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?Amphictis (Carnivora, Ailuridae) from the Belgrade Formation of North Carolina, USA

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Miocene terrestrial mammals are poorly known from the Atlantic Coastal Plain. Fossils of the Order Carnivora from this time and region are especially rare. We describe a carnivoran mandible with a p4 from the late Oligocene or early early Miocene Belgrade Formation in Onslow County, North Carolina. Comparisons are made with carnivoran jaws with similar premolar and molar lengths from the late Oligocene and Miocene of North America and Eurasia. These indicate that the North Carolina jaw is assignable to the Ailuridae, a family whose only living member is the red panda. The jaw is tentatively referred to *Amphictis*, a genus known elsewhere from the late Oligocene and early Miocene of Europe and the early Miocene (Hemingfordian) of North America.

The North Carolina mandible compares best with the late Oligocene (MP 28) *Amphictis ambiguus* from Pech du Fraysse, France, the oldest known member of the Family Ailuridae, and with the early Miocene (MN 1–MN 2a) *A. schlosseri* from southwestern Germany. This identification is compatible with a late late Arikareean (Ar4, early Miocene, MN 2-3 equivalent) age assignment for the other terrestrial mammals of the Belgrade Formation.

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Abstract

Miocene terrestrial mammals are poorly known from the Atlantic Coastal Plain. Fossils of the Order Carnivora from this time and region are especially rare. We describe a carnivoran mandible with a p4 from the late Oligocene or early early Miocene Belgrade Formation in Onslow County, North Carolina. Comparisons are made with carnivoran jaws with similar premolar and molar lengths from the late Oligocene and Miocene of North America and Eurasia. These indicate that the North Carolina jaw is assignable to the Ailuridae, a family whose only living member is the red panda. The jaw is tentatively referred to *Amphictis*, a genus known elsewhere from the late Oligocene and early Miocene of Europe and the early Miocene (Hemingfordian) of North America.

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Introduction

Tertiary terrestrial mammals are known from a few localities on Atlantic Coastal Plain (Tedford et al., 2004). Only four of these contain terrestrial carnivorans. The Farmingdale Local Fauna of New Jersey, initially assigned to the early Hemingfordian (Tedford & Hunter, 1984), is late late Arikareean (Ar4, MN 2-3 equivalent) in age (Emry & Eshelman, 1998). An indeterminate canid is recorded from there (Gallagher et al., 1995). The early Hemingfordian (He1, MN 4 equivalent) Pollack Farm Local Fauna of Delaware is from the Calvert Formation. It contains at least 26 species of land mammals (Emry & Eshelman, 1998). Carnivorans present are two procyonids, two borophagine canids, an ursid, and two amphicyonids. The Barstovian Chesapeake Bay Fauna of Maryland and Virginia is from the Calvert and overlying Choptank Formations (Wright & Eshelman, 1987). *Amphicyon* and the borophagine canid ?*Cynarctus marylandica* are recorded in the fauna (Tedford et al., 2004). The Lee Creek Mine Local Fauna is from the Lower to Upper Pliocene Yorktown Formation in North Carolina (Snyder, Mauger & Akers, 1983). Eshelman & Whitmore (2008) documented 16 taxa from there, including two borophagine canids, an ursid, and a felid.

The Belgrade Quarry in Onslow County, North Carolina exposes strata of Oligocene through Pleistocene age (Locality 20 of Ward, Lawrence & Blackwelder, 1978). At the quarry, marine invertebrates and vertebrates have been recovered from the River Bend Formation and the overlying Belgrade Formation (e.g., Rossbach & Carter, 1991; Boesseneker, Ahmed & Geisler, 2017). The River Bend Formation is a shell hash limestone. The Belgrade Formation, which is divided into the lower Pollocksville and upper Haywood Landing Members, consists of marine shell beds, sands, and clay (Ward, Lawrence & Blackwelder, 1978).

The carnivoran jaw (NCSM 33670) described below is likely from the Belgrade Formation. At the quarry, the middle to late Oligocene River Bend Formation is mined for aggregate (McCleod & Barnes, 2008). Belgrade Formation sediments are bulldozed off of it and placed into small piles that are exposed to the elements. A mammal jaw with a p4 (NCSM 33670) was recovered while surface collecting for shark teeth and other fossils after a heavy rainstorm. Ray dental plates and shark teeth from these spoil piles include *Aetobatis* sp., *Dasyatis* sp., *Myliobatis* sp., *Rhinoptera* sp., *Galeocerdo* sp., *Hemipristis serra*, *Carcharhinus* sp., *Carcharodon angustidens*, *Carcharias* sp., *Nebrius* sp., *Isurus* sp., and *Physogaleus* sp.

The age of the Belgrade Formation is disputed. It has been assigned a late Oligocene age (Rossbach & Carter, 1991; Harris & Laws 1997; Ward, 2002), a late Oligocene/early Miocene age (Ward, 1998), and an early Miocene age (Baum, Harris & Zullo, 1978; Zullo, Willoughby & Nystrom, 1982). Belgrade Quarry is in Onslow County, the location of the type section of the Belgrade Formation. The Belgrade Formation in Onslow County, including the designated type section (Baum, Harris & Zullo, 1978), has been assigned to the early Miocene (Ward, Lawrence & Blackwelder, 1978; Zullo, 1984).

