

THREE NEW PROCYONIDS (MAMMALIA, CARNIVORA) FROM THE BLANCAN OF FLORIDA

Laura G. Emmert^{1,2} and Rachel A. Short^{1,3}

ABSTRACT

Fossils of the mammalian family Procyonidae are relatively abundant at many fossil localities in Florida. Analysis of specimens from 16 late Blancan localities from peninsular Florida demonstrate the presence of two species of *Procyon* and one species of *Nasua*. *Procyon gipsoni* sp. nov. is slightly larger than extant *Procyon lotor* and is distinguished by five dental characters including a lack of a crista between the paracone and hypocone on the P4, absence of a basin at the lingual intersection of the hypocone and protocone on the P4, and a reduced metaconule on the M1. *Procyon megalokolos* sp. nov. is significantly larger than extant *P. lotor* and is characterized primarily by morphology of the postcrania, such as an expanded and posteriorly rotated humeral medial epicondyle, more prominent tibial tuberosity, and more pronounced radioulnar notch. Other than larger size, the dentition of *P. megalokolos* falls within the range of variation observed in extant *P. lotor*, suggesting that it may be an early member of the *P. lotor* lineage. *Nasua mastodonta* sp. nov. has a unique accessory cusp on the m1 as well as multiple morphological differences in the dentition and postcrania, such as close appression of the trigonid of the m1 and a less expanded medial epicondyle of the humerus. We also synonymize *Procyon rexroadensis*, formerly the only known Blancan *Procyon* species in North America, with *P. lotor* due to a lack of distinct dental morphological features observed in specimens from its type locality in Kansas. Results indicate that three procyonid species were sympatric in Florida during the Blancan, as occurs in parts of Central America today.

Key words: Carnivora, Procyonidae, *Procyon*, *Nasua*, early Pleistocene, Blancan, Florida, new species.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank Publication number for this issue is EB20BEB8-E2A1-42F3-8518-6068119F8122.

Published On-line: May 22, 2018

Open Access Download at <https://www.floridamuseum.ufl.edu/bulletin/publications/>

ISSN 2373-9991

Copyright © 2018 by the Florida Museum of Natural History, University of Florida. All rights reserved. Text, images and other media are for nonprofit, educational, or personal use of students, scholars, and the public. Any commercial use or republication by printed or electronic media is strictly prohibited without written permission of the museum.

¹Don Sundquist Center of Excellence in Paleontology, East Tennessee State University Natural History Museum at the Gray Fossil Site, Gray, TN 37615 USA

²corresponding author <zlsg5@goldmail.etsu.edu>

³Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843 USA

INTRODUCTION

Within Carnivora, the Procyonidae includes some of the rarest taxa in the fossil record (Baskin, 1982), likely due to their often arboreal nature (Romer, 1966). The Procyonidae contains 16 taxa from the Miocene (23 Ma) to today in North America (Baskin, 1998). The oldest fossil referred to *Procyon* is a partial dentary recognized by Baskin (1982) from the Mt. Eden local fauna, California, (5.6 Ma) (Albright, 1999) of the late Hemphillian North American Land Mammal Age (NALMA), but this material was not assigned to a species, and the generic identification was not considered certain. *Procyon* is confidently known from Kansas in the early Blancan NALMA (Pliocene) and questionably from Washington, while the genus is known from Arizona, Texas, and Florida by the late Blancan (White and Morgan, 2005). An extinct Blancan species, *Procyon rexroadensis*, was named based on specimens from the Rexroad Fauna of Meade County, Kansas (Hibbard, 1941; Oelrich, 1953), and later identified from Cita Canyon, Randall County, Texas (Johnston and Savage, 1955; Anderson, 1984). From its type locality, *P. rexroadensis* is represented by 34 specimens, mostly cranial elements (Bjork, 1973); there is also a fragmentary distal humerus catalogued as *P. rexroadensis* in the University of Michigan collections that was not previously recorded in the literature. This Blancan species was described as being about the same size as the extant crab-eating raccoon *Procyon cancrivorus* (Hibbard, 1941) and is thought to have a more general ecology than other species of *Procyon* (Oelrich, 1953).

Procyon became more common through the Pleistocene and, corresponding with the expansion of humans, *Procyon lotor* has today become widespread through Central America, the entirety of the United States and into southern Canada (Zaveloff, 2002). Four North American Pleistocene species of *Procyon* were named based on supposed size differences with *P. lotor* (*Procyon priscus*, *Procyon simus*, *Procyon nanus*, and *Procyon psora*). All were later shown to be within the natural variation of *P. lotor* and have been synonymized with this extant species (Oelrich, 1953; Kurtén and Anderson, 1980).

In North America, the early Blancan fossil record of *Nasua* consists only of a single p4 of *Nasua pronarica* from the Beck Ranch Local Fauna, Texas (Dalquest, 1978). *Nasua* sp. is also known from the Blancan-Irvingtonian Fish Creek-Vallecito Canyon local fauna of California (Cassiliano, 1999) and has tentatively been identified from the late Hemphillian Bone Valley Formation of Florida (Baskin, 1982). This record is based on a dentary with heavily worn lower premolars (Baskin, 1982) that was not recovered *in situ* (Webb et al., 2008), but the elongation and mediolateral compression of the p3 is indicative of *Nasua* rather than *Procyon* (Baskin, 1982). There are no records of *Nasua* from the middle or late Pleistocene of North America.

MATERIAL AND METHODS

Since 1965, the Florida Museum of Natural History has catalogued 48 procyonid fossils from 16 late Blancan localities in peninsular Florida: Santa Fe River 1B and 8C; Haile 7G; Waccasassa River 9A; Inglis 1A, 1B, 1D, 1F, 1I, and 1L; Ballards Pit 2; John Reynolds Site; Withlacoochee River 1A; Walden Pit 2; Indian River Shell Pit; and Macasphalt Shell Pit (see Hulbert, 2010 for site descriptions). Distal humeri are the most commonly preserved element (n=21). Just two dentaries have cheek teeth that are relatively unworn. Only the specimens from Inglis 1A have been previously studied. They were described as larger than extant *P. lotor*, and morphologically intermediate between *P. rexroadensis* and *P. lotor* (Webb and Wilkins, 1984) and possibly a new species of *Procyon* (Berta 1995). Morgan and Hulbert (1995), following Berta (1995), stated that it is likely that *Procyon* from the early Irvingtonian Leisey Shell Pit is conspecific with the Inglis 1A species. This study is restricted to specimens from the Blancan, but future work needs to be done on early Irvingtonian specimens of *Procyon* to determine if they truly represent an extension of an extinct Blancan taxon, or if they are instead better placed in *P. lotor*.

Specimens of the Rexroad Fauna, including all known specimens of *Procyon rexroadensis*, are currently housed at the University of Michigan. Unfortunately, the holotype specimen (an isolated

M1, KUMVP 5522) has been misplaced and could not be located during a visit to the UM collection. In the absence of the holotype, we examined a set of associated upper and lower dentition from both sides of the skull, UM 37171.

Rodriguez et. al. (2017) showed that the P4 is less useful than molars to identify taxa within Procyonidae because they display higher levels of intraspecific variation; consequently, a total of 520 P4s and M1s from 130 modern *Procyon* skulls representing the entirety of the continental United States and Central America were examined to eliminate sample biases. The representative sample of extant *Procyon* and *Nasua* was obtained from mammalogy collections of the USNM and AMNH. Five individuals were selected from each of the 26 subspecies of *P. lotor* (n=130), but only nine postcranial specimens of *P. cancrivorus* were available and many of these were incomplete or were insufficiently cleaned to allow accurate measuring. At least 30 individuals were selected from both species of *Nasua* (n=60). Approximately equal numbers of males and females of varying age classes and from nearly every region within the respective distribution ranges were included. Body mass estimates were made using the formulae provided in Tarquini et. al. (2017).

