9-21.4
Width	10.2	14.9	13.8	--	9.6-15.6
m3					
Length	11.3	11.4	--	--	11.0-11.5
Width	7.0	10.1	--	--	6.5-10.8

Compared to specimens of *P. medius* from the Olcott and Barstow formations, the mandible of *P. robustus* is more robust, the p2-3 are more reduced, the p2 is larger than the p3, and the m1 is relatively longer in *P. robustus* (Berta and Galiano, 1984). Based on a larger sample from the Olcott Formation and the three mandibles of *Pliocyon* from the Barstow Formation, the Barstow and Olcott dentaries have a smaller p2 compared to p3 and a relatively shorter m1 than the holotype of *P. robustus* (Table 1). Also, the three mandibles of *Pliocyon* from the Barstow Formation are very similar in size (Table 1) and morphology to those of *P. medius* from the Olcott Formation. There is little doubt the Barstow Formation sample of *Pliocyon* represents *P. medius*.

The holotype of *Pliocyon ossifragus* (CM 790) is a partial skull with an incomplete dentition from Miocene strata in the Lower Madison Valley of Montana that was originally identified as an ursid similar to *Dinocyon* (Douglass, 1903). In his description of CM 790, Douglass (1903) noted that the P4 and M1-2 were very large, comparable in size to those of *Amphicyon major* from Europe. Subsequently, *Dinocyon ossifragus* was referred to *Pliocyon ossifragus* by Tabrum et al. (2001) without comment. *Pliocyon ossifragus* is much larger than *P. medius* and is similar in size to *Amphicyon ingens*. For example, the M1 of *A. ingens* from the Barstow Formation has a length of 29.5 mm and a width of 38-39 mm and the M1 of *Pliocyon ossifragus* is 30 mm in length and 41 mm in width (Douglass, 1903). Thus, if CM 790 is correctly referred to *Pliocyon*, *P. ossifragus* would represent the largest species of the genus.

Specimens of *Pliocyon medius* are rarely recovered from the Barstow Formation. There are only seven AMNH specimens and no examples of the species are present in the RAM collections. Although the cheek teeth of *P. medius* and *Ischyrocyon gidleyi* are similar size (Figure 2), the canine of *Pliocyon medius* (approximately 20 mm in

Figure 2: Labial view of FAM 27130, right dentary of *Ischyrocyon gidleyi* with p2-4, m1-2 (above) and labial view of FAM 27503, right dentary of *Pliocyon medius* with p2-4 and m1 (below).

maximum diameter and 13 mm in minimum diameter at gum line) is smaller than the canine of *Ischyrocyon gidleyi* (approximately 22-23 mm in maximum diameter and 15.5 mm in minimum diameter at gum line). As would be expected, the canine of *Amphicyon ingens* from the Barstow Formation is much larger than either of the other two amphicyonids (approximately 28 mm in maximum diameter and 19 mm in minimum diameter at gum line). All AMNH specimens of *Pliocyon medius* that have locality data are from the middle member of the Barstow Formation. They include:

FAM 68201, right radius, Spade Quarry, 1937.

FAM 68203, right metatarsal IV, 2nd Division, 1933.

FAM 27316, left mandible with p2, p4, m1-3, and damaged p3, Yermo Quarry, 1932.

FAM 27504, right mandible with c, p2, p4, m1-2, Green Hills, no date.

FAM 27503, right mandible with p2-4 and m1, Green Hills, no date.

FAM 27102, juvenile palette, no locality or date.

FAM 27103, juvenile mandibles and upper teeth, no locality or date.

AMPHICYON Lartet, 1836

AMPHICYON INGENS Matthew, 1924

The holotype of *Amphicyon ingens* (FAM 18272) is from the Snake Creek beds (Matthew, 1924) and the species is the largest of the North American amphicyonids (Hunt 1998, 2003). In addition to *Pliocyon medius*, two other amphicyonid species are present in the Barstow Formation, *Amphicyon ingens* (Hunt, 1998, 2003; Pagnac, 2005) and *Ischyrocyon gidleyi* (Hunt, 1998; Pagnac, 2009). Postcranial specimens of *Amphicyon ingens* are usually about 20 to 40% larger than those of *Ischyrocyon gidleyi* (Table 2) (Figure 3). However, an ulna from Turbin Quarry (FAM 68193A, middle member) is 33 cm in length, similar in length to the only complete ulna known of *Ischyrocyon gidleyi* from Deep Quarry in the Barstow Formation (FAM 27153, upper member). The most complete specimen of *Amphicyon ingens* from the Barstow Formation is FAM 23788, a partial skeleton from Valley View Quarry. The mandible of FAM 23788 is much larger than the mandible of *Ischyrocyon gidleyi* (Figure 4) and the skull of FAM 23788 is massive, although crushed (Figure 5).

A skeletal cast of *Amphicyon* was created as part of a major renovation of the AMNH paleontology displays in the 1990s. Many elements of *A. ingens* from Nebraska and Colorado (FAM 68117, FAM 54262, UCMP 36279) were molded to make the cast which is now on display in the Lila Acheson Wallace Wing of Mammals and their Extinct Relatives at the AMNH. An additional cast of *Amphicyon* made by AMNH staff is on display at the RAM in the Hall

Table 2: Measurements in cm of postcranial elements of *Amphicyon ingens* and *Ischyrocyon gidleyi* from various localities in the Barstow Formation (Q= quarry).

