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A new species of *Hydrochoerus* (Rodentia: Caviidae: Hydrochoerinae) from the Pleistocene of San Diego County, California, USA with remarks on capybara biogeography and dispersal in the Pleistocene of Western North America

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Abstract: We describe a new species of capybara from late Pleistocene deposits (Rancholabrean NALMA) in northern San Diego County, California, USA which tentatively dates to Marine Isotope Stage (MIS) 5 interglacial (~130 ka to 80 ka). The specimen represents a new species of *Hydrochoerus* based on morphological characters of the upper incisor (I1) and the upper (maxillary) third molar (M3). *Hydrochoerus hesperotiganites* sp. nov. differs from other described species of *Hydrochoerus* in its larger size, wider skull roof, more robust zygomatic process of the maxilla and descending zygomatic process of the lacrimal and in details of the otic region. The new species is the only confirmed record of fossil *Hydrochoerus* in North America and is the northwestern-most record of any capybara in North America. All previous records of fossil capybara from North America represent one of two extinct genera, *Neochoerus* or *Phugatherium*. Northward dispersal of capybaras from central and southern México probably occurred along the coasts of Sinaloa and Sonora, entering the north or northeast flowing drainages which entered the Gulf of California, then further north into the San Simon drainage to the Gila River and ultimately into the Colorado River, or directly northward along the coast of Sonora to the mouth of the Colorado River.

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INTRODUCTION

Three genera of capybaras (Caviidae: Hydrochoerinae: *Phugatherium, Neochoerus* and *Hydrochoerus*, the latter being today's largest living rodent) dispersed into North America after the establishment of the Panama Land Bridge about 5 Ma (Morgan 2008; Woodburne 2010; O'Dea et al. 2016). *Phugutherium* was present in central México by the Pliocene (early Blancan NALMA) at 3.6 Ma (Vucetich et al. 2015). *Neochoerus* is found in southern México in the Rancholabrean NALMA (Carbot-Chanona et al. 2020) and in Central México in the early Blancan at 3.5 Ma. These are the oldest verified record of any capybara in North America (Carranza-Castañeda and Miller 1988). *Neochoerus* has also been recorded from northern México in the Irvingtonian NALMA, as well as from the United States in the middle Blancan of South Carolina (Sanders 2002; Albright et al. 2019) and in the late Blancan through Rancholabrean in Florida and the Rancholabrean in Texas (Morgan and White 1995; Morgan 2005; Baskin et al. 2020). *Hydrochoerus* has been thought to have been present from the late Pliocene (late Blancan) to the latest Pleistocene (Rancholabrean) in the United States, but not in the Recent (Ahearn 1981; Morgan 2005). The fact that the earliest records of *Neochoerus* in North American are in the north rather than the south would seem to suggest that its origin was in the north; but the relative lack of fossil producing

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localities of appropriate age in southern México and Central America has likely produced a skewed record. The taxonomy and affinities of the two lineages (P*hugatherium and Neochoerus* + *Hydrochoerus*) were the subject of much research in the last decade (Vucetich et al. 2013; Vucetich et al. 2015; Carranza-Castañeda 2016; Albright et al. 2019; Baskin et al. 2020; Carbot-Chanona et al. 2020). Fossils of capybaras from North America previously allocated to the extant genus *Hydrochoerus* have subsequently been referred to *Neochoerus*, leaving *Neochoerus* and *Phugatherium* as the only capybaras known in the North American fossil record (Ahearn 1981; Mones 1991).

Capybaras reached as far north and east as Florida and South Carolina, and as far north and west as Texas, Arizona, and Sonora, México (Ahearn 1981; Sanders 2002; Baskin et al. 2020; Mead et al. 2006). The Colorado River seems to have been a barrier beyond which capybaras and glyptodonts (Cingulata: Glyptodontinae) did not extend in the Pliocene or Pleistocene (Morgan 2008). The western-most occurrence of *Glyptotherium texanum* the Blancan and Irvingtonian species, is in Arizona, while the western-most occurrences of *G. floridanum*, or any Rancholabrean species, are in central Texas (Kurtén and Anderson 1980) and in Sonora, Mexico (Mead et al. 2007. One capybara specimen has been collected from extreme northwestern Sonora, México. However, that specimen, found in the early Irvingtonian locality of El Golfo, in deltaic deposits of the ancestral Colorado River (Lindsay 1984; Croxen et al. 2007; Carranza-Castañeda 2016) may have floated down from drainages to the north and east.