Terrestrial vertebrates recovered from mine spoil piles are likely earliest Miocene (late late Arikareean, Ar4, 18-23 Ma, MN 2-3 equivalent) in age (MacFadden et al., 2017). The key specimen for this determination is the entelodont *Daeodon*. The holotype of *Daeodon leidyanus* is from the late late Arikareean Farmingdale Local Fauna. However, the range of *Daeodon* in North America is early Arikareean, to early Hemingfordian (Lucas, Emry & Foss, 1998). Pliocene mammal fossils are also present at Belgrade Quarry (B. MacFadden, 2019, pers. comm.). Therefore, it is necessary to compare NCSM 33670 with late Oligocene to Pleistocene taxa.

Materials & Methods

Microtomography scans of the mandible were collected on a Zeiss Xradia 510 Versa nanoCT system, housed at the Analytical Instrumentation Facility at North Carolina State University. Measurements of fossil mammals at the American Museum of Natural History were made with digital calipers to the nearest 0.1 mm. Subdivision of the Arikareean North American Land Mammal Age (Ar1-4) follows Albright et al. (2008).

Results

Systematic Paleontology

Order CARNIVORA Bowdich, 1821
Family AILURIDAE Gray, 1843

Remarks

Baskin (1998b) had previously grouped the musteloids with an elongate m2 into a single family, the Procyonidae, with two subfamilies (Procyoninae and Ailurinae). His Ailurinae contained the tribes Simocyonini and Ailurini. In the present paper, we follow Morlo & Peigné's (2010) classification of the Ailuridae. Ailuridae is the sister taxon to the Procyonidae and Mustelidae. *Ailurus fulgens*, the red panda, is the only extant ailurid. The late Oligocene to early Miocene *Amphictis* is the sole genus of the paraphyletic Amphictinae (Morlo & Peigné, 2010) and is the stem sister taxon to the other two ailurid subfamilies, the Ailurinae and Simocyoninae.

Genus *AMPHICTIS* Pomel, 1853

Genotypic species: *Amphictis antiqua* (Blainville, 1842)

Remark

Morlo & Peigné (2010) diagnosed the genus and characterized its eight species.

?*AMPHICTIS* sp.
Figs. 1-4; Table 1

Referred specimen. NCSM 33670, right mandible with p4, and alveoli for p1-p3, m1-m2; from Belgrade Quarry in Onslow County, North Carolina, USA.

Description: The mandible extends from posterior to the canine to the posterior alveolus of m2 (Fig. 1). It is somewhat shallower beneath the p3 (Table 1). Posterior from beneath the p3, the ventral border is gently convex posterior to beneath the p3. The mental foramen is below the anterior root of the p3, at approximately half the depth of the ramus. The coronoid process is missing, Length-wise cracks on the surface, porous bone, and polish on parts of the surface are indications of weathering and perhaps transport before burial.

The p1 is represented by a single, shallow alveolus. The roots are preserved in the p2 alveoli. The p3 alveoli contain the distal tips of the roots. The p4 is the only tooth in the mandible with crown elements preserved (Fig. 1). The relatively intact roots of p2 and p4 are preserved, as are the apical-most portions of both of the roots of p3 and much of the anterior root of m1 (Fig. 1B, F). The main cusp of the p4 is broken anterior to the midline of the tooth. There is a distinct posterior accessory cusp on the external margin of the main cusp. The anterior cingulid is better developed antero-internally than antero-externally. The posterior cingulid is well developed.

The posterior root of the m1 is larger than the anterior root. The m2 is double rooted and situated on the slope of the ascending coronoid process. In the nano-CT volumetric reconstruction (Figs. 1B, 1F), the posterior root appears smaller than the anterior root. However, the bone surface surrounding that alveolus is eroded. As reconstructed (Fig. 2), the two roots were nearly identical in depth, with the posterior alveolus extended upward and sloped toward the anterior margin of where the coronoid process would have been. Therefore, the m2 posterior root was a much more substantial structure that extended both distally and occlusally than what is preserved. There is a third small accessory rootlet between the anterior and posterior root.

Discussion

The presence of only a single, relatively non-diagnostic tooth, the p4, and the possibility that the jaw may not be late late Arikareean make a confident generic determination difficult. The absence of an m2 indicates NCSM 33670 is a member of the Musteloidea - the Mephitidae, Ailuridae, Mustelidae, and Procyonidae (Wolsan, 1993; Wang, McKenna & Dashzeveg, 2005). The highly sloping distal molar, transitioning to the coronoid process out of the strict occlusal plane, is another feature seen only in musteloids, and immediately identifies the jaw as neither a canid nor an amphicyonid. An elongate m2 is and an elongate m1 talonid (as suggested by the larger posterior m1 alveolus) are characteristic of the Ailuridae and Procyonidae. NCSM 33670 was therefore compared with late Oligocene and early Miocene basal musteloids, mustelids, ailurids, and procyonids, as well as with middle Miocene and younger ailurids and other musteloids.