Amphicyon ingens			***Ischyrocyon gidleyi***		
Locality	Specimen	Length	Length	Specimen	Locality
		Radius			
Valley View Q	FAM 23788	35	27	FAM 27153	Deep Q
Skyline Q	FAM 23794	33	--		
Steepside Q	FAM 68193	40	--		
		Ulna			
Valley View Q	FAM 23788	42	33	FAM 27153	Deep Q
East of Yermo Q	FAM 27300A	40	--		
Valley View Q	FAM 23794	40	--		
Skyline Q	FAM 23792	40	--		
Turbin Q	FAM 68193A	33	--		
		Humerus			
Valley View Q	FAM 23788	42	26	FAM 27088	1st Division
Oreodont Q	FAM 68191	35	25	FAM 68198	*Hemicyon* Q
		Tibia			
Valley View Q	FAM 23788	36	24	FAM 27099G	1st Division
			29	FAM 68200	New Year Q
			30	FAM 27153A	Deep Q
			29	FAM 68197	2nd Division

Figure 3: Comparison of FAM 23788, ulna of *Amphicyon ingens* (above) and FAM 27153, ulna of *Ischyrocyon gidleyi* (below).

Figure 4: Labial view of the left dentary (FAM 23788) of *Amphicyon ingens* (above) and the left dentary of *Ischyrocyon gidleyi* (FAM 27095) (below).

of Footprints (Figure 6), mounted over the only known trackway of *Amphicyon* from North America (RAM 100, holotype of ichnotaxon *Hirpexipes alfi*, Sarjeant et al., 2002). The trackway was collected from the middle member in 1964 by Raymond Alf and Webb Schools students (Lofgren et al., 2006; Lofgren and Anand, 2010). The RAM cast was a gift from the AMNH in exchange for the rights to mold the holotype of *Hirpexipes alfi*. Thus, the record of *Amphicyon ingens* from the Barstow Formation includes a spectacular trackway on exhibit at the Raymond M. Alf Museum of Paleontology.

RAM specimens of *Amphicyon ingens* from the Barstow Formation are all postcranial elements from the middle member. RAM 7332 is a large astragulus from RAM locality V94026, a site that also yielded a smaller amphicyonid astragulus (RAM 7308) (Figure 7). The larger astragulus (RAM 7332) compares favorably in size to a damaged astragulus of *A. ingens* from Valley View Quarry (Figure 7) and almost certainly represents this species. The smaller astragulus (RAM 7308) probably represents *Ischyrocyon gidleyi* or a smaller species of *Amphicyon*.

Twenty four cataloged and eight uncataloged specimens of *Amphicyon ingens* from the Barstow Formation are housed at the AMNH. One is an uncatalogued partial metapodial (BAR 328) from Hidden Hollow Quarry, the only specimen identified as *A. ingens* from the upper member of the Barstow Formation. The fragmentary condition of BAR 328, and the fact that all other AMNH specimens of *A. ingens* are from the middle member, suggests that BAR 328 may represent some other amphicyonid. Thus, AMNH and RAM specimens confidently identified as *A. ingens* that have precise locality data are all from the middle member of the Barstow Formation. These specimens include:

FAM 23788, partial skeleton, including left mandible with c, p2-4, and m1-2, right mandible with c, p1-4, m1, crushed skull with right P1-4 and M2 and left C, P2-4, and M1-2, left and right radius, left and right ulna, patella, assorted metapodials and phalanges, broken astragulus, humerus, tibia, distal end of femur, crushed innominate, left and right scapula, rib fragments, proximal femur lacking head, twelve fragmented vertebrae, and axis, Valley View Quarry, 1933.

FAM 27097, left m3, Green Hills, no date.

FAM 27096A, right M1, Green Hills, no date.

FAM 27099A-H, associated (?) isolated teeth (M1, M2, m2, P4), Green Hills, no date.

FAM 27098, left mandible with p3-m1, right mandible with p3-p4, Green Hills, no date.

Figure 5: Palatal view of FAM 23788, a crushed but nearly complete skull of *Amphicyon ingens* from Valley View Quarry.

Figure 6: Skeletal cast of *Amphicyon ingens* mounted over trackway of *Amphicyon* (RAM 100, *Hirpexipes alfi*) on display in the Hall of Footprints at the Raymond M. Alf Museum of Paleontology.

Figure 7: Comparison of the astragulus of *Amphicyon ingens*, FAM 23788 (left) and RAM 7332 (middle), with the astragulus of *Ischyrocyon gidleyi,* RAM 7308 (right).

FAM 50070, broken ulna, right mandible with i2-3, c, p1-4, m1-3 (m3 in crypt), left mandible with i2-3, c, p1-4, m1-2, Bar 374c-3259-st-5Q-lo. Lev., no date.

FAM 23794A, left radius, Skyline Quarry, 1933.

FAM 23792, left ulna, Skyline Quarry, 1933.

FAM 68191, left humerus, Oreodont Quarry, 1934-35.

FAM 27300, left mandible with damaged p2-3, p4-m2, and m3 alveolus, and right mandible with i3, c, p2-4, m1, 5 miles east of Yermo, 1932.