Here we present the discovery of a nearly complete although badly crushed skull of a capybara collected in 1994 from upper Pleistocene lacustrine deposits in the San Luis Rey River Valley in San Diego County, California, USA. This specimen (SDSNH 50000) provides an opportunity to re-examine the evolution, historical biogeography, and dispersal of capybaras in North America.

Previous work: For the purposes of the present study, we adopt the taxonomic classification of capybaras proposed by Vucetich et al. (2013, 2014, 2015) and followed in the three most recent papers on North American (NA) capybaras (Albright et al. 2019; Baskin et al. 2020; Carbot-Chanona et al. 2020). Two lineages with a total of three genera are recognized by Vucetich et al. (2015): (1) *Phugatherium*, with *P. dichroplax* as the only NA species; and (2) a lineage consisting of *Neochoerus*, with the NA species *N. aesopi*; and a Central and South American sister taxon, *Hydrochoerus*, including the extant *H. hydrochaeris* and *H. isthmius*.

The diminutive capybara *H. isthmius* was described by Goldman (1912) from six specimens collected in eastern Panama. Cabrera (1961) considered *H. isthmius* as only subspecifically distinct from *H. hydrochaeris* and this taxonomy was followed by subsequent authors. Mones (1991), however, noted that the two species were clearly separable based on cranial measurements of 17 specimens of *H. isthmius*. Aeschbach et al. (2016) made a detailed analysis of ontogenetic changes in cranial size and morphology of both species based on 44 specimens of *H. isthmius* and 171 of *H. hydrochaeris*, demonstrating that the two are morphologically distinct. We follow recent authors (Ahearn 1981; Mones 1991; Baskin et al. 2020) in considering the fossil taxon *H. holmesi* to be properly allocated to *Neochoerus*.

One additional fossil species of *Hydrochoerus* (*H. gaylordi*) has been described by MacPhee et al. (2000) from Pliocene deposits on the island of Grenada at the southern end of the Lesser Antilles, about 160 km (100 miles) off the coast of Venezuela. We do not consider this species further here, as it is based on a partial right maxilla with M1-3 and diagnosed by a single character of the M2. We observe that the M2 of neonate extant *Hydrochoerus* have the two prisms on M2 united buccally as in *H. gaylordi*; by the age of 4 weeks the two laminae are separate as in the adults (Mones 1991: fig. 7A, B). Thus, it is possible that the condition seen in the type and only specimen of *H. gaylordi* may be an individual neotenic variant. Should further specimens be found to have the same condition and given the insular occurrence (Grenada) of *H. gaylordi*, it would stand as a valid species.

MATERIALS AND METHODS

Catalogued specimens of extant *Hydrochoerus hydrochaeris* are in the comparative collections of The Mammoth Site, Hot Springs, South Dakota. Age classes are as defined by Ojasti (1973, 2011) and Gorosabel et al. (2017). Restrictions in access to museum collections due to COVID-19 prevented us from examining a larger sample of *Hydrochoerus* skulls. This was especially unfortunate in that skulls of the northern-most species of extant capybara, *H. isthmius*, were not available to us.

Abbreviations: ka, kilo annum; Ma, mega-annum; MSCC, Mammoth Site Comparative Collection, The Mammoth Site at Hot Springs, SD; NALMA, North American Land Mammal Age; SDSNH, San Diego Society of Natural History, San Diego, California. Descriptive terminology for the capybara skull and dentition (upper M2 and M3) discussed is presented in Figures 1 and 2. L, left; R, right.