Institutional Abbreviations.—**AMNH**, American Museum of Natural History, New York City, New York; **ETVP**, East Tennessee State University Vertebrate Paleontology, Johnson City, Tennessee; **KUMVP**, University of Kansas Museum of Vertebrate Paleontology, housed at University of Michigan, Ann Arbor; **UF**, Florida Museum of Natural History, University of Florida, Gainesville; **UF/TRO** Timberlane Research Organization collection, housed at the Florida Museum of Natural History; **UM**, University of Michigan, Ann Arbor; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Morphological Abbreviations.—**i**, lower incisor; **c**, lower canine; **p**, lower premolar; **m**, lower molar; **I**, upper incisor; **P**, upper premolar; **M**, upper molar.

RESULTS

We found evidence of three new species of procy-

onids in the late Blancan of Florida. Two species belong in the genus *Procyon*: one that is slightly larger than extant *P. lotor* with a distinct dentition, and one that is significantly larger than *P. lotor* with distinct postcranial features. The third species is the first confidently known Blancan *Nasua* in the eastern United States and has the first recorded postcranial material of fossil *Nasua* in the United States.

Until now, the only named species of *Procyon* from the Blancan was *P. rexroadensis*. Therefore, the original assumption was that the specimens from Florida most likely belonged to that species. However, we found that the dental morphology of topotypic specimens of *P. rexroadensis* does not fall outside of the range of variation in both size (though it is closer in size to *P. cancrivorus*) and morphology of the large sample of examined modern *P. lotor* and, thus, in the absence of postcrania, it cannot be confidently distinguished as a distinct species. A distal humerus from the type locality, UM 37159, is catalogued as *P. rexroadensis* but appears to be a mustelid, perhaps *Lutra* or *Satherium*, based on the robustness and low angle of the medial supracondylar ridge, the large size of the epicondylar foramen, and the sloping angle of the medial edge of the trochlea. Until postcrania associated with teeth are found of *P. rexroadensis* and can be compared to other species of *Procyon*, we recommend that *P. rexroadensis* be synonymized with *P. lotor*.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Superfamily MUSTELOIDEA Fischer, 1817

Family PROCYONIDAE Bonaparte, 1850

Genus *PROCYON* Storr, 1780

PROCYON GIPSONI sp. nov.

Holotype.—UF 243697, left maxillary fragment with P4–M1 (Fig. 1B).

Paratype.—UF 312851, right P4 (Fig. 2D).

Zoobank Nomenclatural Act.—31902ABA-84DD-4AEC-A42C-AC701204D3F2.

Type locality.—Withlacoochee River 1A, Marion County, Florida (see Hulbert, 2010 for detailed locality data).

Etymology.—Named in honor of Aaron

Gipson, the discoverer and primary excavator of the Withlacoochee River 1A site, who has graciously donated many hundreds of fossils to UF, including the holotype of the eponymous species.

Referred material.—UF 243837, right dentary with c-m1 (m1 in Fig. 2H).

Diagnosis.—Differs from all other known species of *Procyon* in lacking a crista between hypocone and paracone on P4, absence of a basin at lingual intersection of hypocone and protocone on P4, reduction of metaconule of M1, valley between metacone and metaconule of M1 in place of crista, and considerably more posterior extension of entoconid relative to hypoconid of m1.

Description.—Within the modern sample (n=130), only five *P. lotor* shared detailed morphological similarities with *P. gipsoni*. None had a reduced M1 metaconule similar to the holotype of *P. gipsoni*, UF 243697, including those with considerable wear. There is minimal wear on the holotype and only a very small, shallow wear surface is

present where the metaconule would be, so there is not enough wear to cause the total loss of a possible metaconule. Also, the crista that normally descends from the metacone to the metaconule in *P. lotor* is truncated by a distinct groove in *P. gipsoni*. Four modern *P. lotor* specimens (USNM 050982, 80301, 255053, 267381) have the same absence of a lingual basin on the P4 as seen in *P. gipsoni*, but all four possess the hypocone-paracone crista. Only one specimen, USNM 057839, lacks the crista but it does possess the lingual basin. Despite rare specimens sharing some characters, no examined specimen of *P. lotor* has all five diagnostic characters of *P. gipsoni*.

Only a single specimen representing the upper dentition of *P. gipsoni* is presently known from the type locality. It therefore might have been considered a rare individual aberration from a population whose normal dental morphology resembles that of *P. lotor*. But a second specimen, an isolated right P4 (UF 312851), was collected from the Nashua

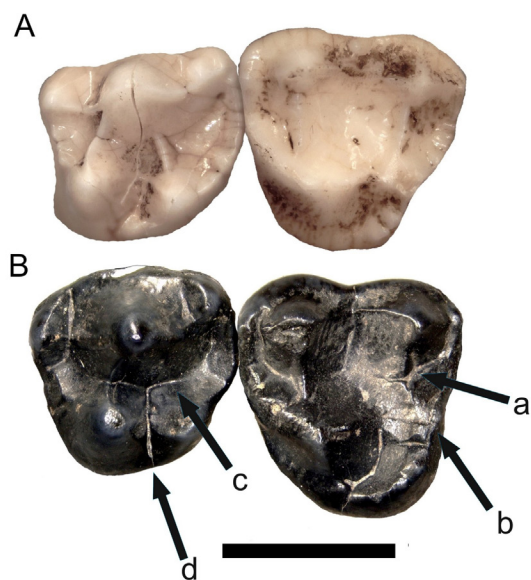


Figure 1. M1 and P4 of (A) USNM 73488 *Procyon lotor* compared to M1 and P4 of (B) UF 243697 *P. gipsoni*. 'a' indicates the groove that truncates the descending crista of the metacone, 'b' indicates the reduced metaconule, 'c' indicates the absence of the crista between the hypocone and paracone, and 'd' indicates the absence of the lingual basin between the protocone and hypocone. Scale = 1 cm.

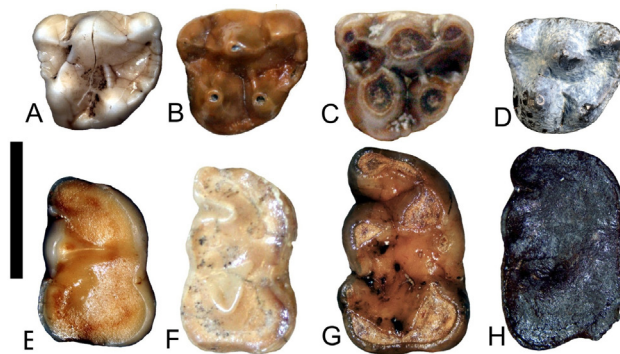


Figure 2. Right P4s and m1s of *Procyon* species included in this research. A, E - modern *P. lotor*; B, F - Blancan *P. lotor* formerly assigned to *P. rexroadensis*; C, G - *P. megalokolos*; D, H - *P. gipsoni*. The m1 of *Procyon gipsoni* (H, UF 243837) has an entoconid that extends considerably more posteriorly than the hypoconid and an inflated paraconulid on the anterior border. Teeth with heavy wear were selected where possible to compare to *P. gipsoni*. A, USNM 73488; B, UM 37131; C, UF 238043; D, UF 312851; E, ETVP 7582; F, UM 29647; G, UF 49251; H, UF 243837 (flipped horizontally) Scale = 1 cm.

Formation in Indian River County about 220 km distant from the Withlacoochee River 1A site. UF 312851 has both diagnostic characteristics of the P4 of *P. gipsoni* found on UF 243697 (Fig. 2D), and the two clearly represent the same species.