FAM 27300A, left ulna, 5 miles east of Yermo, 1932.

FAM 27300B, right metatarsal IV, 5 miles east of Yermo, 1932.

FAM 68193, left radius, Steepside Quarry, 1937.

FAM 68193A, right ulna, Turbin Quarry, 1937.

FAM 68192, proximal end of humerus, Valley View Quarry, 1933.

FAM 68196, proximal right femur without head, Valley View Quarry, 1933.

FAM 68196A, distal end of left femur, Valley View Quarry, 1933.

FAM 68210, metatarsal II, Skyline Quarry, 1936-37.

FAM 68210A, metatarsal III, Skyline Quarry, 1936-37.

FAM 23794, ulna, Valley View Quarry, 1933.

FAM 23794A, metacarpal V, Valley View Quarry, 1933.

FAM 23793, right metacarpal IV, Skyline Quarry, 1933.

FAM 68207, right metatarsal III, Mayday Quarry, 1937.

FAM 27096, maxilla fragments with right M2 and left P4-M2, 2nd and 3rd Division Green Hills, 1929.

BAR 328, distal half of metapodial, Hidden Hollow Quarry, 1934-35.

BAR 277, calcaneum, Mayday Quarry, 1933.

BAR 242, 258, 261, 262, 265, 267A, metapodials and phalanges, Valley View Quarry, 1933.

RAM 6811, left scapholunar, RAM locality V95082 (middle member), 2000.

RAM 7556, right metacarpal V fragment, RAM locality V94180 (middle member), 1994.

RAM 9439, left scapholunar, RAM locality V94026 (middle member), no date.

RAM 7332, left astragulus, RAM locality V94026 (middle member), no date.

ISCHYROCYON Matthew and Gidley, 1904
ISCHYROCYON GIDLEYI Matthew, 1902

Numerous specimens in the Frick Collections at the AMNH are labelled *Amphicyon* sp. and they are about 30% smaller than AMNH specimens referred to *Amphicyon ingens* (Pagnac, 2005). These smaller AMNH amphicyonid specimens were identified as *Ischyrocyon gidleyi*, an exclusively North American genus, based mainly on numerous skulls and mandibles recovered from the *Hemicyon* Stratum of the Barstow Formation (Hunt, 1998). In contrast, Pagnac (2005) noted that criteria proposed by Hunt (1998) to differentiate *Amphicyon* from *Ischyrocyon* were not useful in assigning specimens from the Barstow Formation labelled *Amphicyon* sp. in the ANNH collections to either genus.

Table 3: Measurements in mm of the m1-2 and P4-M2 of *Amphicyon ingens* and *Ischyrocyon gidleyi* from the Barstow Formation, *Amphicyon frendens* from the Sheep Creek Formation, and *A. galushai* from the Runningwater Formation (measurements of *A. galushai* and *A. frendens* from Hunt (2003, tables 4.2 and 4.5).

Tooth	*Amphicyon ingens*	*Ischyrocyon gidleyi*	*Amphicyon frendens*	*Amphicyon galushai*
m1				
Length	35.9-42.1	27.2-32.6	33.5-39.8	30.2-32.2
Width	17.1-19.6	11.8-14.3	--	15.7-16.5
m2				
Length	29.0-36.0	--	21.9-32.1	18.5-20.6
Width	19.0-20.4	--	--	13.3-15.9
P4				
Length	32.5-33.7	22.6-29.7	24.9-32.4	24.8-31.4
Width	19.6-20.0	12.1-16.2	--	14.9-17.9
M1				
Length	29.4-29.5	18.5-24.9	23.2-29.3	20.4-24.8
Width	38.3-39.5	25.6-31.3	29.4-37.0	27.3-32.9
M2				
Length	22.1	--	19.5-26.5	15.7-19.6
Width	30.6	--	31.4-39.9	24.9-28.9

Pagnac (2005) argued that the parastylar cusp of P4 and the relative size of M2 and M1 of these AMNH specimens were characteristic of *Amphicyon*, but that they could not be assigned to any existing species of the genus, although they compare most favorably to *A. frendens* based on size. Apparently this conflict was resolved as this smaller amphicyonid is listed as *Ischyrocyon gidleyi* in a subsequent biostratigraphic review of the Barstow Formation by Pagnac (2009, figure 3).

According to Hunt (2003), the *Amphicyon* lineage in North America is restricted to these species, *A. galushai*, *A. frendens*, and *A. ingens*. As noted earlier, *A. ingens* is much larger than any other species of *Amphicyon* and the size of the dentition of *A. frendens* is significantly larger than that of *A. galushai* (Hunt, 2003, table 4.2 and table 4.5). When comparing the size of the M1 and m1 of AMNH specimens of *Ischyrocyon gidleyi* from the Barstow Formation to those of *Amphicyon galushai* and *A. frendens*, the Barstow specimens are similar in size to *A. galushai* and smaller than those of *A. frendens* (Table 3). It is important to note that postcranial elements labelled as *Amphicyon* sp. (now *Ischyrocyon gidleyi*) from the Barstow Formation in the AMNH collections are from sites throughout the middle and upper member of the formation and it is unsure if all of these isolated elements actually represent *Ischyrocyon gidleyi*.