GEOLOGICAL AND CHRONOLOGICAL CONTEXT

Geological context: The new fossil specimen described here was collected from SDSNH Locality 3775 by Bradford O. Riney on March 5, 1994, during paleonto-

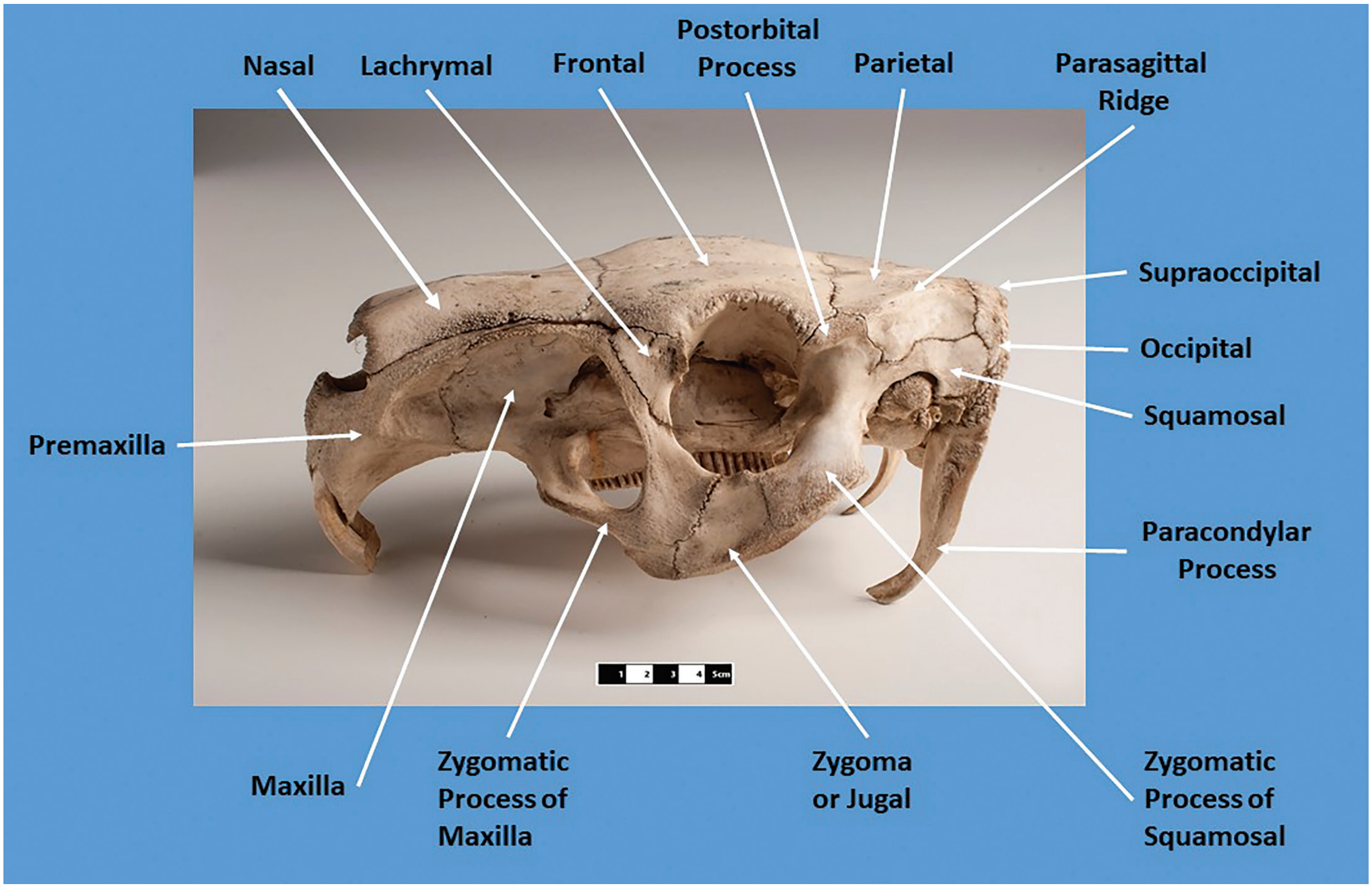

Figure 1. Cranial terminology utilized in this paper. Museum of Veterinary Anatomy FMVZ USP / Wagner Souza e Silva (https://commons.wikimedia.org/wiki/File:Capybara_skull._Hydrochoerus_hydrochaeris_02.jpg), adding labels and arrows by Richard S. White, https: // creativecommons .org / licenses / by-sa / 4.0 / legalcode

