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A Machairodont felid (Mammalia; Carnivora; Felidae) from the latest Hemphillian (Late Miocene/Early Pliocene) Bidahochi Formation, northeastern Arizona

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A lower jaw from the White Cone local fauna of the latest Hemphillian Bidahochi Formation in northern Arizona is the first description of a felid from this fauna and the first positively identified occurrence of the smilodontine machairodont *Paramachairodus* in North America. This lower jaw has characters identical to those seen in a similar sized machairodont felid from the Bone Valley Formation of Florida, suggesting that the same taxon is present in Florida. The diversity of the Hemphillian machairodonts and the taxonomic status of *Megantereon hesperus* is reviewed. The characteristics of the ramus corpus and dentition places *Paramachairodus* firmly within the Smilodontini and adds further support that the more derived smilodontine machairodonts, *Megantereon* and *Smilodon*, had their origins in North America.

INTRODUCTION

In the early 1950s the United States Geological Survey conducted a geological survey on the Navajo reservation (Repenning et al. 1958). During this survey, a collection of fossil vertebrates was made from White Cone, Navajo County, Arizona. White Cone is a small peak exposing the upper Bidahochi Formation, a deposit of Miocene to Pliocene fluvial and lacustrine sediments. Among the undescribed portion of the collection, now housed at the Smithsonian Institution, is a lower jaw of a medium-sized felid. A brief summary of the vertebrate remains by Repenning et al. (1958) mentions a “large cat” collected from White Cone. It is assumed here that the “large cat” mentioned by Repenning et al. (1958) is the mandible (USNM 244453) referred to here as the “White Cone cat.” This specimen offers valuable insight on the evolution of one group of machairodont felids and the diversity of the Felidae during the late Miocene. Additionally, new ecological implications can be drawn for the associated fossils from White Cone and the Bidahochi Formation based on this felid.

Previous work in the Bidahochi Formation

There is a diverse record of vertebrates from the Bidahochi Formation (Table 1). The earliest description of fossils from the Bidahochi Formation was made by Reagan (1932) who described the invertebrates from White Cone, and additional invertebrate remains were described by Taylor (1957). The first vertebrate fossils were described by Stirton (1936). These included a new species of beaver, *Dipoides williamsi*, as well as fragments of other rodents, a rabbit, a bird, an amphibian, and fish from collections made by the University of California, Berkeley. Repenning et al. (1958) noted additional fossil materials from White Cone collected by the USGS in the early 1950s. Uyeno and Miller (1965) described four species of cyprinid fishes from the Bidahochi Formation. Both isolated elements and complete individuals were described from Roberts Mesa, including a new species of the pike-minnow

Ptychocheilus preluclusus, and a new species of minnow, *Evomus navaho* (Uyeno and Miller 1965). Breed (1973) described aquatic bird tracks and fossils of *Olor columbianus*, the extant whistling swan, from 60 km north of Holbrook Arizona, and additional bird remains were mentioned by Stirton (1936). Lindsay and Tessman (1974) cite mammalian remains from the Bidahochi Formation at the “Taylor Gravels” near Taylor, Arizona, and provide a list of the White Cone fauna known at that time. The mammals from near Taylor include a canid, a gomphothere proboscidian, an equid referred to *Pliohippus*, and a camelid (Lindsay and Tessman 1974). Baskin (1975) described vertebrate remains from White Cone collected by the University of Arizona and the Smithsonian Institution in an unpublished Master’s thesis (Baskin 1975). Baskin later published on the origin of the South American cricetid rodent tribe Hesperomyini (Baskin 1978) utilizing material from White Cone and a description of the small mammal fauna from White Cone (Baskin 1979). Harrison (1981) described the *Plesiogulo* from White Cone in detail and designated it *Plesiogulo marshalli*. Harrison (1985) later described a large sample of the giant camelid *Megacamelus merriami* from the Bidahochi Formation near Keams Canyon Arizona. Prothero (1998, 2005) described the first record of the rhinoceros *Teleoceras hicksi* from Keams Canyon and Jeddito Arizona. The record of *T. hicksi* from the Bidahochi Formation is the only known record of rhinoceroses in the late Miocene of Arizona. Wang et al. (1999) described remains of the giant borophagine canid *Epiocyon haydeni* from President Wilson Springs in the Jeddito Valley. Wang et al. (1999) allocated these remains to the late Clarendonian, although *E. haydeni* is also known from the Hemphillian (Baskin 1998, Wang et al. 1999). The reptiles and amphibians collected from White Cone were recently reviewed by Parmley and Peck (2002). Morgan and White (2005) and Lindsay and Mead (2005) have provided recent overviews of the vertebrate faunas of the Bidahochi Formation. Lindsay and Mead (2005) added an additional taxon for White Cone: “? *Carpocyon* sp.”, a

Table 1. The vertebrate fauna of the Bidahochi Formation (references: Uyeno and Miller 1965, Breed 1973, Lindsay and Tessman 1974, Baskin 1975, 1979, Harrison 1981, 1985, Prothero 1998, 2005, Wang et al. 1999, Parmley and Peck 2002, Lindsay and Mead 2005, Tedford et al. 2009).

Class Osteichthyes	Class Aves	Order Carnivora
Family Cyprinidae	Order Anseriformes	Family Canidae
<i>Ptychocheilus preluccius</i>	Family Anatidae	<i>Epicyon haydeni</i>
<i>Evomus navaho</i>	? <i>Olor columbianus</i>	? <i>Carpocyon</i> sp.
? <i>Gila cristifera</i>	Class Mammalia	<i>Eucyon davisi</i>
<i>Gila</i> cf. <i>G. robusta</i>	Order Insectivora	canid indet. (small species)
Class Amphibia	Family Talpidae	Family Procyonidae
Order Anura	? <i>Domnimooides</i> sp.	cf. <i>Procyon</i> sp.
Family Bufonidae	Family Soricidae	procyonid indet.
<i>Bufo pliocompactilis</i>	<i>Notiosorex</i> sp.	Family Mustelidae
<i>Bufo woodhousii</i>	Order Lagomorpha	<i>Martes (Plionictis)</i> sp.
<i>Bufo</i> sp. indet.	Family Leporidae	<i>Plesiogulo marshalli</i>
Family Pelobatidae	<i>Hypolagus vetus</i>	Family Felidae
<i>Scaphiopus</i> sp.	Order Rodentia	<i>Paramachairodus</i> sp.
Family Ranidae	Family Mylagaulidae	Order Proboscidae
<i>Rana</i> sp. indet.	<i>Mylagaulus monodon</i>	Family Gomphotheriidae
Family Hylidae	Family Sciuridae	gomphotherid indet.
<i>Hyla</i> sp. indet.	<i>Spermophilus</i> sp.	Order Perissodactyla
Class Reptilia	sciurid indet.	Family Equidae
Order Sauria	Family Castoridae	cf. <i>Pliohippus</i> sp.
Family Teiidae	<i>Dipoides willamsi</i>	Family Rhinocerotidae
<i>Cnemidophorus</i> sp. indet.	Family Heteromyidae	<i>Teleoceras hicksi</i>
Family Iguanidae	<i>Perognathus</i> sp.	Order Artiodactyla
<i>Crotaphytus</i> sp.	<i>Cupidinimus bidahochiensis</i>	Family Camelidae
Family Scincidae	Family Cricetidae	<i>Megacamelus merriami</i>
<i>Eumeces</i> sp.	<i>Calomys (Bensonomys) yazhi</i>	camelid indet. (small species)
Order Serpentes	<i>Calomys (Bensonomys) gidleyi</i>	Family Antilocapridae
Family Colubridae	<i>Antecalomys</i> sp.	<i>Texoceras ? minorei</i>
<i>Pituophis melanoleucus</i>	<i>Paronychomys alticuspis</i>	antilocaprid indet.
<i>Lampropeltis getula</i>	cricetid indet.	
<i>Heterodon</i> cf. <i>H. nasicus</i>		
<i>Thamnophis</i> sp. indet.		

small hypo-carnivorous borophagine dog (Wang et al. 1999). Tedford et al. (2009) described the canid *Eucyon davisi* from the Bidahochi Formation near Keams Canyon, Arizona.

Abbreviations

Dental abbreviations used are: **c1**, lower 1st canine; **p2**, lower 2nd premolar; **P3**, upper 3rd premolar; **p3**, lower 3rd premolar; **P4**, upper 4th premolar; **p4**, lower 4th premolar; and **m1**, lower 1st molar.