A right dentary, UF 243837, is referred to *Procyon gipsoni* because it is from the same locality as the holotype, is the appropriate size to match the holotype, and has dental morphology differing from both *Procyon lotor* and *Procyon megalokolos*. Although the teeth of UF 243837 are extremely worn, the overall shape of the m1 is distinct and the premolars are more robust than those of *P. lotor* and *P. megalokolos*. The m1 of UF 243837 has an entoconid that extends more posteriorly than the hypoconid whereas in *P. lotor* and *P. megalokolos* the hypoconid and entoconid of the m1 are almost equal in length (Fig. 2E–H). The paracoenid is also inflated to make the anterior border of the m1 of UF 243837 less curved posteriorly than that of *P. lotor* and *P. megalokolos* (Fig. 2E–H). The canine is also more sharply recurved than in *P. lotor*. Measurements of the M1s and lower teeth

of *P. gipsoni* and other species of *Procyon* can be found in Tables 1 and 2.

Within the sample of humeri, some of the smaller specimens (those similar in size to the largest *P. lotor* specimens but small compared to specimens of *P. megalokolos*) have less expanded medial epicondyles compared to the specimens confirmed to be *P. megalokolos*. It is possible that these specimens may represent postcrania of *P. gipsoni* but further morphological analysis is needed to accurately separate the two species, and consequently, they are identified as *Procyon* sp. below.

Remarks.—*Procyon gipsoni* has teeth larger than the largest measured specimens of extant *P. lotor* (Table 1). However, as the species is based on only three specimens, and no postcranial specimens are directly associated with these teeth, further description of this species cannot be made until additional material is found. It is beyond the scope of this study to attempt to separate smaller *P. megalokolos* postcrania from *P. gipsoni* postcrania, if both are present in the sample from Florida.

Table 1. Measurements of the M1 of fossil and modern specimens of *Procyon*. For extant samples, values given are mean \pm one standard deviation.

| ID | Species | Length (mm) | Width (mm) |
|----------------|-----------------------------------|------------------|------------------|
| UF 243697 | <i>Procyon gipsoni</i> | 9.85 | 10.59 |
| UF 259055 | <i>Procyon megalokolos</i> | 9.11 | 9.57 |
| UF 263232 | <i>Procyon megalokolos</i> | 9.12 | 9.58 |
| UF 18074 | <i>Procyon megalokolos</i> | 9.32 | 10.20 |
| UF 259056 | <i>Procyon megalokolos</i> | 9.85 | 10.67 |
| UF 223841 | <i>Procyon megalokolos</i> | 9.93 | 10.63 |
| UF 21665 | <i>Procyon megalokolos</i> | 9.97 | 9.81 |
| UF 238043 | <i>Procyon megalokolos</i> | 10.43 | 10.99 |
| UF 271827 | <i>Procyon megalokolos</i> | 11.00 | 11.21 |
| Average (n=30) | extant <i>Procyon lotor</i> | 8.79 \pm 0.44 | 9.15 \pm 0.53 |
| Average (n=4) | extant <i>Procyon cancrivorus</i> | 10.75 \pm 0.27 | 11.47 \pm 0.50 |

Table 2. Measurements of lower cheek teeth of fossil and modern specimens of *Procyon* and *Nasua*. For extant samples, values given are mean \pm one standard deviation.

| ID # | Species | p4 length | p4 width | m1 length | m1 trigonid width | m1 talonid width | m2 length | m2 trigonid width | m2 talonid width |
|----------------|------------------------|-----------------|-----------------|------------------|-------------------|------------------|-------------------|-------------------|------------------|
| UF 243837 | <i>P. gipsoni</i> | 8.37 | 6.17 | 11.15 | 7.22 | 7.31 | 10.59 | 6.86 | 4.48 |
| UF 240248 | <i>N. mastodonta</i> | 7.08 | 4.52 | 8.61 | 5.45 | 5.98 | -- | -- | -- |
| UF 217535 | <i>N. mastodonta</i> | 8.08 | 4.45 | 11.44 | 6.44 | 7.17 | 11.2 | 6.53 | 6.74 |
| UF 49251 | <i>P. megalokolos</i> | 8.68 | 5.63 | 11.83 | 6.72 | 7.37 | -- | -- | -- |
| UM 26997 | <i>P. rexroadensis</i> | 8.46 | 5.24 | 11.95 | 6.35 | 7.37 | 10.73 | 6.50 | 6.02 |
| UM 29646 | <i>P. rexroadensis</i> | 8.19 | 4.73 | 11.90 | 5.30 | 6.23 | 11.49 | 4.79 | 3.95 |
| Average (n=15) | <i>Nasua</i> | 7.58 \pm 0.56 | 4.47 \pm 0.46 | 8.15 \pm 0.63 | 5.33 \pm 0.56 | 5.45 \pm 0.56 | 8.54 \pm 0.93 | 5.12 \pm 0.64 | 7.74 \pm 0.61 |
| Average (n=5) | <i>P. cancrivorus</i> | 9.54 \pm 0.24 | 7.17 \pm 0.35 | 11.59 \pm 1.03 | 7.53 \pm 1.06 | 7.43 \pm 1.19 | 11.14 \pm 0.46 | 6.74 \pm 1.06 | 5.36 \pm 1.02 |
| Average (n=30) | <i>P. lotor</i> | 7.28 \pm 0.57 | 5.20 \pm 0.48 | 10.25 \pm 0.43 | 5.66 \pm 0.57 | 6.45 \pm 0.68 | 10.01 \pm 0.758 | 5.81 \pm 0.74 | 5.45 \pm 0.71 |

***PROCYON MEGALOKOLOS* sp. nov.**

Holotype.—UF 49361, left humerus.

Paratypes.—UF 45338, right distal humerus; UF 18078, left tibia; UF 243557, left radius.

Zoobank Nomenclatural Act.—1D1ED03A-B47F-4EE3-BED0-959286A172DB.

Type locality.—Inglis 1A, Citrus County, Florida (Meachen, 2005; Webb, 2006; DeSantis et al., 2009; Hulbert, 2010).

Etymology.—From the Greek *megalo* (large) plus *kolos* (colossus) referring to the size of the species relative to modern *Procyon*.

Referred Specimens.—Inglis 1A: UF/TRO 3758, calcaneum; UF/TRO 3761–3762, humeri; UF/TRO 3763, ulna; UF/TRO 3764, femur; UF 18073, maxilla, partial with M1–M2; UF 18074, M1; UF 18075, palate, partial with I3; UF 18077, humerus; UF 18078, tibia; UF 18079, calcaneum; UF 18080, astragalus; UF 21665, M1; UF 45333, 45336–45338, humeri; UF 45339, tibia; UF 49251, dentary with p2–m1; UF 49255, dentary with m1; UF 49361–49365, humeri; and UF 217534, maxilla, right partial with M1–M2.

Inglis 1B.—UF 97111, ulna.

Inglis 1D.—UF 271828, humerus.

Inglis 1I.—UF 271827, maxilla with M1–M2.

Inglis 1L.—UF 271826, calcaneum.

Haile 7G.—UF 223841, cranium, partial with right P4–M2 and left P4; 238043, associated maxilla, left with P3–P4, humerus, scapula; 234407, P4; 234411, maxilla, left with M1–M2; 271118, m1; 271122, humerus; 271824, m1; 271825, m2.

Withlacoochee River 1A.—UF 241432, humerus; 241433, humerus; 243466, femur; 243557, radius; 243585, humerus; 243932, ulna; 258912, m1; 259055, M1; 259056, M1; 262754, humerus; 263219, calcaneum; 263232, M1; 263233, p4; 275500, cranium with right I3, P3–M2, left P2.

Ballards Pit 2.—UF 245133, femur.

John Reynolds Site.—UF 10280, m1.

Macasphalt Shell Pit 1.—UF 100302, femur.