NCSM 33670 compares best with *Amphictis*, the earliest and most primitive member of the Ailuridae (Morlo & Peigné, 2010). *Amphictis* is known from the late Oligocene (Arvernian, MP 28) to early Miocene (Orleanian, MN 3-4) of Europe (Heizmann & Morlo, 1994, Cirot & Wolsan, 1995; Morlo, 1996), the middle Miocene (late Orleanian, MN 5 or Astaracian, MN 6) of Turkey (Nagel, 2003), and the late early Miocene (early Hemingfordian, MN 4 equivalent) of North America (Tedford et al., 1987; Baskin, 2017). A possible earlier North American occurrence is AMNH 81029 (misnumbered AMNH 81040 in Baskin, 2017), a mandible from the late late Arikareean (AR4, MN 2-3 equivalent) of Nebraska identified as *Bassariscus* sp. (Cook & Macdonald, 1962). Baskin (2004) considered AMNH 81029 *Amphictis*-like.

NCSM 33670 is larger than most other mandibles referred to *Amphictis*, but the teeth have similar length proportions (Fig. 3). The middle Miocene (MN 6) *Amphictis cuspida* from Çandir, Turkey is the latest and largest species (Nagel, 2003). It is known from a lower jaw with p4-m2. *Amphictis cuspida* differs from other *Amphictis*, including NCSM 33670, in having a shorter m2 as compared to the m1 (Fig. 3). The only other specimen in Fig. 3 with such a relatively short m2 is the holotype of *Plesictis milloquensis* from the Late Oligocene (MP 29) of La Milloque in southwestern France (Helbing, 1928) which Cirot & Wolsan (1995) transferred to *Amphictis*. The additional specimen they identified as *A. milloquensis* (Cirot & Wolsan, 1995: fig. 1) has the m2:m1 ratio the same as that of the early Miocene (MN 1–MN 2a) *A. schlosseri* from the Molasse basin and Mainz basin of southwestern Germany (Heizmann & Morlo, 1994). *Amphictis* from the Hemingfordian of Florida and Nebraska (Baskin, 2017) is much smaller than NCSM 33670. The *Bassariscus*-like posterior ramus with alveoli for the posterior root of m1 and for two roots of an elongate m2 from the Hemingfordian Pollack Farm of Delaware is similar to these Florida and Nebraska *Amphictis* (Emry & Eshelman, 1998; Baskin, 2003, 2017). NCSM 33670 is near the high end of the alveolar measurements of the species of *Amphictis* plotted in Fig. 3. Measurements of *Amphictis ambiguus* from Quercy at Pech du Fraysse (MP 28) are most similar to those of NCSM 33670. The p4 of NCSM 33670 is similar to that of *A. schlosseri* (Heizmann & Morlo, 1994: fig. 2).

Alopecocyon from the middle Miocene of Europe (MN 6–MN 7/8) is closely related to *Amphictis* (Beaumont, 1976; Morlo & Peigné, 2010). Beaumont (1976) noted that the lower dentition of *Alopecocyon goeriachensis*, the type species of the genus, was difficult to distinguish from that

of *Amphictis*. Wolsan (1993) synonymized *Alopecocyon* with *Amphictis*. Plots of dental measurements (Figs. 3, 4) support Wolsan. However, Morlo & Peigné (2010) noted that this had not been accepted by subsequent authors. Webb (1969), following a suggestion from D. E. Savage, synonymized *Actiocyon* (Stock, 1947) from the Clarendonian Nettle Spring Fauna of the Caliente Formation of California with *Alopecocyon*. Smith, Czaplewski & Cifelli (2016) distinguished North American *Actiocyon* from Eurasian *Alopecocyon* by morphology of the cusps on m2. *Actiocyon parverratis* from the early Barstovian (MN 6 equivalent) of Nevada (Smith, Czaplewski & Cifelli, 2016) and *Actiocyon* sp. (F:AM 25312) from the late Clarendonian Ash Hollow Formation of Nebraska have an elongate m2 relative to m1 (0.68 and 0.77 of the m1 length respectively), but only the Ash Hollow specimen has the m2 significantly more elongate than *Amphictis*. More derived ailurids such as *Pristinailurus* from the late Miocene to early Pliocene Gray Fossil Site in Tennessee (Wallace & Wang, 2004; Wallace, 2011) have a more complex p4 and an even more elongate m2. Tooth measurements (Figs. 3, 4) indicate NCSM 33670 is more similar to the larger species of *Amphictis* than to *Alopecocyon* or other ailurids.