Institutional abbreviations used are: **AMNH**, American Museum of Natural History, New York, NY, USA; **AZMNH**, Arizona Museum of Natural History, Mesa, AZ, USA; **DMNH**, Denver Museum of Nature and Science, Denver, CO, USA; **F:AM**, Frick Collection, American Museum of Natural History, New York, NY, USA; **IGM**, Instituto de Geología, Mexico City, Mexico; **KUVP**, University of Kansas

Natural History Museum, Lawrence, KS, USA; **TMM**, Texas Memorial Museum, Laboratory of Paleontology, Austin, TX, USA; **UALP**, University of Arizona, Laboratory of Paleontology, Tucson, AZ, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, USA; **USNM**, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; **YPM**, Yale-Peabody Museum, New Haven, CT, USA.

Machairodont felids from the Hemphillian North American Land Mammal Age

Machairodont felids from the Hemphillian are surprisingly diverse. Typical faunal records for the Hemphillian suggest one or two machairodont cats within a given mammalian fauna. There are five species recognized from North America. The largest is the lion-sized *Machairodus coloradensis*, first

described by Cook (1922) from Yuma County, Colorado. *M. coloradensis* is a member of the tribe Homotheriini (Kurtén 1963, Turner and Anton 1997). *M. coloradensis* has also been reported from Kansas (Martin and Schultz 1975, Harrison 1983), Nebraska (Martin and Schultz 1975), Oklahoma (Savage 1941) and Texas (Dalquest 1969). Webb et al. (2008) report a large machairodont felid from the Bone Valley Formation in Florida as "*Machairodus* cf. *M. coloradensis*". *M. coloradensis* is often confused with *Nimravides catocopis*, another large lion-sized felid with mixed taxonomic placement (Turner and Anton 1997, Martin 1998). *N. catocopis* is largely confined to the Late Clarendonian though it may have persisted into the early Hemphillian (Stevens and Stevens 2003). *Nimravides* differs from *Machairodus* in having a less developed mandibular flange, premolars with tall primary cusps, and a more elongate coronoid process (Martin and Schultz 1975). Martin and Schultz (1975) reassigned many previously described specimens of *Nimravides catocopis* to *M. coloradensis*, including the large sample from the Hemphillian Coffee Ranch locality in Texas (Burt 1931, Dalquest 1969). A set of lower jaws (IGM 6414) and upper dentition (IGM 6666 and 6667) from the Hemphillian deposits in Guanajuato, Mexico, have been referred to *Machairodus* cf. *coloradensis* (Carranza-Castañeda 1992, Carranza-Castañeda and Miller 1996). A lower jaw (WT 1642) of a machairodont from the Axtel locality in the Texas Panhandle has been referred to *Machairodus (Heterofelis)* sp. by Mawby (1965). This jaw exhibits characteristics of the ramus and dentition seen in *M. coloradensis* but it is noticeably smaller.

Adelphailurus kansensis was described by Hibbard (1934) based on a partial skull with complete dentition (KUPV 3462) from the late Hemphillian Edson fauna from Sherman County, Kansas. Harrison (1983) located and described additional post-cranial materials from the Frick Collections at the Edson locality. This taxon is considered a machairodont felid of the tribe Metalurini by Turner and Antón (1997). *A. kansensis* differs from *Metailurus major* and *M. parvulus* in that the cutting edge of the canines is primarily on the posterior, and the base of the posterior cutting edge is slightly serrated (Hibbard 1934). Also unique to *A. kansensis* is the presence of a medial groove along the anterior edge of the canine (Hibbard 1934). Harrison (1983) noted that the post-cranial elements of *Adelphailurus* are puma-like in structure. The metalurines had a puma/cheetah-like morphology and would have filled a similar ecological niche during the Miocene (Turner and Anton 1997). Harrison (1983) suggested that two species of *Adelphailurus* may occur in the Hemphillian Wikieup local fauna of northeastern Arizona. The holotype (KUPV 3156) of *Pratifelis martini* is a partial right mandible with poorly preserved p3-m1 from the Hemphillian Lost Quarry of Wallace County, Kansas. *P. martini* is an enigmatic cat known only from the holotype. Hibbard (1934) considered this taxon as part of a *Pseudaelurus* to *Felis* lineage, although Rothwell (2003) considered this taxon to be a specimen of *Nimravides*.

Berta and Galiano (1983) described a lower mandible from the latest Hemphillian Bone Valley Formation of Florida, which they referred to *Megantereon hesperus*. Turner (1987) suggested that this fossil is not *Megantereon*, however this specimen continues to be cited as the oldest occurrence of *Megantereon* (Martin 1998). Webb et al. (2008) propose that the Bone Valley Formation Palmetto fauna machairodont is not *Megantereon* and suggest it represents another machairodont taxon that was most recently compared to *Paramachairodus* and *Adelphailurus* (Webb et al. 2008).

GEOLOGY AND ENVIRONMENTAL SETTING

The White Cone locality is a small (about 74.7 meters) peak representing fluvial, volcanic, and lacustrine sediments of the upper Bidahochi Formation located between the towns of Bidahochi and Keams Canyon, Navajo County, Arizona (Fig. 1). Repenning and Irwin (1954) and Repenning et al. (1958) described three members of the Bidahochi Formation: a lower member consisting of gray, brown, and pink mudstones and argillaceous fine-grained sandstones, a middle volcanic member, and an upper fluvial member comprised predominantly of sandstones and rhyolitic ash layers.

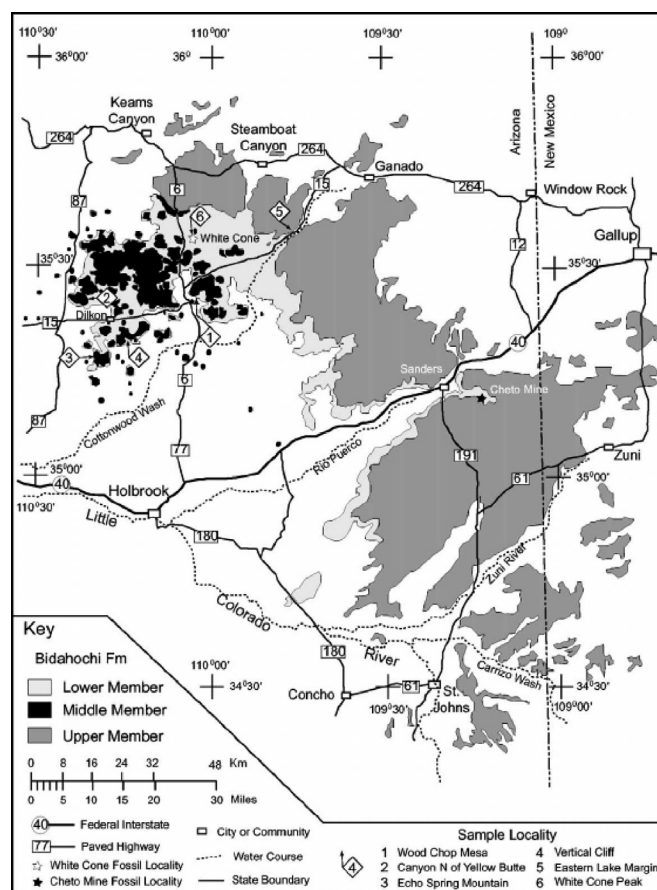


Figure 1. Map showing northeastern Arizona, White Cone locality, and the Bidahochi Formation's simplified three members of Repenning et al. (1958). Map from Dallegge et al. (2003).

Shoemaker et al. (1957) and Dallegge et al. (2003) revised the stratigraphy with six members: member 1 (the lowest) is composed of red mudstones, siltstone, and claystone; member 2 is composed of green, brown, red, pinkish-tan, yellow, and white interbedded claystone, siltstone, and marl; member 3 is composed of pinkish-tan siltstone with minor beds of green claystone and pinkish-tan sandstone; member 4 is composed of a lower red claystone unit and an upper green claystone unit, with minor interbedded siltstone and conglomerate; member 5 is composed of brown, green, black, lavender, and tan tuff, tuff breccias, lava, sandstone, claystone, and siltstone. Dallegge et al. (2003) named member 5 the White Cone member. Member 6 is composed of white, tan, buff, and green, poorly to moderately indurated sandstone and siltstone with minor amounts of claystone (Dallegge et al. 2003). The fossils collected by the USGS are from the White Cone member.