The remains of a smaller species of *Amphicyon* are commonly found in Barstovian rocks in North America. In addition to *A. frendens* and *A. galushai*, four other species of *Amphicyon* smaller than *A. ingens* have been described: *A. longiramus*, *A. intermedius*, *A. pontoni*, and *A. riggsi.* (Simpson, 1930; McGrew, 1939; White, 1940, 1942). However, Hunt (2003) restricted *Amphicyon* in North America to *A. galushai*, *A. frendens*, and *A. ingens* without comment on the status of *A. longiramus*, *A. intermedius, A. pontoni*, and *A. riggsi.* We provide a brief review of these taxa.

Two species were described from the Thomas Farm area of Florida, *Amphicyon intermedius* and *A. longiramus* (White, 1940, 1942). The holotype of *A. intermedius* is a mandible with p3-m2 (MCZ 3631), whose respective length and width of the m1-2 are 29 mm x 14 mm (m1) and 20.5 mm x 14.5 mm (m2) (White, 1940), dimensions more similar in size to *A. galushai* (Table 3). The holotype of *A. longiramus* (MCZ 3919) is a mandible with p2-m2 (White, 1942) whose m1 length is 32 mm and m2 length is 23 mm, dimensions more similar to *A. frendens* than *A. galushai*. Thus, if these specimens still represent *Amphicyon*, they indicate that two species are present in Miocene strata from Florida.

Interestingly, another species of *Amphicyon*, *A .pontoni*, was described by Simpson (1930) from Florida based on an isolated m2 (FSGS V4112) with a length of 18.6 mm and a width of 14.3 mm. If valid, *A. pontoni* would be most similar in size to *A. galushai* (Table 3).

The other species is *Amphicyon riggsi* from the Deep River Beds (Renova Formation) of Montana (McGrew,

Figure 8: Palatal view of FAM 27107, a relatively complete skull of *Ischyrocyon gidleyi.*

Figure 9: Occlusal view of FAM 27117, partial right maxilla of *Ischyrocyon gidleyi* with P4-M3, compared to the M1-3 of FAM 23788, partial skull of *Amphicyon ingens*.

1939), whose holotype (FM P12029) includes a partial skull with mandible. The m1 and m2 of *A. riggsi* are 31.0 mm x 14.3 mm (m1) and 21.6 mm x 16.0 mm (m2) in length and width respectively (McGrew, 1939). These dimensions are most similar to *A. galushai* (Table 3).

The validity of *A. longiramus*, *A. intermedius*, *A. pontoni*, and *A. riggsi* are in doubt as they were dismissed without comment by Hunt (2003). However, the disagreement between Hunt (1998) and Pagnac (2005) over the identification of the smaller sized amphicyonid in the AMNH collections was resolved (Pagnac, 2009). Thus, *Ischyrocyon gidleyi* appears to represent this smaller sized amphicyonid from the Barstow Formation, but if any of these specimens were later identified as *Amphicyon*, they would be more similar to *A. galushai* than *A. frendens* based on size (Table 3).

Ischyrocyon gidleyi is known from 103 cataloged and four uncataloged specimens labelled *Amphicyon* sp. (*Ischyrocyon gidleyi*) in the AMNH collections. Thirty-three of these are from the *Hemicyon* Stratum, including numerous skulls and mandibles (Figure 8) as noted by Hunt (1998). The dentition of *Ischyrocyon gidleyi* is much smaller than that of *Amphicyon ingens* (Figure 9). It is important to note there is repetitive numbering of specimens of *Ischyrocyon gidleyi* ("*Amphicyon* sp.") in the AMNH sample. One example is FAM 27106, the catalog number for a maxilla and two mandibles from the Rak Division (no collection date) and also the catalog number for a maxilla with no locality or collection date. Another is FAM 27107, which refers to an M2 with no data, as well as a skull from the *Hemicyon* Stratum (Figure 8) with no collection date. Specimens labelled *Amphicyon* sp. in the AMNH collections also include 40, mostly isolated, postcranial elements. We assume that most of these specimens represent *Ischyrocyon gidleyi*, but it is possible that the sample could include specimens of a species of *Amphicyon* smaller than *A. ingens*.

The RAM sample of smaller amphicyonid specimens from the Barstow Formation includes an astragulus (RAM 7308) and a calcaneum fragment (RAM 7322) from the

Figure 10: Comparison of canines of *Ischyrocyon gidleyi*, RAM 7347 (above) and FAM 27139 (below).

middle member, and a canine (RAM 7347) from the upper member. RAM 7347 compares closely to canines labelled *Amphicyon* sp. (*Ischyrocyon gidleyi*) in the AMNH collections (Figure 10) and RAM 7308 is much smaller than the astragulus of *Amphicyon ingens* from the Barstow Formation (Figure 7).

AMNH and RAM specimens identified as *Ischyrocyon gidleyi* that have locality data are all from the middle and upper members of the Barstow Formation. These specimens include:

FAM 68206, left metatarsal III, Valley View Quarry, 1933.

FAM 68205, proximal half of metapodial, Valley View Quarry, 1933.

FAM 68205A, proximal end of metapodial, Valley View Quarry, 1933.

FAM 68205B, proximal end of metapodial, Valley View Quarry, 1933.

FAM 68200, right tibia, New Year Quarry, 1934.