Santa Fe River 1B.—UF 11875, dentary.

Walden Pit 2.—UF/TRO 2500, P4.

Diagnosis.—Significantly larger limb ele-

ments than *Procyon lotor* and *P. cancrivorus*. Humerus with a medially enlarged and posteriorly rotated medial epicondyle. Also differs from other species of *Procyon* by having an enlarged tibial tuberosity, an enlarged radioulnar notch, robust p4 with inflated conids, and a posteriorly convergent incisive foramen. Differentiated from *P. gipsoni* in having a crista between the paracone and hypocone of P4, as well as a basin between the protocone and hypocone of P4, and a distinct metaconule on M1.

Description.—This species is primarily differentiated from extant *P. lotor* based on postcrania, which is why a humerus was chosen as the holotype as opposed to one of the crania. The medial epicondyles of the humeri of *P. megalokolos* are noticeably larger than those of extant *P. lotor* and *P. cancrivorus* and are rotated considerably more posteriorly than the strictly medially expanded epicondyles of extant *Procyon* (Fig. 4). Tibiae of the fossil specimens have prominent tibial tuberosities that are weakly developed in modern *Procyon* (Fig. 5), and the radioulnar notch of the radius is considerably more pronounced (Fig. 6). The enlargement of the medial epicondyle, as well as the overall size increase has resulted in the mean of the maximum width of the distal humeri of *P. megalokolos* being significantly larger than the mean of modern *P. lotor* ($p < 0.001$; *P. lotor*/*P. megalokolos*, $n=40/19$, mean = 22.76/27.55 mm, $s=1.57/1.98$ mm). There are no distinct dental apomorphies for *Procyon megalokolos* and the dental morphology strongly resembles that of modern *P. lotor*. The fossil material is clearly distinct from *P. cancrivorus* due to the absence of the characteristic inflation of the cusps present in *P. cancrivorus*. The p4s have reduced anterior and shallow posterior basins, inflated metaconids and hypoconids that meet centrally, large protoconids that make the lingual edge convex, and posteriorly angled protoconid tips (Fig. 7). The m1 has an anteroposteriorly expanded trigonid, a pronounced paraconulid, and wide valleys between the metaconid and the entoconid. The m2 has an anteroposteriorly reduced trigonid basin, a slightly inflated protoconid, a groove in the trigonid basin, and a posteriorly expanded hypoconulid.



Figure 3. *Procyon megalokolos* fossils showing the notable size difference between the fossil taxon and the largest *Procyon lotor* specimens available in the ETVF collections. Note the large size of the juvenile specimens B and C compared to the fully fused adult *P. lotor* (A). Also note that 'C' still has a distal epiphyseal suture visible, indicating that it is quite young (Fig. 4). 'E' is not the largest possible humerus as it is smaller than the humerus that would have articulated with the ulna (G). (A) ETVF 7000, right humerus; (B) UF 49363, right humerus; (C) UF/TRO 3761, left humerus, image flipped; (D) UF 49361, left humerus, image flipped; (E) UF 45338, right humerus; (F) ETVF 7000, right ulna; (G) UF/TRO 3763, right ulna; (H) ETVF 7000, right femur; (I) UF 245133, right femur; (J) ETVF 7000, right tibia; (K) UF 18078, left tibia; (L) UF 45339, right tibia. Scale = 5 cm.

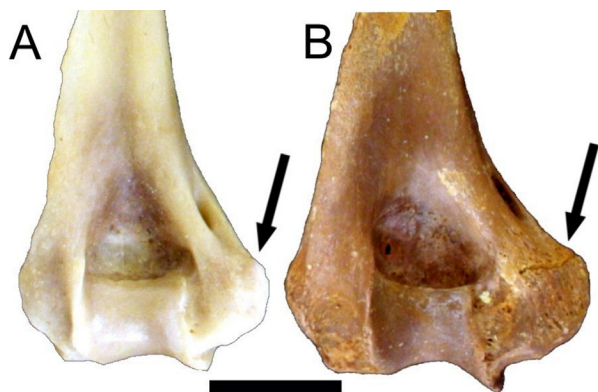


Figure 4. Distal humeri of (A) USNM 144069 *Procyon lotor* compared to (B) UF/TRO 3761 *Procyon megalokolos* showing the inflated medial epicondyle (black arrows) in the fossil species. Also notice the unfused distal epiphyseal suture of B (also indicated by the black arrow), indicating that this specimen is a young juvenile, despite already being considerably larger than A. Scale = 1 cm.

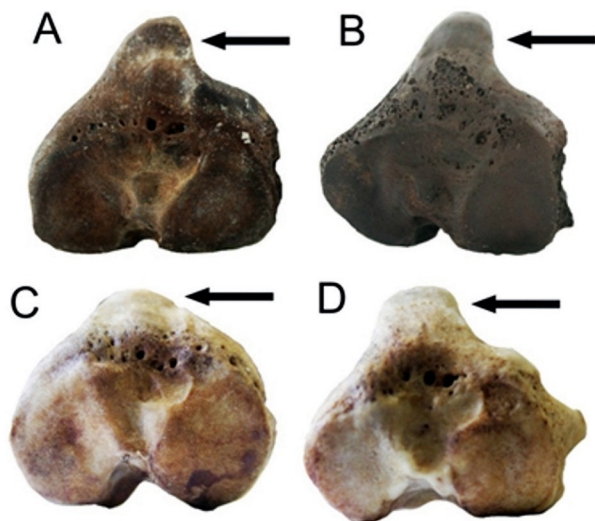


Figure 5. Tibiae of *Procyon megalokolos* compared to extant *Procyon lotor* and *Nasua*. (A) UF 18078 *P. megalokolos*, (B) UF 312851 *P. megalokolos*, (C) USNM 245645 *P. lotor*, and (D) AMNH 214725 *Nasua nasua*. Not to scale.

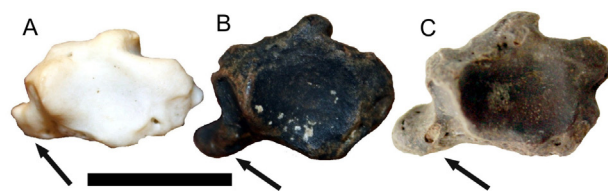


Figure 6. Distal left radii of (A) modern *Procyon lotor* and (B and C) *Procyon megalokolos* with arrows showing the exaggerated medial expansion of *P. megalokolos* that results in a deeper radioulnar notch. (A) ETVP 7000 *P. lotor*, (B) UF 243557 *P. megalokolos*, and (C) *P. megalokolos* specimen in private collection (lent by Andreas Kerner for photography). Scale = 1 cm.

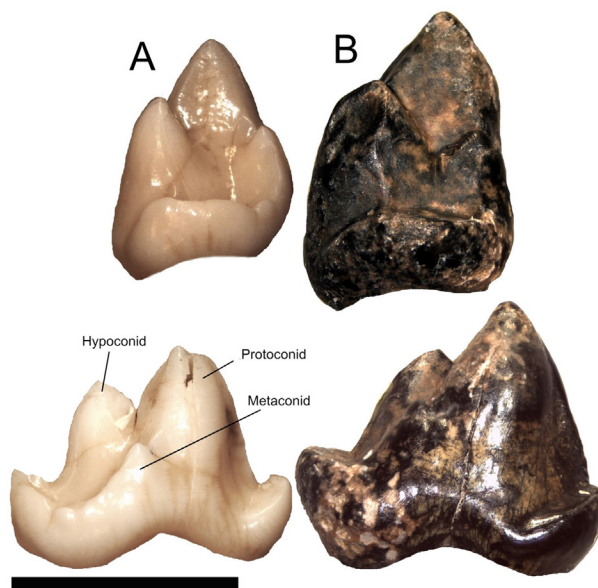


Figure 7. Posterior and labial views of left p4s of (A) ETVP 1511 modern *Procyon lotor* and (B) UF 263233 *Procyon megalokolos*. Note inflation of the protoconid and inflation and appression of the hypoconid and metaconid in *P. megalokolos* (B). Scale = 5 mm.