The lower members (1 and 2) have been dated between 9 Ma and 12 Ma, correlating with the Clarendonian North American Land Mammal Age (NALMA) (Love 1989). The upper members (5 and 6) at White Cone are regarded as latest Hemphillian (Lindsay et al. 1984). An air-fall tuff 15 m below the fossil bearing sediments was dated at 6.7 Ma (Lindsay et al. 1984). Scarborough et al. (1974) determined a radiometric age of 6.9 Ma from basalts within the White Cone locality. Lindsay et al. (1984) dated the fossiliferous zone (member 5) to roughly 5.9 Ma, with the White Cone fauna corresponding with the Redington fauna of southeastern Arizona and the Coffee Ranch local fauna of the Texas panhandle. Both faunas occur in lower chron 5 of the Global Magnetic Polarity Time Scale (GMPTS) (Lindsay et al. 1984, Tedford et al. 2004, Morgan and White 2005). Love (1989) and Wang et al. (1999) have suggested that many of these sites are Clarendonian in age, however, the occurrence of *Teleoceras hicksi* at Jeddito and Keams Canyon, suggest middle to late Hemphillian age (Prothero 2005).

Baskin (1975) described the paleoenvironment of member 5 of the Bidahochi Formation as an arid to semi-arid climate in close proximity to a series of semi-permanent to seasonal ponds, small lakes, and streams. Preliminary pollen studies of the Bidahochi Formation sediments at White Cone showed that the most common plants were *Sarcobatus* (greasewood) and *Amaranthus* (pig weed), indicative of semi-arid scrublands similar to those found in the region today (Baskin 1975). Pine pollen was rare, suggesting that pine occurred no closer than 2–30 miles away (Baskin 1975). The Bidahochi Formation sediments at Roberts Mesa contain *Sparganium* (bur-reed) or *Typha* (cattail), suggesting a marsh habitat occurred along the lake and stream margins at the time of deposition (Baskin 1975).

Taylor (1957) described the mollusk fauna from White Cone. The common species today, *Pisidium compressum* and *Helisoma subcrenatum*, require permanent standing water with little current (Taylor 1957). Two snail species, *Valata humeralis* and *Promenetus umbilicatus* occur as fossils at White Cone. Today, these taxa are known from higher

mountain areas, suggesting that summers were cooler than present (Taylor 1957).

Microvertebrate fossils in the White Cone fauna are extensive, with fish remains common. The cyprinid fishes of the Bidahochi Formation were described by Uyneo and Miller (1965). Uyneo and Miller (1965) suggested that some parts of the Bidahochi Formation were high flowing fluvial environments based on the presence of fossil minnows and an ancestral pike-minnow. The herpetofauna from White Cone, described by Parmley and Peck (2002), lists six amphibian and seven reptile species present in semi-arid environments and riparian habitats within the region today (Parmley and Peck 2002).

Baskin (1975, 1979) described the small mammals from White Cone. The presence of the desert shrew *Notiosorex*, the ground squirrel *Spermophilus*, and Heteromyid rodents, provide further evidence for semi-arid conditions in the past (Baskin 1975, 1979). The presence of grasslands is supported by the rodents *Calomys*, *Paronychomys*, and *Mylagaulus* (Baskin 1975, 1978, 1979). The beaver *Dipoides williamsi* is associated with permanent water; the mole *Dominoides* is considered an inhabitant of the pond-bank community (Stirton 1936, Baskin 1975, 1979). From the fossil evidence it can be concluded that the environment at White Cone was a riparian habitat with both permanent and seasonal water sources surrounded by semi-arid scrublands.

MATERIALS AND METHODS

All measurements are in millimeters and were taken with digital calipers. Comparisons were made with direct observations of modern specimens, original fossils, and casts of fossil specimens as noted. Additional comparisons were made through literature review. Dental nomenclature follows Van Valen (1966). Illustrations are made from scaled photographs.

SYSTEMATIC PALEONTOLOGY

ORDER: CARNIVORA Bowdich 1821

SUBORDER: FELIFORMIA Kretzoi 1945

FAMILY: FELIDAE Gray 1821

SUBFAMILY: MACHAIRODONTINAE Gill 1872

TRIBE: SMILODONTINI Kurten 1963

GENUS: *Paramachairodus* Pilgrim 1913

Paramachairodus sp

Referred Specimen—USNM 244453; lower right fragmentary ramus with complete p3, partial p4, and posterior root of the m1 (Table 2, Fig. 5).

Horizon and Locality—White Cone (USNM loc. 37; UALP loc. 6), Bidahochi Formation, Navajo County, Arizona.

Age—latest Hemphillian (late Miocene/early Pliocene)

Description—The ramus (Figs. 2–4) is missing the anterior mandibular symphysis, the articular condyle, and a small part of the dorsal edge of the coronoid process. The ramus is gracile and laterally compressed. A small thin ridge is present on the dorsal surface between the c1 and p3. A shallow

Table 2. Measurements of USNM 244453, *Paramachairodus* sp. from the White Cone local fauna. Measurements in millimeters, “*” measured from alveolus.

Ramus	
depth of ramus at p4	22
width of ramus at p4	11.4
Dentition	
Diastima between c1-p3	17.2
p3-m1 length	47.1
p3	
anteroposterior diameter	12.9
transverse diameter	6.3
p4	
anteroposterior diameter	16.8
transverse diameter	7.6
m1	
*anteroposterior diameter	20.3
*transverse diameter	8.5

concave depression is present on the upper anterior lateral end of the ramus between the c1 and p3. Two small closely spaced mental foramina are present. The anterior foramen is located just posterior of the canine and the posterior foramen just under the anterior root of the p3. The anterior ventral margin of the ramus is rounded. The coronoid process is reduced. A ridge is present on the anterior lateral margin of the coronoid that runs from the anterior border of the coronoid, down to the lateral side of the ramus just under the posterior root of the m1. The mandibular fossa extends directly under the m1. The rounded angular process projects downward at a slight angle. The angular process has a thin medial ridge.

The dentition (Fig. 3) is closely spaced with the anterior end of the m1 overlapping the posterior end of the p4 medially. The p3 has a small anterior accessory cuspid, a broad and low primary cusp, and two small posterior accessory cusps with the most posterior cusp formed from the posterior cingulum. In occlusal view, the anterior margin is small and tapers out to a broad posterior margin. The p4 is missing three fourths of the anterior medial side. The anterior accessory cuspid is roughly the same height as the posterior cuspid. The primary cusp is tall and prominent. The posterior cuspid is broad transversely with a cingulum on the posterior margin. Wear facets occur on the tips of the primary cusps of the p3 and p4. Only the posterior root of the m1 is present.