FAM 68198, right humerus, *Hemicyon* Quarry, 1938.

FAM 68198A, distal half of humerus, Hidden Hollow Quarry, 1933-36.

FAM 68199, proximal half of femur, *Hemicyon* stratum, 1930.

FAM 27153B, astragulus, *Hemicyon* Stratum, 1930.

FAM 27303A, metatarsal III, *Hemicyon* Stratum, 1931.

FAM 68208, proximal end of metacarpal III, *Hemicyon* Quarry, 1931.

FAM 68209, metacarpal II, Hidden Hollow Quarry, 1935-36.

FAM 68209A, metatarsal III, Hidden Hollow Quarry, 1935-36.

FAM 68209B, metatarsal I, Hidden Hollow Quarry, 1935-36.

FAM 27095, left mandible with c, p2-4, m1-2, m3 alveolus and right mandible with i3, c, p1-4, m1-3, Barstow Bluff, 1927.

FAM 27095A, left and right calcaneum and four metapodials, Barstow Bluff, 1927.

FAM 27153, radius, two metapodials, and ulna, Deep Quarry, Green Hills, west of camp, 1931.

FAM 27153A, crushed tibia, Deep Quarry, 1931.

FAM 27153A, partial femur without head, Camp Quarry, 1931.

FAM 68195, proximal half of femur, Steepside Quarry, upper level, 1935-36.

FAM 68197, right tibia, 2nd Division, 1927.

FAM 68202, right metacarpal V, Steepside Quarry, upper level, 1935-36.

FAM 68202A, right metacarpal III without proximal end, Steepside Quarry, upper level, 1935-36.

FAM 68206, left metatarsal III, Valley View Quarry, 1933.

FAM 68205, proximal half of metapodial, Valley View Quarry, 1933.

FAM 68205A, proximal end of metapodial, Valley View Quarry, 1933.

FAM 68205B, proximal end of metapodial, Valley View Quarry, 1933.

FAM 27301, left and right maxilla fragments with M2s and an isolated M3, 5 miles east of Yermo Quarry, 1932.

FAM 27304, right maxilla with broken C and P4-M1, *Hemicyon* Stratum, 1931.

FAM 50086, right mandible with p3-4, and erupting m1, May Day Quarry, 1933.

FAM 50087, left mandible with m1, May Day Quarry, 1933.

FAM 50088, left maxilla with P4-M2 and right maxilla with P4-M1, May Day Quarry, 1934.

FAM 50082, left maxilla fragment with P4 and erupting M2, Hidden Hollow Quarry, 1935.

FAM 50083, left mandible with p4-m2, Hidden Hollow Quarry, 1935.

FAM 50089, crushed skull with left P4-M2, damaged right P4-M1 and M2, Hailstone Quarry, 1937.

FAM 27302, right mandible with i2-3, c, p1-2, p4, m1, and left mandible with c, p1-4, *Hemicyon* Stratum, 1931.

FAM 23791, tibia, Skyline Quarry, 1933.

FAM 23789, four metacarpals, Skyline Quarry, 1933.

FAM 23793, two metapodials, Valley View Quarry, 1933.

FAM 50075, skull with left P1-3, P4, and M1-2, and right P1-3, P4-M1-3, and atlas, Leader Quarry, 1935.

FAM 20085, partial femur without head, no locality, 1925.

FAM 27106, left mandible with p4-m2, right mandible with i2-3, c, p1, p3-4, m1-2, and left maxilla with I1-3, damaged P1, and P2-M3, Rak Division, no date.

FAM 27116, left maxilla with P3-M2, 1st Division, no date.

FAM 68194, right femur, 2nd division, no date.

FAM 50105, M3, Green Hills Quarry, no date.

FAM 27126, left maxilla with P4-M2, *Hemicyon* Stratum, no date.

FAM 27141, left mandible with m1 and erupting m3, *Hemicyon* Stratum, no date.

FAM 27097A, metatarsal and three phalanges, 1st Division, no date.

FAM 27097E, metatarsal, 1st Division, no date.

FAM 27097F, proximal half of metatarsal, 1st Division, no date.

FAM 27099G, tibia, 1st Division, no date.

FAM 27099H, proximal half of metatarsal, 1st Division, no date.

FAM 27088, left humerus, 1st Division, no date.

FAM 27127A, right P4, *Hemicyo*n Stratum, no date.

FAM 27096B, right metacarpal V, *Hemicyon* Stratum, no date.

FAM 27124, right maxilla with P4-M2, *Hemicyon* Stratum, no date.

FAM 27117, right maxilla with P4-M3, 1st Division, no date.

FAM 27107, partial skull with left I3, C, P2, P4, M1-2, and right I3, C, P2-4, M1-2, *Hemicyon* Stratum, no date.

FAM 27123, skull fragment with left and right P1, *Hemicyon* Stratum, no date.

FAM 27137, left mandible with c, p2-3, m1, right mandible with p2-4, m1, and metapodial, *Hemicyon* Stratum, no date.

FAM 50081, brain case, partial innominate, distal femur, astragulus, two metapodials, Hidden Hollow Quarry, no date.

FAM27107A, skull with left C1, P203, M1-2, and right I2-3, C1 ,P3-4, M1, *Hemicyon* Stratum, no date.