In North America, procyonids are known from the the Hemingfordian of Florida, Nebraska, and Delaware. The procyonid from the early Hemingfordian Pollack Farm of Delaware (Emry & Eshelman, 1998) is an M1 compared to *Edaphocyon* (Wilson, 1960). The only mandible attributed to this genus, the Hemingfordian ?*E. palmeri*, has an elongate m2 (Baskin 2003), but differs from *Amphictis* and NCSSM 33670 in other dental proportions (Figs. 3, 4). The Hemingfordian *Bassaricyonoides phyllismillerae* (Baskin, 2003) has p4 much wider especially posteriorly and with a more prominent posterior accessory cusp on the postero-external margin. The Barstovian to Recent *Bassariscus* and the Barstovian *Probassariscus* are smaller than NCSM 33670 and have a more elongate m2. In the eastern U.S. procyonids occur in Clarendonian and younger sites of Florida. The only extant procyonid that may have been present in North Carolina in the Pliocene and Pleistocene is the raccoon *Procyon*. In *Procyon* the m1 and m2 are more or less equal in length (Wright & Lundelius, 1963) and the p4 is noticeably wider posteriorly and has a more laterally situated posterior accessory cusp.

Plesictis is a small mustelid from the late Oligocene and early Miocene of Europe (Bonis, Gardin & Blondel, 2019). *Mustelavus priscus* (Clark, 1936) is a musteloid from the late Eocene of western North America (Baskin, 1998a). Simpson (1946, p.13) considered *Mustelavus* a "probable synonym" of *Plesictis*. Because of similarities with the type of *M. priscus*, Macdonald (1970), following Simpson, identified an anterior mandible from the early Arikareean (Ar2) of South Dakota as *Plesictis* sp. Tedford et al. (2004) noted this occurrence as an immigration event for *Plesictis*. However, the generic identity of this South Dakota specimen has not been demonstrated. Wang, McKenna & Dashzeveg (2005) include the Chadronian to Orellan *Mustelavus priscus*, *Plesictis*, and several other taxa as basal musteloids. The Orleanian *Plesictis*? *humilidens* (Dehm, 1950) is from Wintershoff-West. Wolsan (1993) made it the type species of *Franconictis*, which he classified as a mustelid that was the sister taxon of *Stromeriella*. Both have a relatively long m2. *Franconicits humilidens* has similar dimensions (Dehm, 1950:table 11) to those plotted in Figs. 3, 4 for *Amphictis winterhoffensis*, other than a somewhat shorter m2 length relative to m1.

The early Oligocene *Peignictis pseudamphictis* is an enigmatic musteloid known from a posterior ramus with m1 (Bonis, Gardin & Blondel, 2019). The posterior alveolus of the m2 is

smaller than the anterior one. It is much smaller than *Amphictis* (m1L =5.3; m2L = 2.5) and has an m1 morphology more like that of *Mustelictis* (Bonis, Gardin & Blondel, 2019). Although the m2 is relatively long, the m2:m1 ratio is less than that of *Amphictis* or NCSM 33670.

The Oligobuninae are the sister group of the neomustelids (Baskin, 1998a, 2017; Valenciano et al. 2016). They, neomustelids, and procyonids are derived relative to ailurids in lacking an alisphenoid canal (Wang, McKenna & Dashzeveg, 2005). *Promartes*, the earliest oligobunine, is known from the late early Arikareean (Ar3) to Hemingfordian. Its species are similar in size to NCSM 33670 (Fig. 4). They and the other oligobunines differ from NCSM 33670 in having a relatively shorter m2 and a relatively longer m1 (Fig. 4).

Conclusions

The late Oligocene and early Miocene are marked by the immigration of carnivorans from Eurasia to North America (Tedford et al., 2004: fig. 6.3). Among the musteloids, *Mustelictis* from the early Oligocene (MP 22, 32 Ma) of Quercy, France (Bonis, 1997) is one of the earliest stem mustelids (Wang, McKenna & Dashzeveg, 2005). *Corumictis wolsani*, from the early Arikareean (Ar1, MP 24 equivalent, 30-28 Ma and Ar2) of Oregon, is the earliest stem mustelid in North America and is an immigrant taxon (Paterson et al., 2019). *Promartes* is the only oligobunine mustelid known from the Arikareean. Whether the Oligobuninae are autochthonous or allochthonous is unresolved. Crown clade mustelids and procyonids first appear in North America during the Hemingfordian. The procyonids are derived from a European early Miocene taxon such as *Broiliana* (Baskin, 1998b). Previously the earliest ailurids in North America were from the Hemingfordian of Florida and Nebraska (Baskin, 2017). NCSM 33670 is most similar to the late Oligocene *Amphictis ambiguus* (MP 28) or the early Miocene *A. schlosseri* (MN 1–MN 2a). Based on marine invertebrates, as noted above, the Belgrade Formation has been considered late Oligocene (Chattian or Chickasawhayan) to early Miocene (Aquitanian) in age. MacFadden et al. (2017) propose a late late Arikareean (AR 4, MN 2-3 equivalent) age assignment for the mammals from the Belgrade Formation, In any case, an Arikareean (late Oligocene to early early Miocene) age assignment supports NCSM 33670 being an immigrant from Eurasia and the earliest record of the Ailuridae in North America.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, New York; F:AM, Frick Collection of fossil mammals in the AMNH; NCSM, North Carolina Museum of Natural Sciences.

Anatomical Abbreviations: p, lower premolar; m, lower molar; L, length; W, width.