The M1s of *P. megalokolos* are between extant *P. lotor* and *P. cancrivorus* in size (Table 1).

A nearly complete cranium, UF 275500, (Fig. 8) from Withlacoochee River 1A is assigned to *P. megalokolos* because of its large size and lack of the dental apomorphies of *P. gipsoni*. The cranium is distinct from *P. lotor* in that it has a remarkably broad postorbital constriction (Fig. 8A), a reduced tympanic bulla (Fig. 8B), a reduced mastoid process (Fig. 8C), and a larger infraorbital foramen. Additionally, *P. megalokolos* has a posteriorly convergent incisive foramen (Fig. 8D), giving it a “heart” shape when viewed ventrally, whereas *P. lotor* has either a parallel or divergent incisive foramen ($n = 90$). Though the specimen appears broken, the edges of the foramen are well preserved except for the small posterior fragment. The cranium is from a young adult individual and is 126.7 mm long, which is longer than the average cranial length of adult modern *P. lotor* (115.0 mm, $n=30$), but as this is the only specimen for which cranial length can be measured, no attempt at statistical significance is made here. While the skull does have characteristic features, it is the postcrania that distinctly separate the species.

Remarks.—Webb and Wilkins (1984) and Berta (1995) both stated that the Inglis *Procyon* was likely a new species, and this research confirms their suggestions. *Procyon megalokolos* is morphologically similar to, although distinct from, *P. lotor*, and is more similar in size to *P. cancrivorus*. Dental differences can be found in the lower dentition, although the upper dentition is less useful due to high levels of variation in the genus. Morphological differences in the humerus, tibia, and radius suggest that locomotion and/or behavior of *P. megalokolos* differed from that of *P. lotor* and *P. cancrivorus*. For example, the enlarged radioulnar joint suggests decreased pronation and supination of the wrist. The expansion of the medial epicondyle suggests that *P. megalokolos* may have exhibited some scratch-digging or shredding behaviors like *Nasua*, which frequently digs holes and pries apart logs to feed on invertebrates (McClern, 1992). Enlarged tibial tuberosities are often found in terrestrial carnivorans (Heinrich and Rose, 1997), including the more terrestrial *Nasua*, which suggests that *P.*

megalokolos was more terrestrial than *P. lotor*. Tibiae of *P. megalokolos* look very similar to those of *Nasua*, but the latter fuses the proximal tibia and fibula during adulthood, and no evidence of this is present in any of the fossil tibiae.

While *P. megalokolos* is on average significantly larger than *P. lotor*, based on the width of the distal humerus, there are some specimens that are within the size range of *P. lotor*. It is reasonable that this may be due to sexual dimorphism because modern *P. lotor* males are known to be distinctly larger than females (Ritke, 1990). If this is the case, then small female *P. megalokolos* can be expected to overlap with large male *P. lotor* while male *P. megalokolos* are larger than any other *Procyon*. Unfortunately, the available fossil postcranial elements do not differentiate sex in the modern *Procyon*, therefore no identification of sex in *P. megalokolos* is currently possible.

Extant *P. lotor* masses average 6.76 kg for males and 5.94 kg for females (Nagel, 1943). Based on UF 45338 (distal humerus) and UF 18078 (tibia), using Tarquini et al. (2017), *P. megalokolos* may have reached 11.7 kg.

***PROCYON* sp.**

Inglis 1A.—UF/TRO 3756, dentary with p2–p3; UF 45334, humerus; 45335, humerus; 49360, humerus; 49365, humerus; 234406, dp4; 234408, upper canine; 234409, upper canine; 4925, dentary, edentulous; 49253–49254, dentary with p2–p3; 21305, associated p2–p4.

Haile 7G.—UF 238045, vertebra, caudal; 254875, metatarsal.

Inglis 1F.—UF 193387, humerus; 193388, vertebra, lumbar.

Withlacoochee River 1A.—UF 243843, premaxilla, right with I1; 263220, premolar, lower; 263234, femur.

Remarks.—This group of Blancan specimens can be confidently referred to the genus *Procyon*, but cannot be positively referred to a particular species. For some, this is due to heavy wear on the teeth or absence of teeth with diagnostic features. The postcrania may represent *P. gipsoni* or smaller females of *P. megalokolos*.