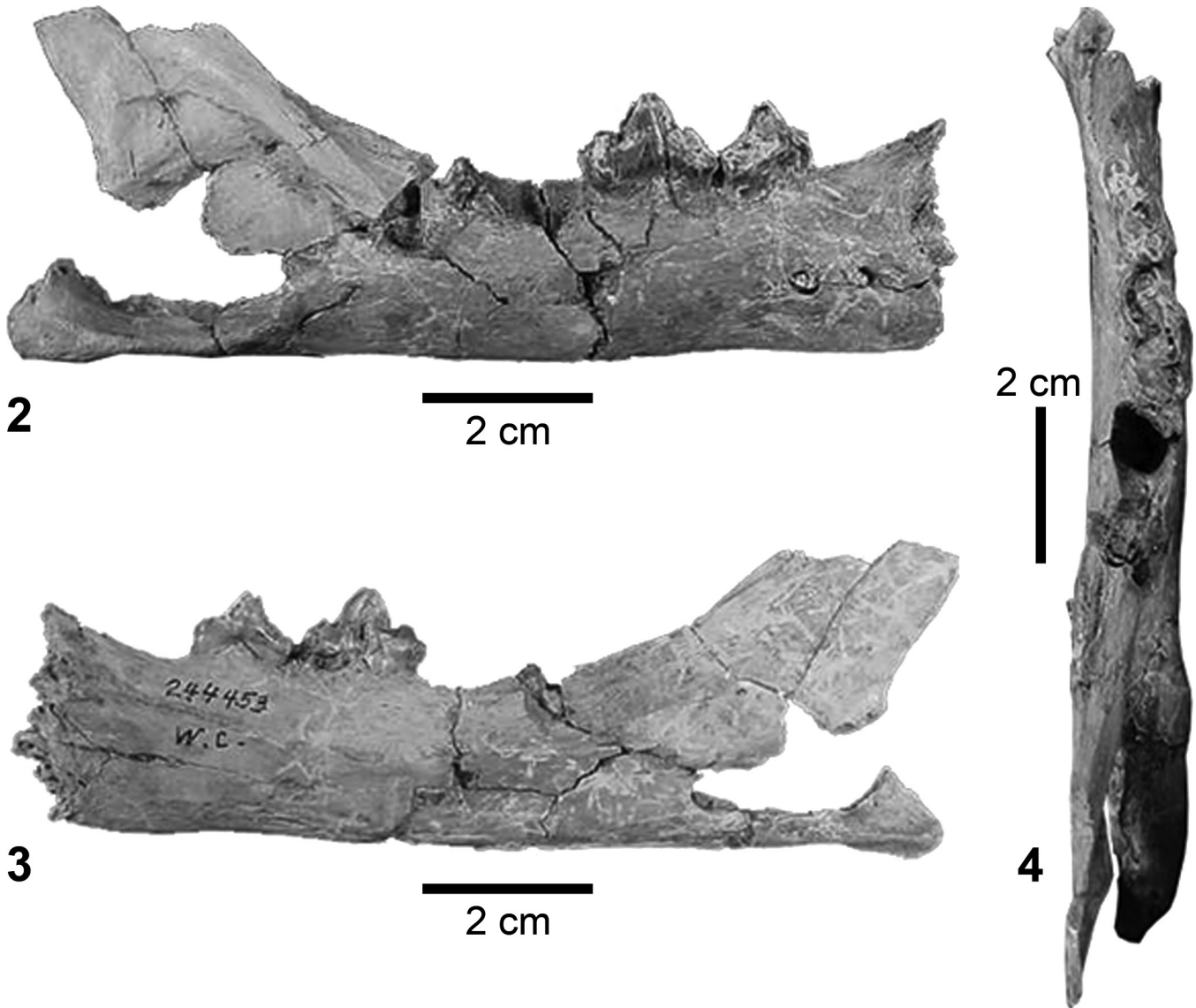
COMPARISON

The lower jaw from White Cone belongs to a medium sized felid, roughly the size of a clouded leopard (*Neofelis nebulosa*) or a small leopard (*Panthera pardus*). Based on the

presence of full adult dentition and on the amount of wear on the p3 and p4, this individual was an older animal. The ramus differs from other non-machairodont cats (Felinae) in having a deep mandibular fossa that extends to about the m1, a reduced coronoid process, and a reduced angular process. Compared to the North American (Hemingfordian-Barstovian) *Pseudaelurus* (Rothwell 2003), the White Cone ramus lacks an alveolus for the lower p2, which is seen in all pseudaelurine felids and some basal machairodonts (Rothwell 2001, 2003, Christiansen 2008). The axis of the p3 in the White Cone felid is angled inward medially, whereas in *Pseudaelurus*, the axis of the p3 is in line with that of the p4 and m1.

The Clarendonian/Hemphillian large felid *Nimravides* is considered a descendant of *Pseudaelurus* by some (Martin and Schultz 1975, Martin 1998). The primitive species, *N. pedionomus*, *N. thinobates*, and *N. galiani*, lack a mandibular flange but have a lower p2 (Kitts 1958, Baskin 1981, Beaumont 1990, Martin 1998). *Nimravides catocopsis* is more derived with a short mandibular flange and serrated lower canine, but retains a lower p2 (Martin and Schultz 1975). *N. catocopsis* (Fig. 6) is larger than *N. pedionomus*, *N. thinobates*, *N. galiani*, and the White Cone cat (USNM 244453) (Martin 1998). *Nimravides* also has a p3 that has a prominent posterior accessory cusp whereas the White Cone cat has a reduced posterior accessory cusp on the p3 (Kitts 1958, Martin and Schultz 1975, Baskin 1981, Beaumont 1990). The primary cusp of the p4 in *Nimravides* is more prominent than in the White Cone cat (Kitts 1958, Martin and Schultz 1975, Baskin 1981, Beaumont 1990).

The metailurine machairodont *Adelphailurus kansensis* is a puma-sized felid known from a partial cranium and post-cranial materials from the Edson fauna of the Ogallala Formation, Kansas (Hibbard 1934, Harrison 1983). Harrison (1983) mentions additional remains of *Adelphailurus* from the Hemphillian Wikieup local fauna of the Big Sandy Formation, Mohave County, Arizona, in her review of the *A. kansensis* materials from Edson. A cast of a partial skull with complete lower jaws from the Wikieup local fauna (AZMNH loc 08-79, MSM P7628, Fig. 10) was made available for this study and facilitated the following comparison. The lower jaw is similar to *Metailurus*. The symphysis of the ramus is at a steep angle, similar to that seen in the living cheetah (*Acinonyx jubatus*) and the Plio/Pleistocene cheetah-like cat *Miracinonyx*. The ramus corpus is relatively deep with a more elongated coronoid process than the White Cone cat and other machairodont felids. The angular process is reduced as in machairodont felids, however it is not rounded like the White Cone cat and terminates in a more defined point. The canine is less enlarged compared with other machairodont felids, similar to the condition seen in living cheetahs (Sunquist and Sunquist 2002). The diastema is less elongated than seen in other machairodont felids. The p3 differs from the White Cone cat in having a more enlarged primary cusp and a more pronounced posterior accessory cusp. The p3 of MSM P7628 has a reduced anterior accessory cusp compared



Figures 2–4. USNM 244453, right ramus of *Paramachairodus* sp. scale bar = 2 cm. 2. left lateral view; 3. right medial view; 4. occlusal view.

to *Pseudaclurus*. The p4 of *Adelphailurus* differs from the White Cone cat in having a taller primary cusp and a more pronounced posterior cingulum. The m1 of *Adelphailurus* has a deep carnasal notch and a prominent accessory talonid.

Adelphailurus was reported from the Hemphillian Redington local fauna from the Quiburis Formation in Pima County Arizona (Lindsay 1984, Lindsay et al. 1984). A maxilla (IGM 6674) with P3-P4 and an isolated P4 (IGM 6673) from Guanajuato Mexico referred to *Pseudaclurus*? *intrepidus* by Carranza-Castañeda and Miller (1996) is referred in this study to *A. kansensis* based on the following: the P3 has a slight anterior accessory cusp, a prominent primary cusp and a posterior accessory cusp; the P4 has a reduced protocone and a deep metastyle notch. *Pseudaclurus intrepidus* is restricted to the early to late Barstovian. Its P4 has a

more prominent protocone than *Adelphailurus* (Rothwell 2003). The holotype ramus (TMM 41261-3, Fig. 11) of *Pseudaclurus hibbardi* (Dalquest 1969) from the Hemphillian Coffee Ranch locality was thought to belong to *Nimravides* (Rothwell 2003). However, this mandible is nearly identical to *Metailurus* from Eurasia (Kovatchev 2001, Roussiakis et al. 2006), an *Adelphailurus* jaw from Wikieup (MSM P7628), and differs from *Nimravides* (Kitts 1958, Martin and Schultz 1975, Baskin 1981, Beaumont 1990). This jaw differs from *Metailurus* and *Adelphailurus* only in the presence of a small alveolus for p2. The Coffee Ranch mandible differs from *Pseudaclurus* and *Nimravides* in having a steep angle on the mandibular symphysis, a reduced diastema between the c1 and p3, reduced anterior accessory cusp on the p3, and a deep carnasal notch with a more pronounced talonid