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513 FIGURE CAPTIONS

514 Figure 1. Lateral (A&B), occlusal (C&D) and medial (E&F) views of volumetric reconstruction
515 of NCSM 33670. Mandibular bone (in gray) has been rendered semitransparent in B, D, and F to
516 display root morphology. Preserved dental elements (root and crown fragments) are tan.
517 Alveolar casts are rendered in red (canine), blue (p1), pink (p3), green (m1) and purple (m2). A-
518 D, anterior is to the right; E&F, anterior is to the left. Scale bar = 1cm.

519

520 Figure 2. Reconstruction of NCSM 33670 showing mandible with c1-m2.

521

522 Figure 3. Scatter plots comparing tooth dimensions of selected early and middle Miocene ailurids
523 and procyonids. Symbols are as follows: ★ = NCSM 33670; ■ = *Alopecocyon goeriachensis*
524 (measurements from Peigné, 2012); ■ = *Actiocyon parverratis* (measurements from Smith et al.,
525 2014); ●= *Amphictis ambiguus* (measurements from Heizman and Morlo, 1994); ● = *Amphictis*
526 *winterhofensis* (measurements from Dehm, 1950); ▲ = *Amphictis milloquensis* (measurements
527 from Cirot and Bonis, 1995); ► = *Amphictis schlosseri* (measurements from Heizman and
528 Morlo, 1994); ▲ = *Amphictis cuspida* (measurements from Nagel, 2003); ▼ = *Amphictis*
529 *timicua* (measurements from Baskin, 2017); ▼= *Amphictis* cf. *timicua* (measurements from
530 Baskin, 2017); ◄ = AMNH 81029; ♦ = *Bassaricyonoides phyllismillerae* (measurements from
531 Baskin, 2003); ♦ = ?*Edaphocyon palmeri* (measurements from Baskin, 2003).

532

533 Figure 4. Scatter plots comparing tooth dimensions of selected *Amphictis* and early and middle
534 Miocene mustelids, and procyonids. Symbols are as follows: ★ = NCSM 33670; ■ =
535 *Alopecocyon goeriachensis*; ■ = *Actiocyon parverratis*; ●= *Amphictis* spp.; ● = *Amphictis*

536 *winterhofensis*; ♦ = *Bassaricyonoides*; ♦ = ?*Edaphocyon*; ▼ = *Amphictis timicua* (measurements
537 from Baskin, 2017); ▼= *Amphictis* cf. *timicua*; ▲ = *Floridictis kerneri* (Baskin, 2017); ▲ =
538 *Zodiolestes*; ► = *Oligobunis*; ► = *Brachypsalis*; ◄ = *Promartes* spp.; ◄ = *Parabrachypsalis*
539 *janisae* (Baskin, 2017).

Figure 1

Lateral (A&B), occlusal (C&D) and medial (E&F) views of volumetric reconstruction of NCSM 33670.

Mandibular bone (in gray) has been rendered semitransparent in B, D, and F to display root morphology. Preserved dental elements (root and crown fragments) are tan. Alveolar casts are rendered in red (canine), blue (p1), pink (p3), green (m1) and purple (m2). A-D, anterior is to the right; E&F, anterior is to the left. Scale bar = 1cm.