FAM 27109, skull with left I1-3, C1, P1-2, P4, M1-3, and right I1-3, C1, P1-4, M1-3, *Hemicyon* Stratum, no date.

FAM 27210, juvenile skull with erupting left P4, *Hemicyon* Stratum, no date.

FAM 27127, right P4, *Hemicyon* Stratum, no date.

FAM 27108, skull with damaged teeth, *Hemicyon* Stratum, no date.

FAM 27110, skull with left I3, C, P2-3, M1-2, and right C, P1-4, and M1, *Hemicyon* Stratum, no date.

FAM 27133, left mandible with c, p1-4, and m1-2, 1st Division, no date.

FAM 27119, left maxilla with M1-2, 1st Division, no date.

FAM 27115, skull fragments with right P4-M1 and broken left P4-M1, *Hemicyon* Stratum, no date.

FAM 27142, right mandible with i3, p1, p3-4, m1, *Hemicyon* Stratum, no date.

FAM 27143, right mandible with p2, p4, m1-2, *Hemicyon* Stratum, no date.

FAM 27120, right maxilla with M1-2, 1st Division, no date.

FAM 27132, left mandible with broken m1, and right mandible with c, p2-4, m1, *Hemicyon* Stratum, no date.

FAM 27148, left mandible with m1-2, *Hemicyon* Stratum, no date.

FAM 50078, right mandible with damaged p3-4 and m1-2, and left mandible with p4, and damaged m1, New Hope Quarry, no date.

FAM 27113, juvenile skull with erupting left P4-M2, right M1, and left and right DP3-4, *Hemicyon* Stratum, no date.

FAM 27125, right maxilla fragment with P3-4, *Hemicyon* Stratum, no date

FAM 27111, mandible with c, p1-2, m1 and erupting c and m2, skull with right M1-2 and left P4-M2, *Hemicyon* Stratum, no date.

FAM 27118, right maxilla with M1-2, 1st Division, no date

FAM 27144, left mandible with p4-m2, and upper molars, *Hemicyon* Stratum, no date.

FAM 27146, left mandible with p2-4 and m1, *Hemicyon* Stratum, no date.

FAM 27139, right mandible with c, p1, and p3 and left isolated c, 1st division, no date.

FAM 27147, right mandible with m1, *Hemicyon* Stratum, no date.

FAM 27135, right mandible with p4-m2, *Hemicyon* Stratum, no date.

FAM 27100, right mandible with p4 and m3, Green Hills, no date.

FAM 27140, mandible fragments, no locality or date.

FAM 20823, braincase, no locality or date.

FAM 27104, left M2, no locality or date.

FAM 27105, right M3, no locality or date.

FAM 27107, right M2, no locality or date.

FAM 27138, right mandible with m1-2, no locality or date.

FAM 27106A, right maxilla with P4-M1, no locality or date.

FAM 27106, right maxilla with I3 and C, no locality or date.

FAM 27095B, left metacarpal II and IV, no locality or date.

FAM 27136, right mandible with m2-3, no locality or date.

FAM 27131, left mandible with m1-2, no locality or date.

FAM 27145, left mandible with damaged teeth, no locality or date.

FAM 27130, right mandible with p2-4, m1-2, no locality or date.

FAM 27134, left mandible with p1, p4, m1-3, no locality or date.

FAM 27128, broken left P4, no locality or date.

FAM 27121, left M2, no locality or date.

FAM 20822, braincase, no locality or date.

BAR 192, two molars, Green Hills Quarry, 1930.

BAR 420, calcaneum, Yermo Quarry, 1938.

BAR 80, braincase, *Hemicyon* Stratum, 1927.

BAR 156, phalanges, Skyline Quarry, no date.

RAM 7347, lower canine, RAM locality V94039 (upper member), 1999.

RAM 7308, left astragulus, RAM locality V94026 (middle member), no date.

RAM 7322, left calcaneum fragment, RAM locality V94026 (middle member), no date.

Biostratigraphy

Mandibles of *Pliocyon medius* were recovered from Yermo Quarry (FAM 27316) and two sites noted as "Green Hills" (FAM 27504 and FAM 27503). The Green Hills Fauna of the Barstow Formation occurs in strata that extend from Steepside Quarry up to just below Valley View Quarry (Figure 11), an interval that is part of the Ba1 biochron of the Barstovian NALMA (Tedford et al., 2004; Pagnac, 2009) and includes the Oreodont Tuff dated at 15.8 Ma (Woodburne et. al., 1990). *Pliocyon medius* is also well known from late Hemingfordian to early Barstovian strata in Nebraska (Hunt, 1998).