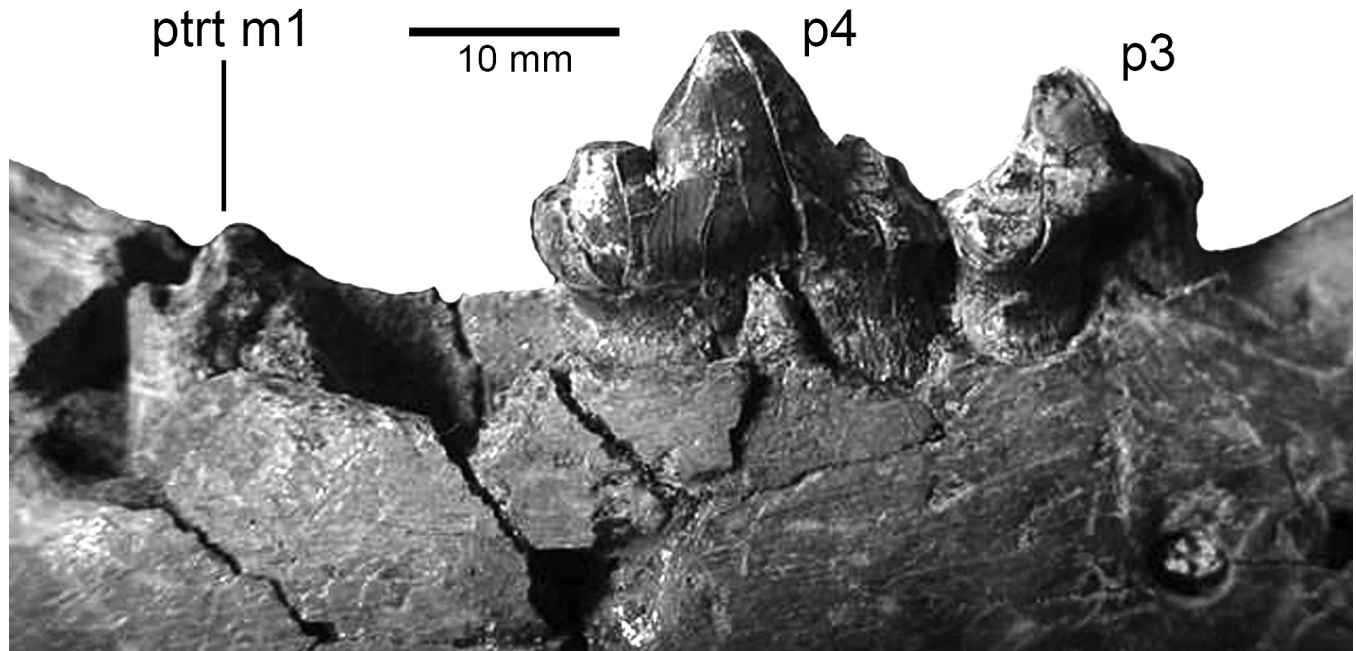


Figure 5. USNM 244453, lateral close up of dentition of *Paramachairodus* sp. p3 Scale bar= 10 mm.

on the m1. These traits strongly support TMM 41261-3 having a closer affinity with an identification of a metailurine machairodont felid. In North America, the only known metailurine is *Adelphailurus kansensis*. Therefore it is suggested here that the holotype ramus of *Pseudaelurus hibbardi* is a junior subjective synonym of *Adelphailurus kansensis*. The Coffee Ranch mandible (TMM 41261-3) differs from the White Cone cat in having a reduced diastema between the c1 and p3, a deeper ramus corpus, a p3 with a taller primary cusp and more prominent posterior accessory cusp, and a taller primary cusp on the p4. The poor condition of the dentition of the holotype of *Pratifelis martini* (KUV 3156) makes the specimen difficult to assess. However, the deep carnassial notch and prominent talonid on the m1 suggest a closer affinity of *Pratifelis* to the Metailurini than to either *Pseudaelurus* or *Nimravides*.

Machairodus is a relatively large machairodont felid from the middle to late Miocene of Eurasia and North America (Turner and Anton 1997). The North American species, *M. coloradensis*, is known from the latest Clarendonian to the Late Hemphillian and is often confused with *Nimravides catocopis* (Martin and Schultz 1975). The large sample of *M. coloradensis* from the Hemphillian Coffee Ranch was originally referred to *N. catocopis* (Burt 1931, Dalquest 1969) but later reassigned to *M. coloradensis* (Martin and Schultz 1975). Compared to the White Cone cat, *M. coloradensis* has a mandibular flange, a shorter coronoid process, a p3 with a larger posterior accessory cusp, a p4 with a more enlarged anterior accessory cusp and a lower primary cusp, a longer m1, and the dimensions of the lower jaw is larger than the White Cone cat lower jaw. The less derived European *Machairodus aphanistus* is known from complete cranial and post cranial

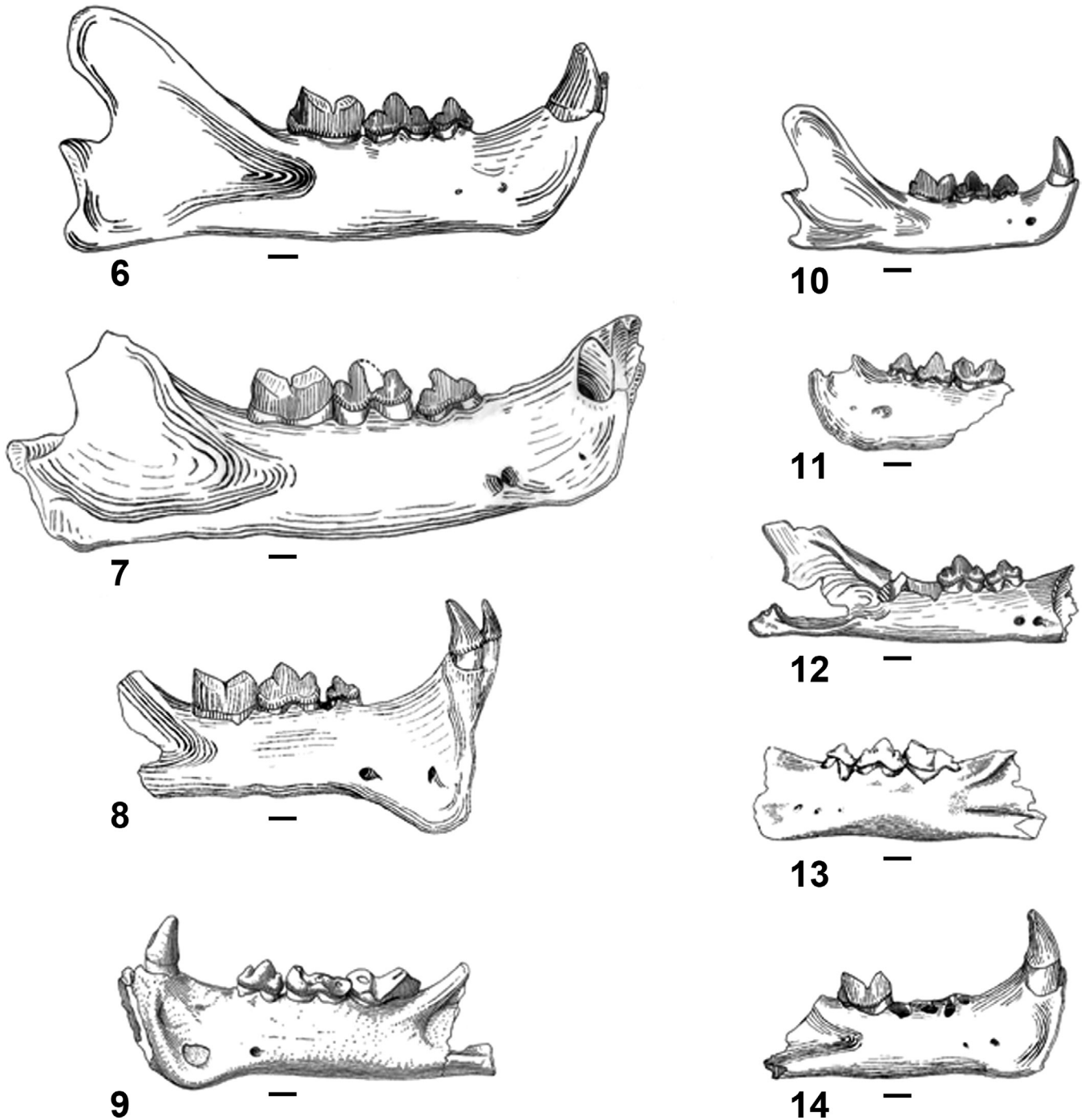
material from the Late Miocene Batallones-1 locality near Madrid, Spain (Anton et al. 2004). *M. aphanistus* has a more elongate coronoid process and a less developed mandibular flange than *M. coloradensis* or *Amphimachairodus giganteus* (Anton et al. 2004, Werdelin and Sardella 2006). Compared with the White Cone cat, the less derived *M. aphanistus* has a p3 with a larger posterior accessory cusp, a p4 with a more enlarged anterior accessory cusp but with a taller primary cusp, and is larger (Anton et al. 2004).

Mawby (1965) referred a left machairodont mandible (Fig. 9) with c1-m1 from the Hemphillian Axtel locality in the Panhandle of Texas to *Machairodus (Heterofelis)* sp. This mandible resembles the paratype of *M. coloradensis* (DMNH 207, Fig. 7) from Yuma County, Colorado (Cook 1922) in having a more developed mandibular flange than *Nimravides catocopis* and a more gracile ramus corpus than *Homotherium*. The dentition also resembles *M. coloradensis* with a more robust p3 with well developed anterior and posterior accessory cusps compared to *N. catocopis*. One of the primary differences between *Machairodus* from Axtel and *M. coloradensis* is the *Machairodus* from Axtel is smaller than *M. coloradensis*. Mawby (1965) also noted that the ramus is proportionally heavier than *M. coloradensis* (referred to as *M. catocopis*) and has a broad depression on the medial side below the diastema, a feature not present in *M. coloradensis*. The heavy wear on the dentition of the Axtel taxon suggest that this is an older adult animal and the small size is not an indicator of juvenile age (Mawby 1965). In comparison to the White Cone cat, the Axtel *Machairodus* is larger and has robust anterior, primary, and posterior cusps on the p3.