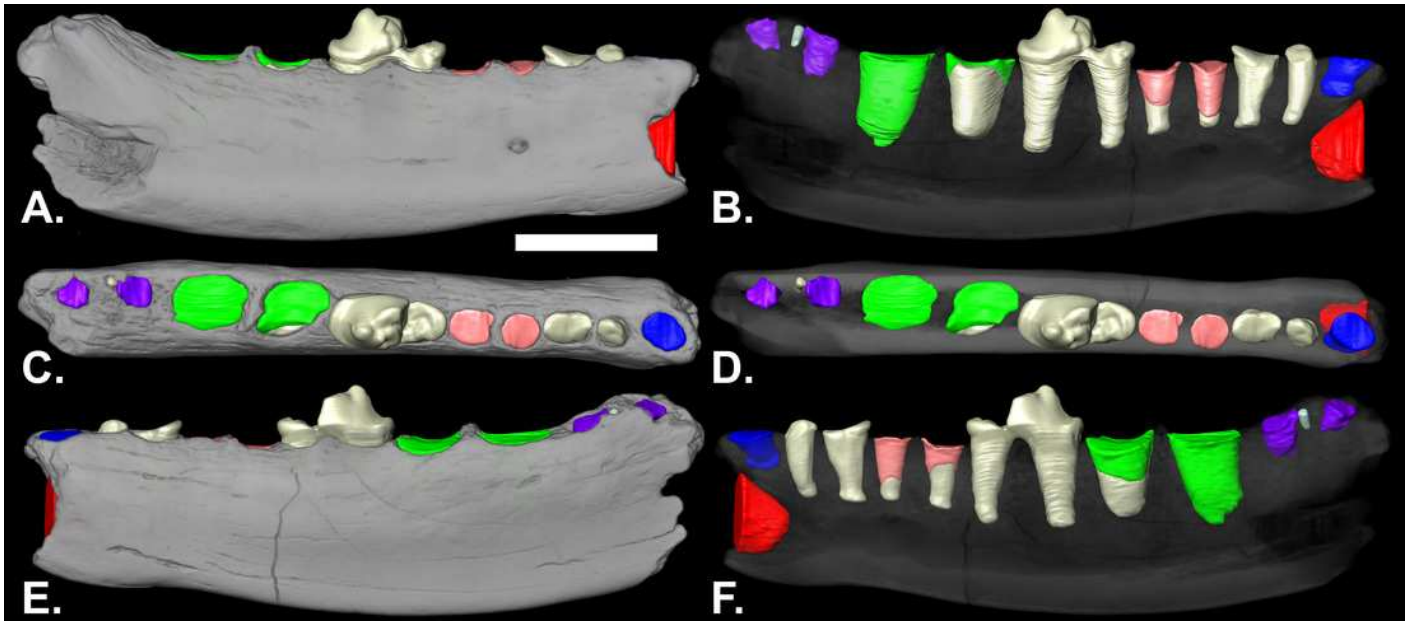


Figure 2

Reconstruction of NCSM 33670 showing mandible with c1-m2.

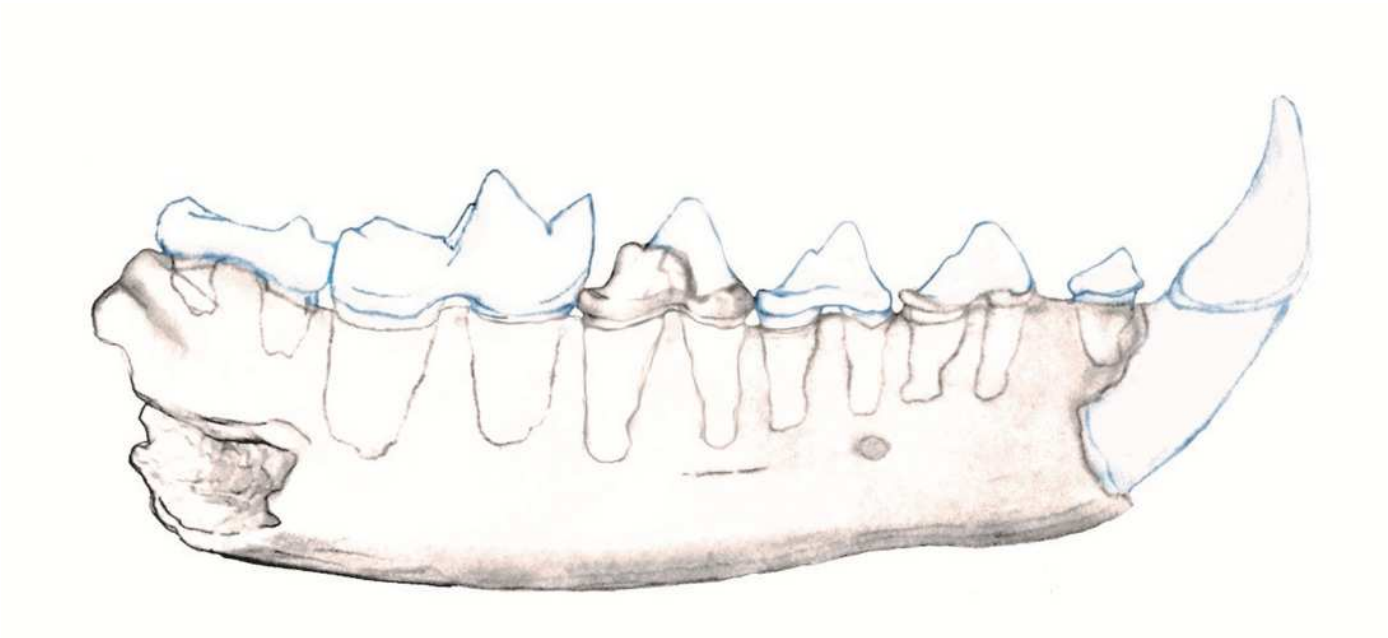
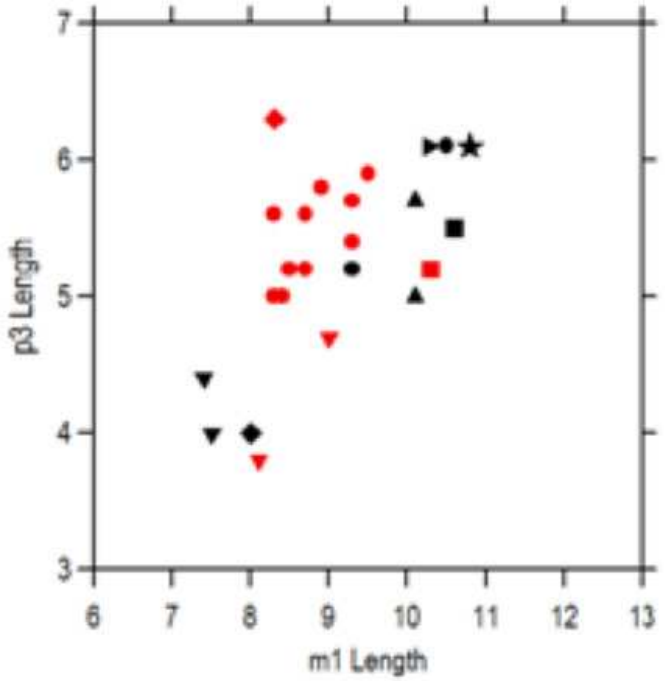