Amphicyon ingens is best known from the Barstow Formation based on FAM 23788, a partial skeleton from Valley View Quarry. The record of *A. ingens* from the Barstow Formation appears to be restricted to the Ba1 biochron of the Barstovian NALMA as it occurs from Steepside Quarry up to Mayday Quarry and Skyline Quarry, an interval that represents most of the middle member (Woodburne et. al., 1990; Pagnac, 2009). As noted earlier, BAR 328 is a partial metapodial from Hidden Hollow Quarry identified as *A. ingens*. If the locality data for BAR 328 is correct, the range of *A. ingens* would extend into the upper member of the Barstow Formation, up into the Ba2 biochron (Figure 11). *Amphicyon ingens* is also known from early to medial Barstovian strata in Nebraska, Oregon, New Mexico, and Colorado (Hunt, 1998), so its occurrence in the

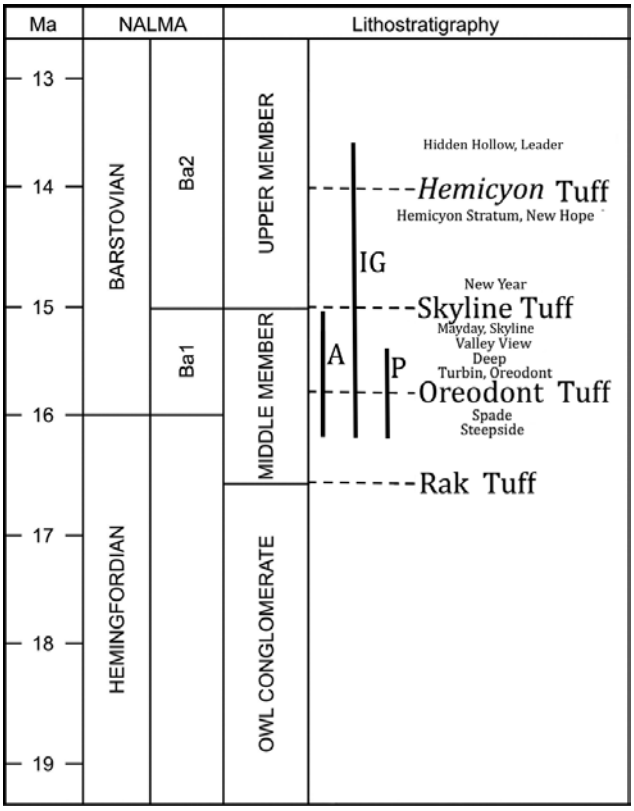

Figure 11: Geochronology and biostratigraphic subdivision of the Barstow Formation (adapted from Pagnac, 2009 and Woodburne et al., 1990), showing stratigraphic ranges of *Amphicyon ingens* (A), *Ischyrocyon gidleyi* (IG), and *Pliocyon medius* (P). The stratigraphic positions of some of the Frick quarries mentioned in the text are noted.

upper member of the Barstow Formation would not be a biochronologic range extension for the taxon.

Skulls and mandibles labelled as *Amphicyon* sp. in the AMNH collections from the *Hemicyon* Quarry were referred to *Ischyrocyon gidleyi* (Hunt, 1998). Postcranial elements labelled as *Amphicyon* sp. are from sites throughout the middle and upper members, from Steepside Quarry up to Hidden Hollow Quarry. It is unsure if all of these isolated elements actually do represent *Ischyrocyon gidleyi*, and analysis of postcranial remains was beyond the scope of this study. *Hemicyon* Quarry specimens represent a small form of *Ischyrocyon*, and Claredonian strata in Texas yield much larger individuals (Hunt, 1998). Thus, whether a second species of *Ischyrocyon* should be erected is an open question (Hunt, 1998).

Summary

The Frick collections at the American Museum of Natural History include 156 amphicyonid specimens from the upper and middle members of the Barstow Formation that are referred to *Amphicyon ingens*, *Pliocyon medius*, and *Ischyrocyon gidleyi*. A much smaller amphicyonid collection is housed at the Raymond M. Alf Museum of Paleontology and is composed of seven isolated postcranial elements and the only known trackway (*Hirpexipes alfi*) of *Amphicyon* from North America.

The presence of *Pliocyon medius* in the Barstow Formation (seven isolated AMNH elements) is confirmed as three mandibles from the middle member are very similar to mandibles of the species from the Olcott Formation in Nebraska. *Amphicyon ingens* is much larger (about 30%) than either *Pliocyon medius* or *Ischyrocyon gidleyi* and is known from thirty-two AMNH and four RAM specimens. This large amphicyonid is best known from the Barstow Formation based on a partial skeleton (FAM 23788) from Valley View Quarry (middle member). *Ischyrocyon gidleyi* is the most abundant amphicyonid known from the Barstow Formation as 117 AMNH and three RAM specimens were recovered. This species is best known from the *Hemicyon* Stratum in the upper member as multiple skulls and mandibles were collected by Frick crews from the site over 60 years ago.

The biostratigraphic records of *Pliocyon medius* and *Amphicyon ingens* (including *Hirpexipes alfi*) are restricted to the middle member except for an uncataloged metapodial (BAR 328) from Hidden Hollow Quarry in the upper member. If BAR 328 is correctly identified and if locality data is accurate, the range of *Amphicyon ingens* would be extended up into the upper member of the Barstow Formation. This occurrence would not be a biochronologic range extension for *A. ingens* as it is known from medial Barstovian strata elsewhere in North America. Besides the excellent sample from the *Hemicyon* Stratum, *Ischyrocyon gidleyi* has been recovered from multiple sites in both the middle and upper members of the Barstow Formation. The sample includes over 40 postcranial elements which would be very difficult to distinguish from various smaller species of *Amphicyon* known from Barstovian strata. If any of these elements were indeed referable to *Amphicyon*, based on size, *A. galuslai* would be the most likely species represented by the specimens.