The two mandibles of a machairodont felid collected from the Hemphillian deposits in Guanajuato Mexico were referred

to as *Machairodus* cf. *coloradensis* by Carranza-Castañeda (1992) and by Carranza-Castañeda and Miller (1996), however, the Guanajuato machairodont differs greatly from the paratype of *M. coloradensis* (Cook 1922) in its smaller size and

more developed mandibular flange. The mandibular flange of the Guanajuato machairodont projects further ventrally of the ramus corpus than what is observed in the paratype of *Machairodus coloradensis*. The Guanajuato mandible (Fig.



Figures 6–14. Hemphillian machairodont felid jaws in lateral view drawn to scale (scale bar= 1 cm). **6.** USNM 4819, *Nimravides catocopsis*; **7.** DMNH 207, *Machairodus coloradensis* (drawn from Cook, 1922); **8.** IGM 6414, the Guanajuato machairodont (drawn from Carranza-Castañeda 1992); **9.** WT 1642, the Axtel *Machairodus* USNM 244453 (from Mawby 1965); **10.** MSM P7628, *Adelphailurus kansasensis* from Wikieup; **11.** TMM 41261-3, *Adelphailurus kansasensis* (holotype to “*Pseudaelurus hibbardii*”) (drawn from Dalquest 1969) from Coffee Ranch; **12.** USNM 244453, *Paramachairodus* sp. from White Cone; **13.** UF 22890 the Palmetto machairodont (modified from Berta 1987); **14.** UF 124634, the Palmetto machairodont (drawn from Hulbert 2001).

8) looks similar to *Megantereon* but the dentition differs in having a more caniniform third incisor, proportionally larger canine, larger primary cusp on the p3, larger accessory cusp and broader primary cusp on the p4, a more elongated m1, and coarse serrations on the incisors, canine, and premolars. The characteristics of the dentition and the greater development of the mandibular flange suggest that the Guanajuato machairodont is more closely related to *Homotherium* than to *Machairodus*.

Homotherium is a large lion-sized and highly derived Plio-Pleistocene machairodont from Africa, Eurasia, and North America (Meade 1961, Ballesio 1963, Petter and Howell 1988, Rawn-Schatzinger 1992). The ramus is relatively deep with a greatly reduced coronoid process, a deep mandibular flange, a reduced p3, a p4 with a robust anterior accessory cusp and low primary cusp, and is larger than the White Cone cat. Additionally, *Homotherium* and the homotherid felid *Xenosmilus* have serrations not only on the incisors and canine but also the premolars (Ballesio 1963, Rawn-Schatzinger 1992, Martin et al. 2000) a feature the White Cone cat lacks.

The White Cone cat shares characters with the machairodont tribe Smilodontini (Kurtén 1963), which include *Paramachairodus*, *Megantereon*, and *Smilodon* (Turner and Anton 1997, contra McKenna and Bell 1997). In *Megantereon cultridens* and *M. whitei*, the ramus has a thin deep mandibular flange and a greatly reduced coronoid process (Palmqvist et al. 2007, Christiansen and Adolfsson 2007). *Megantereon* also has a larger p4 relative to the p3. In *M. cultridens*, the p3 is larger than the more derived *M. whitei* (Palmqvist et al. 2007). In *M. whitei* the p3 is reduced to a small less functional tooth (Palmqvist et al. 2007). In *Smilodon*, (*S. gracilis*, *S. fatalis*, and *S. populator*), the ramus has a reduced but well developed thin mandibular flange, a highly reduced coronoid process, and a larger p4 (Merriam and Stock 1932, Berta 1985, 1987, 1995, Werdelin and Kurtén 1988). The primitive *S. gracilis* from the Pliocene and early Pleistocene of North America retains a well developed, though reduced, p3 that is closely placed to the p4. The anterior and posterior accessory cusps are reduced as seen in *M. cultridens* (Berta 1987, 1995). In the more derived *S. fatalis* and *S. populator*, the p3 is either vestigial, or is completely lost (Merriam and Stock 1932, Berta 1985).

The White Cone cat (Fig. 12) compares best to *Paramachairodus* from the Late Miocene of Eurasia. *Paramachairodus* lacks a well-developed flange and has a taller coronoid process and a larger p3 (Fig. 15) as compared to *Megantereon* and *Smilodon* (Salesa et al. 2003, 2005). Of the two species of *Paramachairodus*, *P. ogygia* is better known than *P. orientalis*, with multiple nearly complete individuals from the Batallones-1 locality near Madrid, Spain (Salesa et al. 2005). Both the White Cone cat and *P. ogygia* have a gracile and compressed ramus corpus, an angular process directed horizontally, a dorsal ridge on the diastema between the c1 and p3, a p3 with reduced anterior and posterior accessory cusps, and a p4 (Fig. 15) with a relatively tall primary cusp

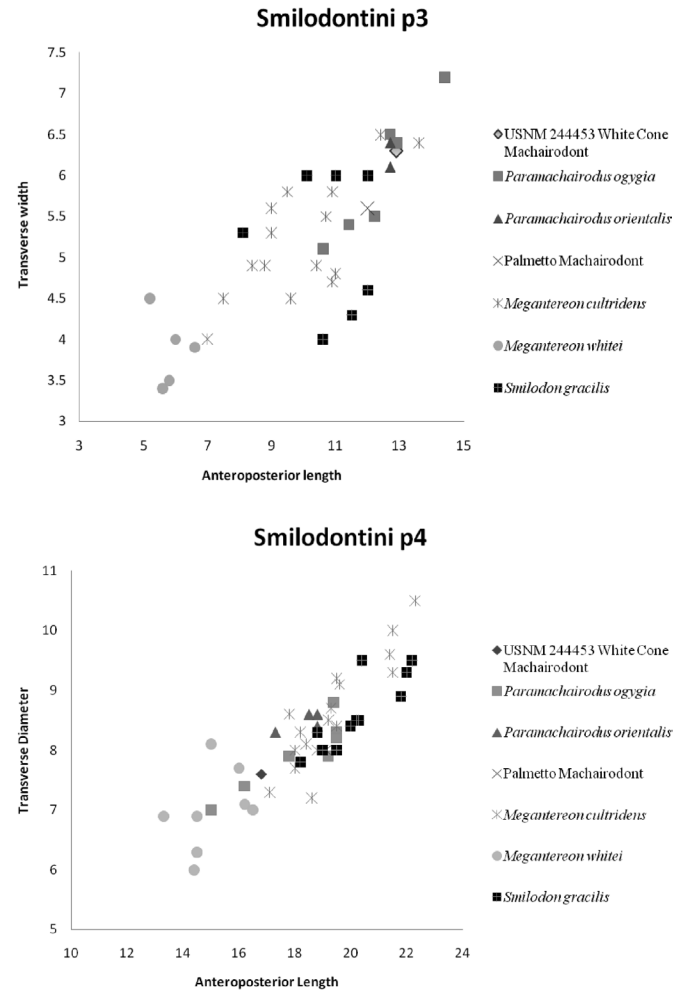


Figure 15. Bivariate analysis of p3 and p4 of the Smilodontini (see Table 3 for measurements).

(Beaumont 1975, Salesa et al. 2003 and 2005). Some individuals of *P. ogygia* have a smaller p2 (Christiansen 2008). The White Cone cat differs from *P. ogygia* in having a more gracile ramus corpus and a more reduced coronoid process, though not to the extent in reduction of the coronoid process seen in *Megantereon* and *Smilodon*. A partial mandible of *P. orientalis* (YPM 15235) differs from the White Cone cat in having a less gracile ramus corpus and a p3 with a broader primary cusp. A p4 from Teruel Spain assigned to *P. orientalis* (Morales and Soria 1977) is nearly identical to the p4 of the White Cone cat. Due to the incomplete nature of the White Cone material, it is here assigned to *Paramachairodus* sp.

The White Cone material is similar in morphology and size to the smilodont felid *Megantereon hesperus* from the Bone Valley Formation in Florida (Berta and Galiano 1983). The lower jaw (UF 22890) described by Berta and Galiano (1983) lacks the anterior mandible symphysis and the coronoid process (Fig. 13). Though it was reconstructed with a small mandibular flange, there is no real indication that one was present. The p3 is similar to the p3 in the White Cone

Table 3. The references and data used for the bivariate analysis for this study. Measurements in millimeters.