Figure 3

Scatter plots comparing tooth dimensions of selected early and middle Miocene ailurids and procyonids

. Symbols are as follows:


p3 Length
m1 Length
3
4
5
6
7
6
7
8
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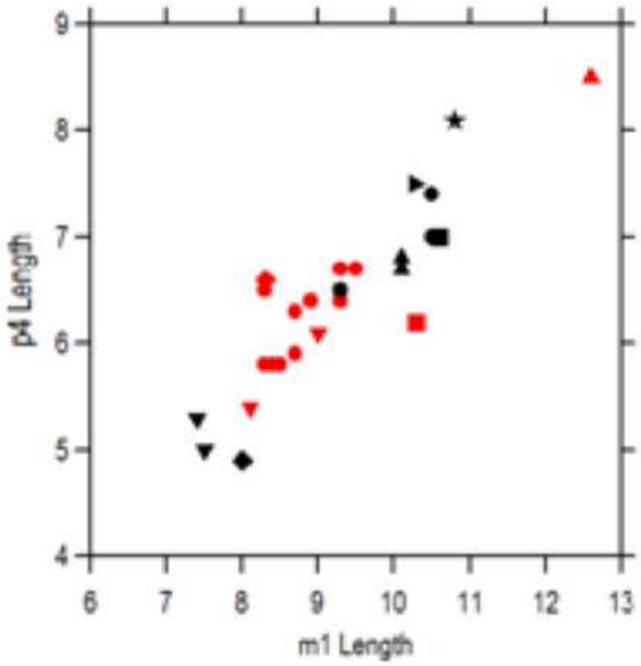
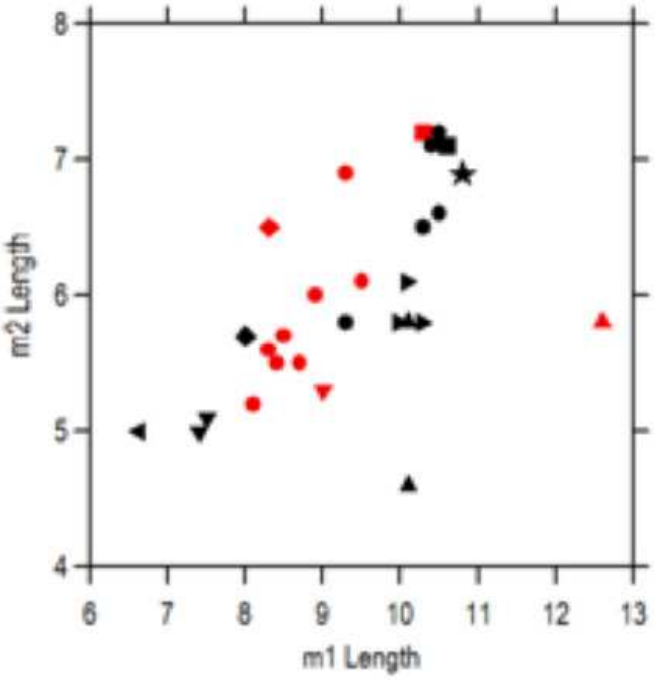
11
12
13


p4 Length
m1 Length
4
5
6
7
8
9
6
7
8
9
10
11
12
13


m2 Length
m1 Length
4
5
6
7
8
6
7
8
9
10
11
12
13

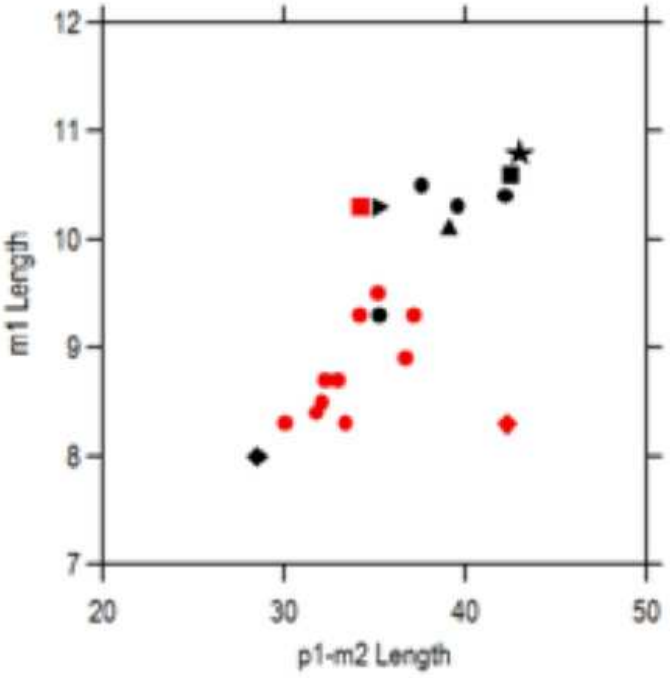

m1 Length
p1-m2 Length
7
8
9
10
11
12
20
30
40
50

Figure 4

Scatter plots comparing tooth dimensions of selected early and middle Miocene ailurids and procyonids