logical mitigation monitoring of mass grading operations at the Town Center North shopping center in Oceanside, San Diego County, California, USA (Fig.3). The site is located on the south side of the San Luis Rey River Valley, a generally east-west trending coastal valley that preserves late Pleistocene invertebrate and vertebrate fossils from elevated and dissected river terrace deposits at a series of discovery sites along its length (Guthrie 2010; Deméré et al. 2013). At the Town Center North shopping center site, the Pleistocene stratigraphic sequence consisted of two distinct fluvial-lacustrine sequences (Fig. 4). The capybara fossil (SDSNH 50000) was collected from the lower (older) sequence, which consisted of up to 7.3 m (24 feet) of interbedded gray-green mudstones, laminated carbonaceous siltstones, and white to orange, friable medium- to coarse-grained graded sandstones with dispersed calcrete nodules. The skull was found palate up and collected from one of the gray-green mudstone beds, which also produced associated maxilla, mandibular, and dental fragmentary remains of an extinct pronghorn (cf. *Stockoceros* sp.) (Tab. 1). This lower lacustrine sequence was deposited along an irregular erosional surface cut into fluvial sandstones of the middle to upper Eocene Santiago Formation. In turn, an irregular erosional surface marks the upper contact between the older Pleistocene sedimentary sequence and an overlying younger Pleistocene sequence. This younger sequence consisted of up to 15.2 m of fluvial and lacustrine sediments beginning with a basal transgressive cross-bedded light gray sandstone gradationally overlain by 5.4 m of lacustrine green laminated mudstones and siltstones. The lacustrine deposits were overlain by 8.5 m of gray laminated and cross-laminated, fine-grained sandstones.

The basal cross-bedded sandstone produced a diverse aquatic assemblage of freshwater snails, clams, bony fishes, amphibians, and pond turtle, as well as a diverse terrestrial vertebrate assemblage of lizards, snakes, birds, and mammals (Tab. 1). Guthrie (2010) reported on the avifauna from this basal sandstone, which consists of over 19 species including grebes, pelican, ducks, rails, sandpiper, quail, roadrunner, and passerines. The dominance of the avifauna by waterfowl is consistent with the sedimentology and aquatic molluscan, fish, and turtle fossils also recovered from this stratum. The terrestrial mammal assemblage from the basal sandstone includes isolated skeletal elements of mole, rabbit, rodents,