White Cone machairodont (this study)													
p3	anteroposterior diameter	12.9											
	transverse diameter	6.3											
p4	anteroposterior diameter	16.8											
	transverse diameter	7.6											
<i>Paramachairodus ogygia</i> (Salesa et al. 2003)													
p3	anteroposterior diameter	12.7	12.2	12.9	11.4	10.6	14.4						
	transverse diameter	6.5	5.5	6.4	5.4	5.1	7.2						
p4	anteroposterior diameter	19.2	19.4	19.5	19.5	17.8	16.2	15					
	transverse diameter	7.9	8.8	8.3	8.2	7.9	7.4	7					
<i>Paramachairodus orientalis</i> (Pilgrim 1915)													
p3	anteroposterior diameter	12.7	12.7										
	transverse diameter	6.4	6.1										
p4	anteroposterior diameter	18.8	18.8	18.5	17.3								
	transverse diameter	8.4	8.6	8.6	8.3								
Bone Valley machairodont (Berta and Galiano 1983)													
p3	anteroposterior diameter	12											
	transverse diameter	5.6											
p4	anteroposterior diameter	19.1											
	transverse diameter	8											
<i>Megantereon cultridens</i> (Palmqvist et al. 2007)													
p3	anteroposterior diameter	9	9	12.4	13.6	13.6	9.6	11	10.9	10.9	10.7	10.4	8.4
	transverse diameter	5.6	5.3	6.5	6.4	6.4	4.5	4.8	4.7	5.8	5.5	4.9	4.9
p4	anteroposterior diameter	19.6	19.3	18.8	19.2	19	17.8	22.3	18.4	17.1	18.2	19.5	21.5
	transverse diameter	9.1	8.7	8	8.5	8	8.6	10.5	8.1	7.3	8.3	9.2	9.3
<i>Megantereon whitei</i> (Palmqvist et al. 2007)													
p3	anteroposterior diameter	5.6	6	6.6	5.8	5.2							
	transverse diameter	3.4		4		3.9	3.5	4.5					
p4	anteroposterior diameter	16.5	16.2	14.4	16	14.5	15	13.3	14.5	14.5			
	transverse diameter	7	7.1	6	7.7	6.3	8.1	6.9	6.9	6.3			
<i>Smilodon gracilis</i> (Berta 1987)													
p3	anteroposterior diameter	11.5	10.6	11	8.1	12	10.1	12					
	transverse diameter	4.3	4	6	5.3	6	6	4.6					
p4	anteroposterior diameter	20.4	20.3	20.2	20	20.3	18.2	19	18.8	22.2	21.8	22	19.5
	transverse diameter	9.5	8.5	8.5	8.4	8.5							
Guanajuato machairodont (Carranza-Castañeda and Miller 1996)													
p3	anteroposterior diameter	13.9	14.2										
	transverse diameter	6.7	6.7										
p4	anteroposterior diameter	22.3	22.7										
	transverse diameter	9.8	10.3										
<i>Machairodus coloradensis</i> (Dalquest 1969, Schultz and Martin 1970)													
p3	anteroposterior diameter	19.4	21.7	19	20	18.8							
	transverse diameter	8.3	9.5	6	9	7.6							
p4	anteroposterior diameter	28.6	28.7	28.9	27.9	29.6	21	23	27				
	transverse diameter	10.9	12	12	12	13.5	9	10	11				

Table 3. (continued) The references and data used for the bivariate analysis for this study. Measurements in millimeters.

Axtel <i>Machairodus</i> sp. (Mawby 1965)				
p3	anteroposterior diameter	17.7		
	transverse diameter	7.8		
p4	anteroposterior diameter	25.5		
	transverse diameter	10		
<i>Nimravides catocopsis</i> (Schultz and Martin 1970, this study)				
p3	anteroposterior diameter	16.25	17.1	
	transverse diameter	7.44	8.3	
p4	anteroposterior diameter	22.61	21.9	23.9
	transverse diameter	10.45	9.4	10.7
<i>Adelphailurus kansasensis</i> (Dalquest 1969, this study)				
p3	anteroposterior diameter	11.1	9.95	
	transverse diameter	5.5	4.35	
p4	anteroposterior diameter	15.5	15.2	14.18
	transverse diameter	7.4	7.4	6.18

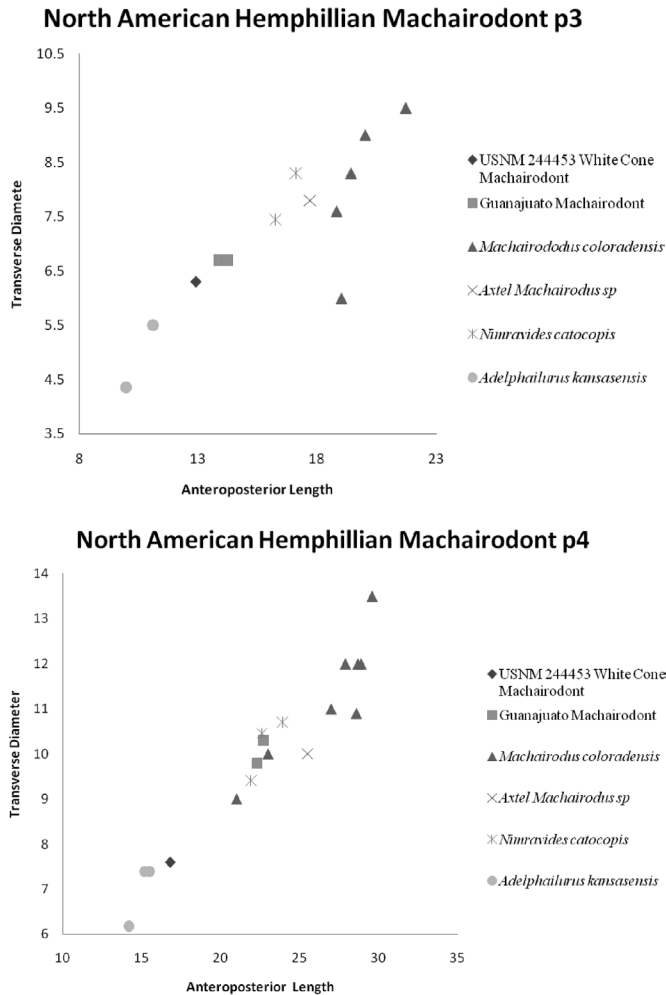


Figure 16. Bivariate analysis of p3 and p4 of the North American Hemphillian machairodont felids (see Table 3 for measurements).

specimen in having reduced anterior and posterior accessory cusps and the p4 is similar with a relatively tall primary cusp. Hulbert (2001) figured a mandible (UF 124634) from the Bone Valley Formation with an intact mandibular symphysis and canine (Fig. 14) that he referred to as *Megantereon hesperus*. This ramus shows a slight bulging of the ventral anterior margin of the mandible symphysis, which could represent a proto-flange, similar to that seen in the White Cone felid. The lack of a well-developed mandibular flange clearly suggests that this material is not *Megantereon* (Webb et al. 2008). Hulbert (personal communication 2008) has indicated FLMNH and UCLA researchers have collected additional complete materials from the Bone Valley Formation that is currently under study (Webb et al. 2008). *Paramachairodus* would have been one of the smaller machairodonts during the Hemphillian (Fig. 16).

The machairodont tribe Smilodontini (Kurtén 1963) includes *Paramachairodus* (including the White Cone cat and Palmetto machairodont), *Megantereon*, and *Smilodon*, as suggested by Turner and Anton (1997), based on the shared traits of a more gracile ramus corpus compared to other machairodont felids, a dorsal ridge on the diastema between the c1 and p3, p3 with reduced anterior and posterior accessory cusps, a p4 with a relatively tall primary cusp, and an m1 that is more laterally compressed, less anteroposteriorly developed, has a shorter paraconid, and the protoconid blade at a more acute angle as compared to other machairodonts

DISCUSSION AND CONCLUSIONS

Paramachairodus is an enigmatic smilodont cat which is becoming better understood based on the magnificent collection from the Batallones-1 locality in Madrid Spain (Salesa et al. 2003, 2005, 2006). The large sample of *Paramachairodus*

ogygia will allow for further analysis of the anatomy and ecomorphology of this species and basal machairodont felids (Salesa et al. 2005 and 2006). The record of *Paramachairodus* is largely confined to the middle Miocene and lower late Miocene of Eurasia (Beaumont 1975). Ginsburg (1999) placed *P. ogygia* in mammal zones MN-9 to MN-11 (Vallesian, 11.1–8.7 Ma) and *P. orientalis* in mammal zones MN-11 to MN-13 (Turolian, 8.0–4.9 Ma). The White Cone cat is the first evidence that *Paramachairodus* immigrated to North America and extends its temporal range into the Miocene/Pliocene transition. The immigration of *Paramachairodus* into North America correlates with the first occurrence of cervids in North America (Webb 2000). Salesa et al. (2006) suggested that *P. ogygia* had a prey preference for cervids and bovids weighing between 46 and 72 kg.