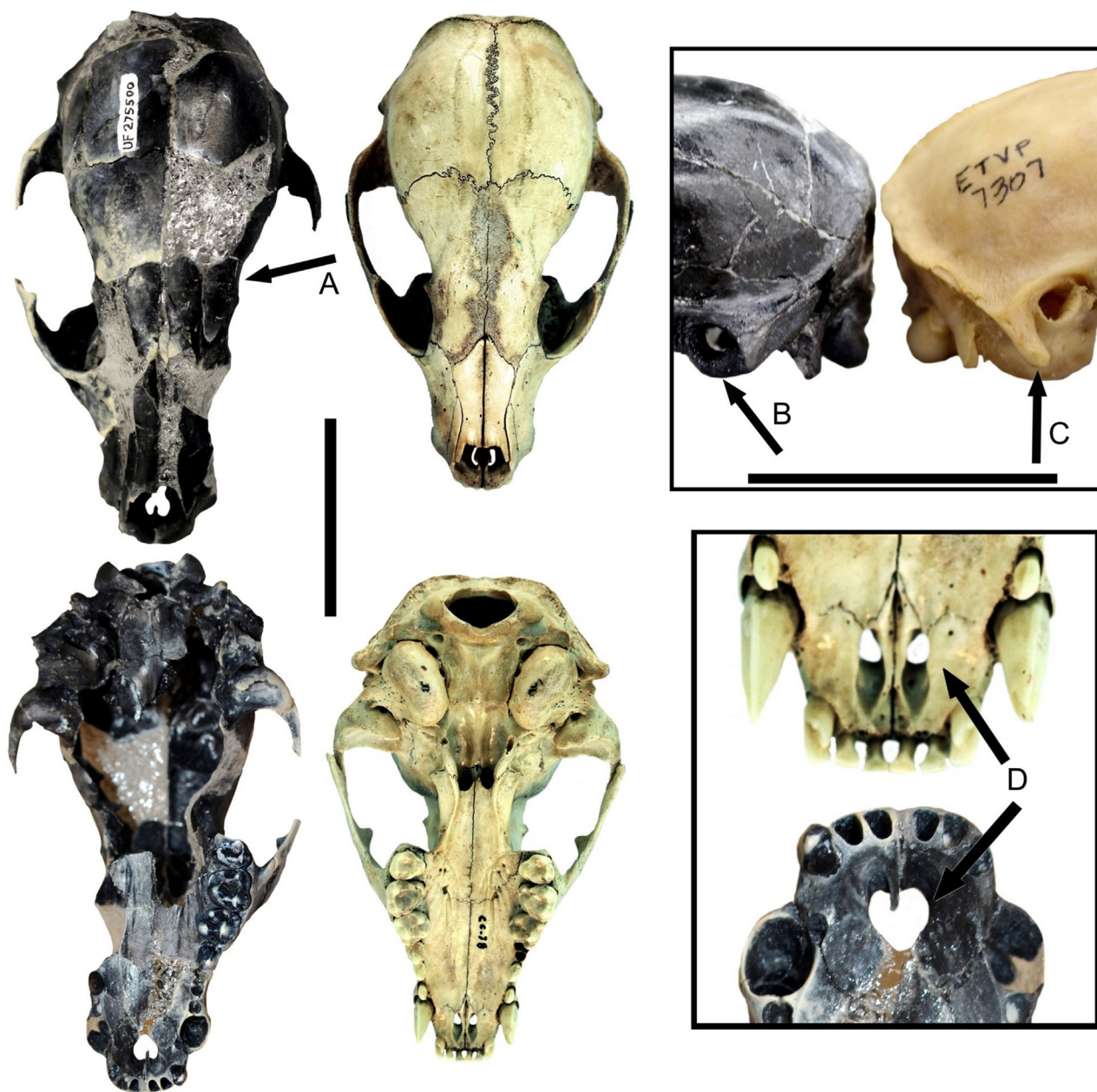


Figure 8. UF 275500 *Procyon megalokolos* partial cranium compared to ETVP 78 and ETVP 7307, modern *P. lotor*. UF 275500 has been reconstructed with Butvar 76. Arrow ‘A’ indicates the postorbital constriction, which is considerably broad for even a young individual such as this one; ‘B’ indicates the reduced tympanic bulla; ‘C’ indicates the mastoid process that is reduced in *P. megalokolos*. ‘D’ indicates the incisive foramen, which is posteriorly divergent but nearly parallel in ETVP 78 and convergent in UF 275500, giving it a “heart” shape (premaxillae pictured here are not to scale). Scale = 5 cm.

Genus *NASUA* Storr, 1780
***NASUA MASTODONTA* sp. nov.**

Holotype.—UF 240248, right dentary with p4 and m1.

Paratype.—UF 240249, right humerus.

Zoobank Nomenclatural Act.—28A55F69-A661-4C8D-A698-6CDA0C30D2D1.

Type locality.—Santa Fe River 8C, Columbia County, Florida (see Hulbert, 2010 for locality data).

Etymology.—From the Greek *masto* (breast), plus *dont* (tooth), in reference to the protuberance on the labial side of the m1.

Referred Specimens.—Haile 7G: UF 238044 associated pelvis, lumbar vertebra and sacrum. Waccasassa River 9A: UF 217535, right dentary with heavily worn p2–m2.

Diagnosis.—A *Nasua* (Fig. 9) with a noticeable and characteristic protuberance between the protoconid and the hypoconid on the labial border of m1 (Fig. 10). On the p4, the hypoconid is separated from the protoconid by a shallow valley whereas in *N. nasua* and *N. narica* the p4 has a distinct, deep valley with a small crista and a depression on the labial side of the tooth (Fig. 11). The p4 can be distinguished from the early Blancan *Nasua pronarica* (Dalquest, 1978) by a reduced hypoconid separated from the protoconid by a shallow, broader valley, a posteriorly enlarged heel that forms a basin, and the presence of a small, lingual, anterior basin.

Description.—The m1 has an anteroposteriorly compressed trigonid, close appression of the metaconid and paraconid, and an inflated protoconid that is shifted lingually. The p4 has a smaller, deeper talonid basin and a larger trigonid depression relative to extant *Nasua*.

A right humerus, UF 240249, was also found at Santa Fe River 8C (Fig. 12) but was not associated with the dentary. This humerus is identified as *Nasua* based on the distinctly expanded

and ventrally angled medial epicondyle, and the pronounced lateral supracondylar ridge, but it is slightly different morphologically from extant *Nasua* species. The most apparent difference is the relatively reduced medial epicondyle compared to the typically expanded medial epicondyles of extant *Nasua*. As with the medial epicondyle, the trochlea and capitulum are more compressed in *N. mastodonta*. In some modern specimens, the lateral supracondylar ridge is noticeably larger than that of *N. mastodonta*, but this character is variable. There is considerably more rotation of the humeral diaphysis in extant *Nasua* than in the fossil specimen.

UF 238044, from Haile 7G, has the sacrum, the last lumbar vertebra, and a pelvic fragment that are more like *Nasua* than *Procyon* (Fig. 13). Morphological characteristics of *Nasua sacra* found in this specimen include elongated neural spines, a more rounded neural canal, a sharper angle of descent of the lumbar spines, and more broadly separated prezygopophyses. Elongated neural spines provide an anchor for tendons and muscles that help hold the tail erect while foraging (Gompper, 1995). Unfortunately, the distinct lateral elongation of the inferior lateral angle, which is the most distinguishing trait of *Nasua sacra*, is broken on both sides of this specimen, although it appears that the broken edges would have continued laterally.

Remarks.—The holotype, UF 240248, is similar in size to extant female *Nasua* and, in fact,



Figure 9. UF 240248 *Nasua mastodonta* holotype dentary with p4 and m1, and alveoli for c1, p1–p3, and m2 in labial view. Scale = 1 cm.

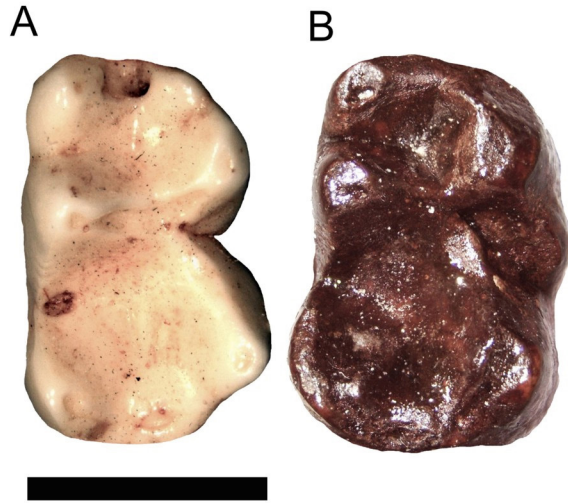


Figure 10. mls of (A) AMNH 2147238 *Nasua narica* and (B) UF 240248 *Nasua mastodonta* in occlusal view. Note the labial protuberance, appression of the paraconid and metaconid, the lingual expansion of the entoconid, and the inflation and lingual rotation of the protoconid. Scale = 5 mm.

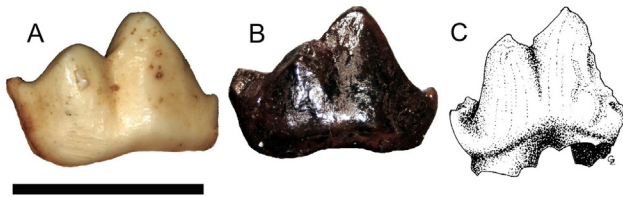


Figure 11. Labial views of the p4 of three *Nasua* species. (A) AMNH 93669 *Nasua narica*, (B) UF 240248 *Nasua mastodonta*, and (C) MSU 8657 *Nasua pronarica* holotype (from Dalquest, 1978). Scale = 5 mm.

is likely to be from a female because of the gracile horizontal ramus and small canine alveolus. Though this cannot be confirmed without finding a complete skeleton with a baculum to accurately identify a male, it is more parsimonious to suggest that the fossil species was sexually dimorphic to a similar degree as the extant species of *Nasua*, than to suggest that it was not dimorphic at all. The second dentary, UF 217535, probably represents a male specimen of *Nasua* because it is considerably