Acknowledgments

We thank J. Shearer of the California Bureau of Land Management for permits, M. Woodburne for reviewing the manuscript, J. Galkin, R. O'Leary, and J. Meng of the AMNH for access to specimens, and the Mary Stuart Rogers Foundation, Augustyn Family Fund of the Raymond M. Alf Museum of Paleontology, and the David B. Jones Foundation for financial support.

References cited

Berta, A., and H. Galliano. 1984. A Miocene amphicyonid (Mammalia, Carnivora) from the Bone Valley Formation of Florida. Journal of Vertebrate Paleontology 4:122-125.

Douglass, E., 1903. New vertebrates from the Montana Tertiary. Annals of the Carnegie Museum 2:145-199.

Hunt, Jr., R. M. 1998. Amphicyonidae. pp. 196-221, *in* Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and ungulate-like

Mammals (C. M. Janis, K. M. Scott, and L. L. Jacobs, eds.), Cambridge University Press, Cambridge, United Kingdom.

Hunt, Jr., R. M. 2003. Intercontinental migration of large mammalian carnivores: earliest occurrence of the Old World beardog *Amphicyon* (Carnivora, Amphicyonidae) in North America. Bulletin of the American Museum of Natural History 279:77-115.

Lartet, E., 1836. Nomenclature des mammiferes et des coquilles qu'il a troves dans un terrain d'eau douce pres de Simorre at de Sansan (Gers). Bulletin de al Societe geologique de France 7:217-220.

Lofgren, D. L., Greening, J. A., Johnson, C. F., Lewis, S. J, and M. A. Torres. 2006. Fossil Tracks at the Raymond Alf Museum of Paleontology and management of tracks on public lands. New Mexico Museum of Natural History & Science Bulletin 34:109-118.

Lofgren, D. L., and R. Anand. 2010. 75 years of fieldwork in the Barstow Formation by the Raymond M. Alf Museum of Paleontology. pp. 169-176, in: R. E. Reynolds and D. M. Miller (eds.). Overboard in the Mojave: 20 Million Years of Lakes and Wetlands. Desert Studies Consortium: Fullerton, California.

Matthew, W. D., 1902. A skull of *Dinocyon* from the Miocene of Texas. Bulletin of the American Museum of Natural History 16:129-136.

Matthew, W. D., 1918. Contributions to the Snake Creek fauna with notes upon the Pleistocene of Western Nebraska American Museum Expedition of 1916. Bulletin of the American Museum of Natural History 38:183-229.

Matthew, W. D., 1924. Third contribution to the Snake Creek fauna. Bulletin of the American Museum of Natural History 50:59-210.

Matthew, W. D., and J. Gidley, 1904. New or little known mammals from the Miocene of South Dakota. Parts I-III. Bulletin of the American Museum of Natural History 20:241-268.

McGrew, P. O., 1939. A new *Amphicyon* from the Deep River Miocene. Field Museum of Natural History Geological Series 6:341-350.

Merriam, J. C., 1919. Tertiary mammalian faunas of the Mohave Desert. University of

California Publications in Geological Sciences 11:437a-437e, 438-585.

Pagnac, D. C., 2005. A systematic review of the mammalian megafauna of the middle Miocene Barstow Formation, Mojave Desert, California (PhD dissertation). University of California-Riverside. 384 pp.

Pagnac, D. C., 2009. Revised large mammal biostratigraphy and biochronology of the Barstow Formation (Middle Miocene), California. Paleobios 29:48-59.

Sarjeant, W. A. S., Reynolds, R. E., and M. M. Kissell-Jones, 2002. Fossil creodont and carnivore footprints from California, Nevada, and Wyoming, pp. 37-50, in (Reynolds, R. E. ed.), Between the Basins: Exploring the Western Mojave and Southern Basin and Range Province. California State University-Fullerton, Desert Studies Consortium.

Simpson, G. G., 1930. Tertiary Land Mammals of Florida. Bulletin of the American Museum of Natural History 59:1-64.

Steinen, R. P., 1966. Stratigraphy of the middle and upper Miocene, Barstow Formation, California. (m.s. thesis): University of California-Riverside, 150 pp.

Tabrum, A. R., Nichols, R., and A. D. Barnosky. 2001. Tertiary paleontology of southwest Montana and adjacent Idaho. Museum of the Rockies Occasional Paper 3:93-112.

Tedford, R. H., Albright III, L. B., Barnosky, A. D., Ferrusquia-Villafranca, I., Hunt, Jr., R. M., Storer, J. E., Swisher III, C. C., Voorhies, M. R., Webb, S. D., and D. P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Early Pliocene epochs). pp 169-231, *in* Late Cretaceous and Cenozoic Mammals of North America; Biostratigraphy and Geochronology (M. O. Woodburne ed.), Columbia University Press, New York.

White, T. E. 1940. New Miocene vertebrates from Florida. Proceedings of the New England Zoological Club 18:31-38.

White, T. E. 1942. The lower Miocene mammal fauna of Florida. Bulletin of the Museum of Comparative Zoology 92:1-49.

Woodburne, M. O., Tedford, R. H., and C. C Swisher III. 1990. Lithostratigraphy, biostratigraphy, and geochronology of the Barstow Formation, Mojave Desert, southern California. Geological Society of America Bulletin 102:459-477.