The oldest North American cervid is *Eocoileus gentryorum*, a member of the Odocoileinae subfamily of deer described from the Hemphillian Bone Valley Formation of Florida (Webb 2000), which includes the Palmetto machairodont (Webb et al. 2008). It is possible that *Paramachairodus* immigrated to North America by following the immigration of cervids into the New World. Given the rarity of cervids in the Hemphillian, it is likely that *Paramachairodus* found new prey opportunities among the ungulates of North America (i.e., antilocaprids, small camelids, equids, etc.).

At present the White Cone cat is the only confirmed report of *Paramachairodus* in North America. However, the Palmetto fauna machairodont (Webb et al. 2008) and other specimens from the Bone Valley Formation in Florida referred to *Megantereon hesperus* are very likely *Paramachairodus* based on the nature of the ramus and the dentition (see comparison above). In addition to the Florida materials and White Cone, the Hemphillian local fauna of Yepómera, Chihuahua, Mexico (Lindsay 1984b, Lindsay et al. 1984), the Wikieup local faunas of the Big Sandy Formation of northwestern Arizona (MacFadden et al. 1979) and the Redington and Camel Canyon local faunas of the Quiburis Formation in southeastern Arizona (Lindsay 1984a, Lindsay et al. 1984) report *Pseudaelurus* and/or *Megantereon* that alternatively may represent *Paramachairodus* or *Adelphailurus*. These faunas will likely increase the known diversity of Hemphillian machairodont felids in southwestern North America when studied.

The status of *Megantereon hesperus* is uncertain. The holotype, USNM 12614, is a right partial mandible with a complete m1 from the early Blancan Hagerman faunas of the Glens Ferry Formation, Idaho, originally described by Gazin (1933) as *Machairodus(?) hesperus*. What is problematic about the holotype is that it only contains part of the ramus with the m1 and lacks the full ramus corpus or the mandibular symphysis. This specimen is a machairodont with a deep mandibular fossa extending just under the m1. The m1 is characteristic of the all members of the Smilodontini. It is less anteroposteriorly elongated, more mediolaterally compressed, with a shorter paraconid and a protoconid at a

more acute angle as compared to the machairodonts *Machairodus* and *Homotherium*. However, without the mandibular symphysis, it is difficult to determine whether USNM 12614 should be placed in *Smilodon*, *Megantereon*, or even in *Paramachairodus*. The holotype of *Machairodus(?) hesperus* is best considered as an indeterminate smilodontine felid.

More complete remains of early Blancan smilodontine felids from the Broadwater fauna in Nebraska and the Rexroad fauna in Kansas (Hibbard 1937, Schultz and Martin 1970, Berta and Galiano 1983) have been referred to *Megantereon hesperus*. Based on the literature (Hibbard 1937, Schultz and Martin 1970, Berta and Galiano 1983), these specimens appear more similar to *Smilodon gracilis* than to *Megantereon* in characters of the mandibular flange. The mandibular flange in *Megantereon cultridens* extends ventrally beyond the ventral border of the ramus corpus and the mandibular symphysis, more so than the North American taxa (Palmqvist et al. 2007, Christiansen and Adolfsen 2007). In *M. whitei*, the mandibular flange is anteroposteriorly broader than *M. cultridens* (Palmqvist et al. 2007). The p3 is slightly more prominent than the early Irvingtonian sample of *S. gracilis* from Florida (Berta 1987, 1995) suggesting the early Blancan North American specimens are similar to *M. cultridens*. Based on the Eurasian specimens, the early Blancan smilodontine is perhaps best placed in *Smilodon* rather than in *Megantereon*. Additional support for *Smilodon* in the early Blancan come from post-cranial remains from the Bear Springs local fauna and the Benson local fauna of Arizona (Morgan and White 2005, White and Morgan 2005, Hodnett 2007).

The current view of the evolution of the Smilodontini is that *Paramachairodus* is the most basal member of this tribe, *Megantereon* evolved from *Paramachairodus*, and *Smilodon* evolved from *Megantereon* (Berta and Galiano 1984, Berta 1987, 1995, Turner and Antón 1997, Palmqvist et al. 2007). The occurrence of *Paramachairodus* in the latest Hemphillian (6.9 to 5.9 Ma) of North America adds further support for the origins of the more derived members of the Smilodontini (*Megantereon* and *Smilodon*) in North America (Berta and Galiano 1984).

The ecological implications of the occurrence of *Paramachairodus* at White Cone supplements what has been previously proposed (Salesa et al. 2006). The paleoenvironmental interpretation of the *Paramachairodus ogygia* from the late Vallesian Batallones-1 locality in Spain suggests that *P. ogygia* inhabited dense woodlands with fringing grasslands (Salesa et al. 2006). *P. orientalis* from the Turolian Siwalik beds of India indicate a habitat with more grassland interspersed with smaller woodland habitats (Barry et al. 2002). The inferred behavior of *Paramachairodus* has been suggested to be similar to the living African leopard, *Panthera pardus*, by Salesa et al. (2006) and Christensen (2008). This felid is known to inhabit dense woodlands and more open habitats with fringing woodlands (Sunquist and Sunquist 2002). Like the leopard, it has also been suggested that *Paramachairodus* was partially arboreal (Salesa et al. 2006). The occurrence of

Paramachairodus from the inferred semi-arid scrublands of the White Cone local fauna supports the idea that *Paramachairodus* was adapted to open habitats or riparian woodlands.

Using the modern felids from sub-Saharan Africa (Hunter and Hinde 2006), a trophic level of the felid guild can be modeled for the Hemphillian. The large felid carnivore guild of the Hemphillian included only machairodonts such as *Machairodus coloradensis* and *Adelphailurus kansensis* which represented the upper size limit of the large felid guild. The Guanajuato machairodont and the Axtel *Machairodus* are placed at the lower end of this large felid guild. *M. coloradensis* was roughly the same size as the modern lion (*Panthera leo*) and would have had a similar role as the apex predator at that time (Turner and Anton 1997). *A. kansensis* and other metailurine machairodonts were morphologically similar to the modern cheetah or American puma, both stalking, long distance pursuit predators, and would have filled that particular niche (Turner and Anton 1997). *Paramachairodus* would have represented the medium felid guild. The only modern felid that fits this size range today is the clouded leopard *Neofelis nebulosa*, an enigmatic cat that lives in the high-altitude dense forest of Southeast Asia. Considered largely arboreal, the feeding ecology of the clouded leopard is not well known, although it is estimated that the clouded leopard can take down prey larger than itself (Sunquist and Sunquist 2002, Christensen 2008). In the modern African guild model, *Paramachairodus* would fit between the leopard and the largest of the small cats such as the caracal *Caracal caracal*, serval *Leptailurus serval*, or African golden cat *Profelis aurata*. As mentioned above, *Paramachairodus* may have preferred prey between 46 and 72 kg (Salesa et al. 2006). In the Bidahochi Formation, there is at present no evidence of cervids. However, there is a fair diversity of non-cervid ungulates such as equids, small camelids, and antilocaprids in the size range that would have been utilized by a predator the size of the White Cone cat. At present, the diversity of the Hemphillian small felids is least understood, with only three known species: “*Felis*” *rexroadensis* (McFadden and Galiano 1981), *F. proterolyncis* (Savage 1941), and *F. longinathus* (Shotwell 1956). Considering the size variance (from 1 to 20 kg) within the small felid guild of Africa (Hunt and Hinde 2006) and the diversity of faunas in the Hemphillian, the number of species of small cats within the Hemphillian could be greater than three. Undescribed small felid remains from southwestern North America in the Frick collection at the AMNH will shed additional light on the diversity of the Hemphillian felids.

Finally, it is unclear at this time whether the lineage from *Paramachairodus* through *Megantereon* results in an anagenic *Smilodon*, or whether *Megantereon* and *Smilodon* both are derived independently from *Paramachairodus*. Only a careful analysis of all available materials, including post-crania, can resolve this question and confirm whether *Smilodon* and *Megantereon* are sister taxa, with *Paramachairodus* as the ancestral form to that group.

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