Symbols are as follows:

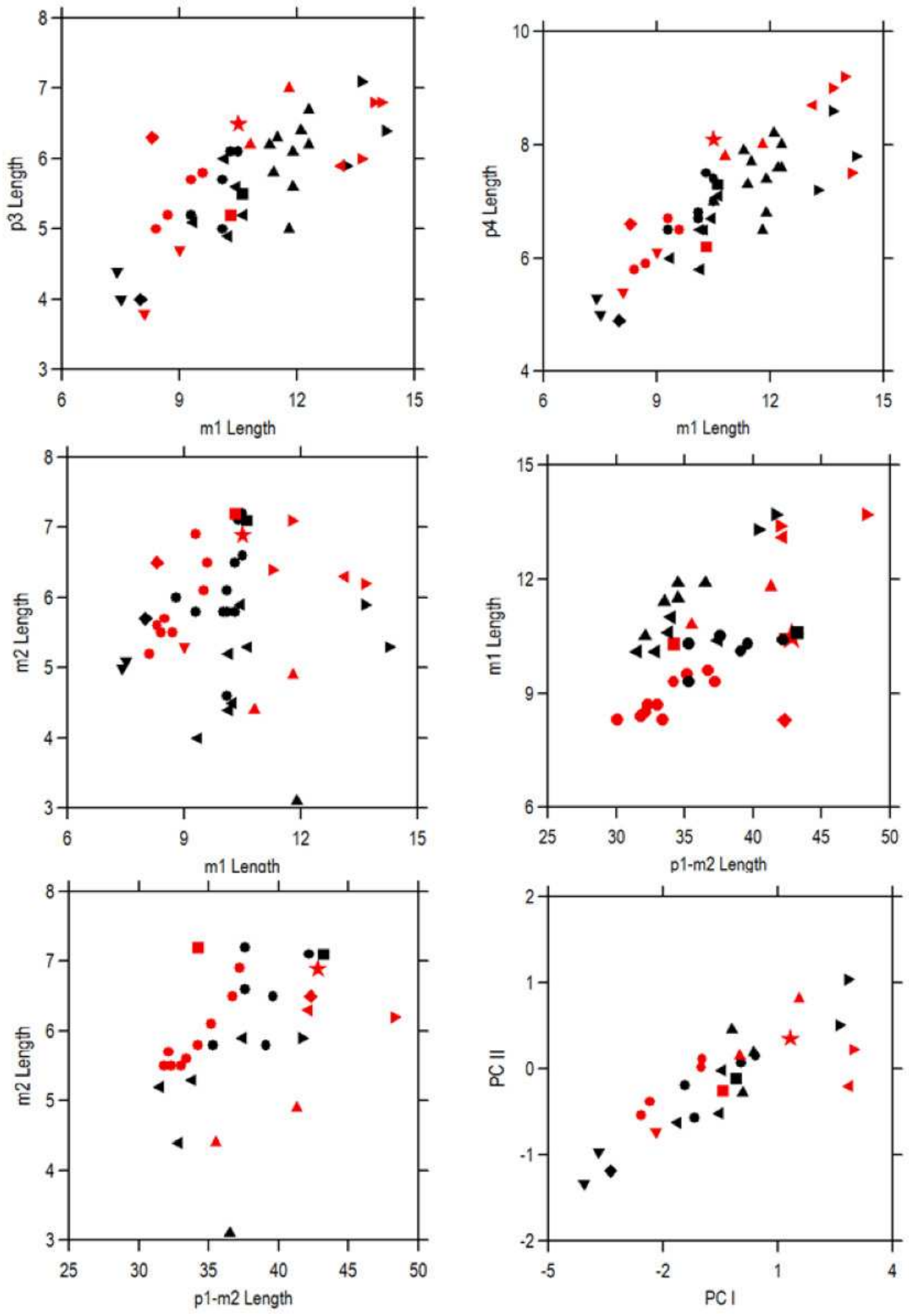

p3 Length
m1 Length
p4 Length
m1 Length
m2 Length
m1 Length
m1 Length
p1-m2 Length
m2 Length
p1-m2 Length
PC II
PC I

Table 1(on next page)

Measurements in mm on NCSM 33670.

L = length; W = width; Depth p2 and Depth m1 = depth of mandible below p2 and m1, respectively

1

p2 L	5.7
p3 L	6.1
p4l	8.1
p4 W	4.0
m1 L	10.9
m2 L	6.9
p2-m1 L	31.6
p2-m2 L	39.5
p1-m2 L	42.8
Depth p2	10.75
Depth m1	12.5

2

3