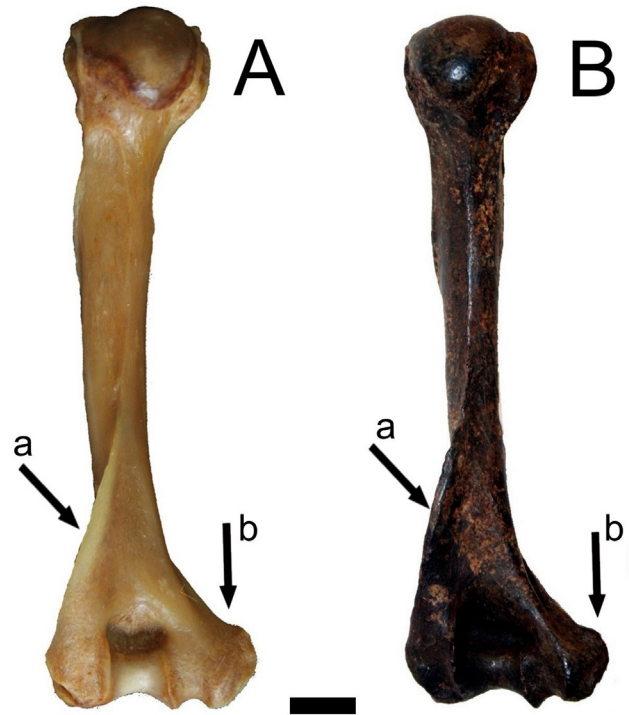


Figure 12. Posterior view of humeri of (A) AMNH 214716 *Nasua narica* and (B) UF 240249 *Nasua mastodonta*. *Nasua mastodonta* has a reduced lateral supracondylar ridge (a), a reduced medial epicondyle (b), and a less rotated diaphysis. Scale = 1 cm.

more robust and, although the teeth are worn, it has a double-rooted p1, which is morphologically characteristic of *Nasua*. *Nasua mastodonta* seems to be less specialized with its reduced medial epicondyle and lateral supracondylar ridge than modern *Nasua*. It was likely scansorial, although seemingly less fossorial than modern *Nasua*.

This species is the first confidently known example of *Nasua* in eastern North America during the Blancan. Specimen UF 18920 (currently identi-

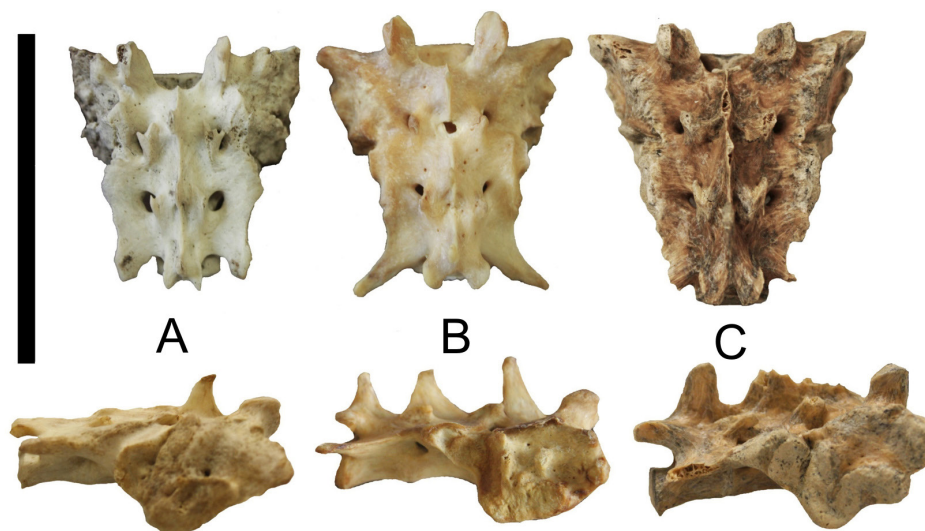


Figure 13. Sacra of (A) ETVP 7000 *Procyon lotor*, (B) AMNH 93668 *Nasua narica*, and (C) UF 238044 *Nasua mastodonta*. Note the elongated posterior neural spines in lateral view and the elongation of the inferior lateral angle in dorsal view. Scale = 1 cm.

fied in the literature by Baskin [1982] as ?*Nasua*) is known from the late Hemphillian of Florida and may belong to *N. mastodonta* rather than *N. pro-narica* as Baskin (1982) suggested. Further investigation will be needed to confidently identify the specimen because it lacks a p1 alveolus and had an infection of the m1 alveolus, but, as stated by Baskin (1982), the shapes of the angular and articular processes are more reminiscent of *Nasua* than *Procyon*. In addition, UF 90957 from the Hemphillian Bone Valley Formation of Florida was originally cataloged as cf. *Nasua* sp., but examination of the specimen reveals it to be more likely *Procyon* than *Nasua* because of the single rooted p1 and the *Procyon*-like shape of the ramus.

The estimated body mass of *Nasua mastodonta*, UF 240249, is 4.6 kg, which is well within the 2–8 kg range of extant *N. narica* (Gompper, 1995).

DISCUSSION

This study reveals that there were at least three procyonid species in Florida during the Blancan. This diversity is not unexpected or unusual, given that modern *Procyon* and *Nasua* are sympatric in many areas. *Procyon lotor* is found throughout the entire

range of *N. nasua*, *P. cancrivorus* lives in the same areas as *N. narica* over much of its range, and *P. lotor*, *P. cancrivorus* and *N. narica* are sympatric in some parts of Panama and Costa Rica. *Nasua nasua* and *N. narica* are not sympatric. This agrees with our findings that there are two sympatric fossil species of *Procyon* in the Blancan of Florida, but only a single species of *Nasua*.

Prior to this study, *Procyon rexroadensis* was the only named species in the genus during the Blancan, therefore much fossil material from that time was assigned to this species. Upon further research on the dentition, *P. rexroadensis* was found not to be morphologically distinct enough to warrant the existence of a separate species and we consider *P. rexroadensis* to be a synonym of *P. lotor*. This constitutes a considerable temporal range extension for *P. lotor*, which previously was only known from the Pleistocene to today.

Nasua was previously known on a provisional basis from Florida during the Hemphillian, and many related taxa, such as *Arctonasua* and *Paranasua*, have been identified from the Miocene of the state (Baskin, 1982). Therefore, the presence of *Nasua* is not unexpected. However, this material does represent the most complete fossil sample of

Nasua material known from North America.

Recently, the earliest known South American *Nasua* (as well as *Procyon*) material was discovered in Venezuela at the Plio-Pleistocene asphalt seep El Breal De Orocuál (Ruiz-Ramoni et al., 2018). Given that this earliest occurrence of *Nasua* and *Procyon* in South America is approximately concurrent with the fossils reported here and that earlier records of both *Nasua* and *Procyon* are known from North America, a North American origin for these two procyonids, followed by dispersal to South America, is currently more strongly supported by the fossil record.

Modern *Nasua* is less generalized, more fossorial (McClern, 1992), and feeds less preferentially on aquatic arthropods than *Procyon* (Kaufmann, 1962), so competition between the genera is low enough to allow them to be sympatric. Similarly, *N. mastodonta* likely filled an ecological role separate from *P. gipsoni* and *P. megalokolos*, however, details of their diets will necessitate microwear analysis to define how these sympatric taxa may have avoided dietary competition. *Nasua mastodonta* was similar in size to modern *Nasua* and its calculated mass is well within the range of variation.

Procyon megalokolos was significantly larger than extant *P. lotor*, was likely more terrestrial and less adept at manual manipulation than extant *P. lotor*, and reached a mass close to 12 kg. *Procyon gipsoni* was likely slightly larger than extant *P. lotor*, based on tooth size (Table 1), though no mass estimates or suggestions as to behavior/locomotion were possible due to the lack of known postcranial elements. The fossil sample from Florida provides a numerous and remarkably representative sample of procyonids from the Blancan as it includes fossils of many skeletal elements, as well as multiple age classes. Further research opportunities include dietary analyses, comparison of Blancan and Irvingtonian *Procyon*, and identification and interpretation of *P. gipsoni* postcrania.

ACKNOWLEDGMENTS

This research is a portion of the first author's Master's thesis (Gilmore, 2013) and we are apprecia-

tive of the help provided by the committee (Steven Wallace, Blaine Schubert and Jim Mead) while the thesis was in progress. We are particularly grateful to Steven Wallace for bringing these fossils to our attention and for his help during the early phases of this research, and to Richard Hulbert at UF for access to fossils, assistance in collections, and sharing his knowledge of Florida excavations. Important specimens were donated to the UF collection by Aaron Gipson, Steve Hutchens, Andreas Kerner, and John Waldrop. We are also grateful for the many UF staff members, students and volunteers who have helped in the excavations of the fossils used in this research. Access to museum collections was provided by Eileen Westwig (AMNH), Suzanne Pourach (USNM) and Philip Gingerich (UM). We thank Jon Baskin and an anonymous reviewer for their comments and suggestions on a previous version of this manuscript. This project was partially funded by a 2012 East Tennessee State University Graduate Student Research Grant.

LITERATURE CITED

- Albright, L. 1999. Magnetostratigraphy and biochronology of the San Timoteo Badlands, southern California, with implications for local Pliocene-Pleistocene tectonic and depositional patterns. *Geological Society of America Bulletin* 111(9):1265–1293.
- Anderson, E. 1984. Review of the small carnivores of North America during the last 3.5 million years. *Special Publications of the Carnegie Museum of Natural History* 8:257–266.
- Baskin, J. A. 1982. Tertiary Procyoninae (Mammalia: Carnivora) of North America. *Journal of Vertebrate Paleontology* 2(1):71–93.
- Baskin, J. A. 1998. Procyonidae. Pp. 144–151 in C. M. Janis, K. M. Scott, and L. L. Jacobs, eds, *Evolution of Tertiary Mammals of North America Volume 1: Terrestrial Carnivores, Ungulates and Ungulatelike Mammals*. Cambridge University Press, Cambridge.
- Berta, A. 1995. Fossil carnivores from the Leisey Shell Pits, Hillsborough County, Florida. Pp. 463–499 in R. C. Hulbert Jr., G. S. Morgan, and S. D. Webb, eds. *Paleontology and Geology*

- of the Leisey Shell Pits, Early Pleistocene of Florida. *Bulletin of the Florida Museum of Natural History* 37.
- Bjork, P. R. 1973. Additional carnivores from the Rexroad Formation (upper Pliocene) of southwestern Kansas. *Transactions of the Kansas Academy of Science* 76(1):24–38.
- Cassiliano, M. L. 1999. Biostratigraphy of Blancan and Irvingtonian mammals in the Fish Creek-Vallecito Creek section, southern California, and a review of the Blancan-Irvingtonian boundary. *Journal of Vertebrate Paleontology* 19(1):169–186.
- Dalquest, W. W. 1978. Early Blancan mammals of the Beck Ranch local fauna of Texas. *Journal of Mammalogy* 59(2):269–298.
- DeSantis, L. R. G., R. S. Feranec and B. J. MacFadden. 2009. Effects of global warming on ancient mammalian communities and their environments. *PLoS ONE* 4(6): e5750. <https://doi.org/10.1371/journal.pone.0005750>
- Gilmore, L. S. 2013. Analysis of the Blancan Procyonids of Florida. Unpublished Master's Thesis. East Tennessee State University, Johnson City, 128 p.
- Gompper, M. E. 1995. *Nasua narica*. *Mammalian Species* 487:1–10.
- Heinrich R. E., and Rose K. D. 1997. Postcranial morphology and locomotor behavior of two Early Eocene miacoid carnivorans, *Vulpavus* and *Didymictis*. *Paleontology* 40:279–305.
- Hibbard, C. W. 1941. New mammals from the Rexroad Fauna, upper Pliocene of Kansas. *American Midland Naturalist* 26(2):337–368.
- Hulbert Jr., R. C. 2010. A new early Pleistocene tapir (Mammalia: Perissodactyla) from Florida, with a review of Blancan tapirs from the state. *Bulletin of the Florida Museum of Natural History* 49(3):67–126.
- Johnston, C. S., and D. E. Savage. 1955. A survey of various late Cenozoic vertebrate faunas of the Panhandle of Texas. Part I. Introduction, description of localities, preliminary faunal lists. University of California Publications in Geological Science 31(2):27–50.
- Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. University of California Publications in Zoology 60:95–222.
- Kurtén, B., and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia University Press, New York City, 442 p.
- McClern, D. 1992. Locomotion, posture and feeding behavior of kinkajous, coatis, and raccoons. *Journal of Mammalogy* 73(2):245–261.
- Meachen, J. 2005. A new species of *Hemiauchenia* (Artiodactyla, Camelidae) from the Late Blancan of Florida. *Bulletin of the Florida Museum of Natural History* 45(4):435–447.
- Morgan, G. S., and R. C. Hulbert Jr. 1995. Overview of the geology and vertebrate paleontology of the Leisey Shell Pit Local Fauna, Hillsborough County, Florida. Pp. 1–92 in R. C. Hulbert Jr., G. S. Morgan, and S. D. Webb, eds. *Paleontology and Geology of the Leisey Shell Pits, Early Pleistocene of Florida*. *Bulletin of the Florida Museum of Natural History* 37.
- Nagel, W. O. 1943. How big is a 'coon? *Missouri Conservationist* 4(7):6–7.
- Oelrich, T. M. 1953. Additional mammals from the Rexroad Fauna. *Journal of Mammalogy* 34(3):373–378.
- Ritke, M. E. 1990. Sexual dimorphism in the raccoon (*Procyon lotor*): morphological evidence for intrasexual selection. *American Midland Naturalist* 124(2):342–351.
- Rodriguez, S. G., C. C. Morgan, L. Soibelzon, and E. R. Lynch. 2017. Intra- and interspecific variation in tooth morphology of *Procyon cancrivorus* and *P. lotor* (Carnivora, Procyonidae), and its bearing on the taxonomy of fossil South American procyonids. *Hystrix, the Italian Journal of Mammalogy* 27(2). doi: 10.4404/hystrix-27.2-11647.
- Romer, A. S. 1966. *Vertebrate Paleontology*, 3rd ed. University of Chicago Press, Chicago, 468 p.
- Ruiz-Ramoni, D., A. Rincón, and M. Montellano-Ballesteros. 2018. Evidencias del origen de *Nasua* y *Procyon* (Procyonidae: Carnivora) en América del Sur. *Revista Brasileira de*

- Paleontologia 21(1):87–94.
- Storr, G. C. C. 1780. *Prodromus Methodi Mammalium*. Reissian, Tübingen, 43 p.
- Tarquini, J., N. Toledo, L. H. Soibelzon, and C. C. Morgan. 2017. Body mass estimation for *Cyonasua* (Procyonidae, Carnivora) and related taxa based on postcranial skeleton. *Historical Biology* (2017):1–11.
- Webb, S. D., and K. T. Wilkins. 1984. Historical biogeography of Florida Pleistocene mammals. Pp. 370–383 in H. H. Genoways, and M. R. Dawson, eds. *Contribution in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday*. Carnegie Museum of Natural History Special Publications 8.
- Webb, S. D. 2006. The Great American Biotic Interchange: patterns and processes. *Annals of the Missouri Botanical Garden* 93(2): 245–257.
- Webb, S. D., R. C. Hulbert Jr., G. S. Morgan, and H. F. Evans. 2008. Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the Central Florida phosphate district. Pp. 293–312 in X. Wang, and L. G. Barnes, eds. *Geology and Vertebrate Paleontology of Western and Southern North America: Contributions in Honor of David P. Whistler*. Natural History Museum of Los Angeles County Science Series 41.
- White Jr., R. S., and G. S. Morgan. 2005. Arizona Blancan vertebrate faunas in regional perspective. Pp. 117–138 in R. D. McCord, ed. *Vertebrate Paleontology of Arizona*. Mesa Southwest Museum Bulletin 11.
- Zeveloff, S. I. 2002. *Raccoons: A Natural History*. Smithsonian Institution Press, Washington, DC, 240 p.