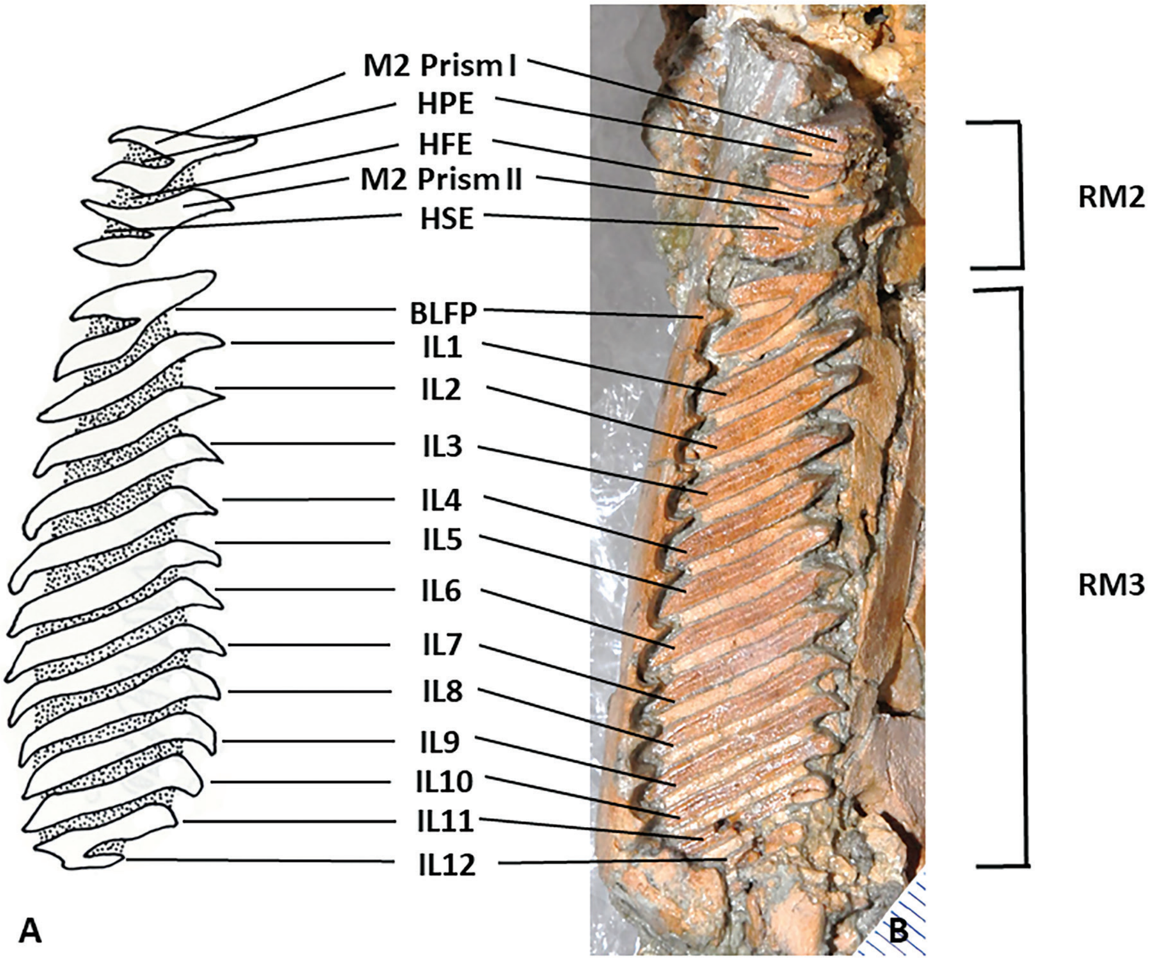

Figure 2. Dental terminology utilized in this paper. A, *Hydrochoerus hydrochaeris* after Mones (1991) : R M2 and M3 of SDSNH 50000. Abbreviations: RM2, second right upper molar; RM3, third right upper molar; HFE, Hendadura Fundamental Externa (Fundamental External Flexus); HPE, Hendadura Primeria Externa (Primary External Flexus); HSE, Hendadura Secundaria Externa (Secondary External Flexus); BLFP, BiLobed First Prism; IL1-12, Independent Prism 1-12.

fox, tapir, horse, mastodon, and ground sloths (Tab. 1). The overlying lacustrine laminated mudstones produced a much less diverse fossil assemblage that consisted of freshwater snails and clams, bony fishes, and horse, as well as leaf compressions of vascular plants including oak (*Quercus* sp.) and sycamore (*Platanus* sp.) (Tab. 1).

Depositional environment: The sedimentology and stratigraphy (Fig. 4) of the Town Center North Pleistocene sequence suggests deposition in a freshwater pond or oxbow lake on the southern margin of the ancestral San Luis Rey River Valley. The older lacustrine sequence preserving the capybara skull, although only exposed in a small area, appears to have been deposited on a relatively high relief unconformity eroded into older Eocene strata. This erosion surface likely formed as the ancestral San Luis Rey River was beginning to aggrade and deposit fine-grained sediments on its floodplain during a eustatic rise in sea level (i.e., an interglacial). The interbedded sequence of mudstones, laminated carbonaceous siltstones, and medium- to coarse-grained graded sandstones likely represent seasonal changes in sediment input to this fluvial-lacustrine setting.

The erosion surface that cuts the older Pleistocene lacustrine sequence is here interpreted to have formed as the river meandered back to the south during a later time of the same interglacial period. The basal cross-bedded sandstone resting on this unconformity likely represents a coarse-grained “beach” facies that was deposited as the floodplain was aggrading and another ox-bow lake was forming. The mixture of terrestrial and aquatic taxa in this basal transgressive unit and the occurrence of isolated and non-articulated skeletal elements suggests a possible scenario whereby bloated, floating mammalian carcasses were successively being “beached,” shedding bones, and refloated. The gradational contact between the sandstone “beach” facies and the laminated mudstone-siltstone “lake” facies suggests continuous interglacial floodplain aggradation.

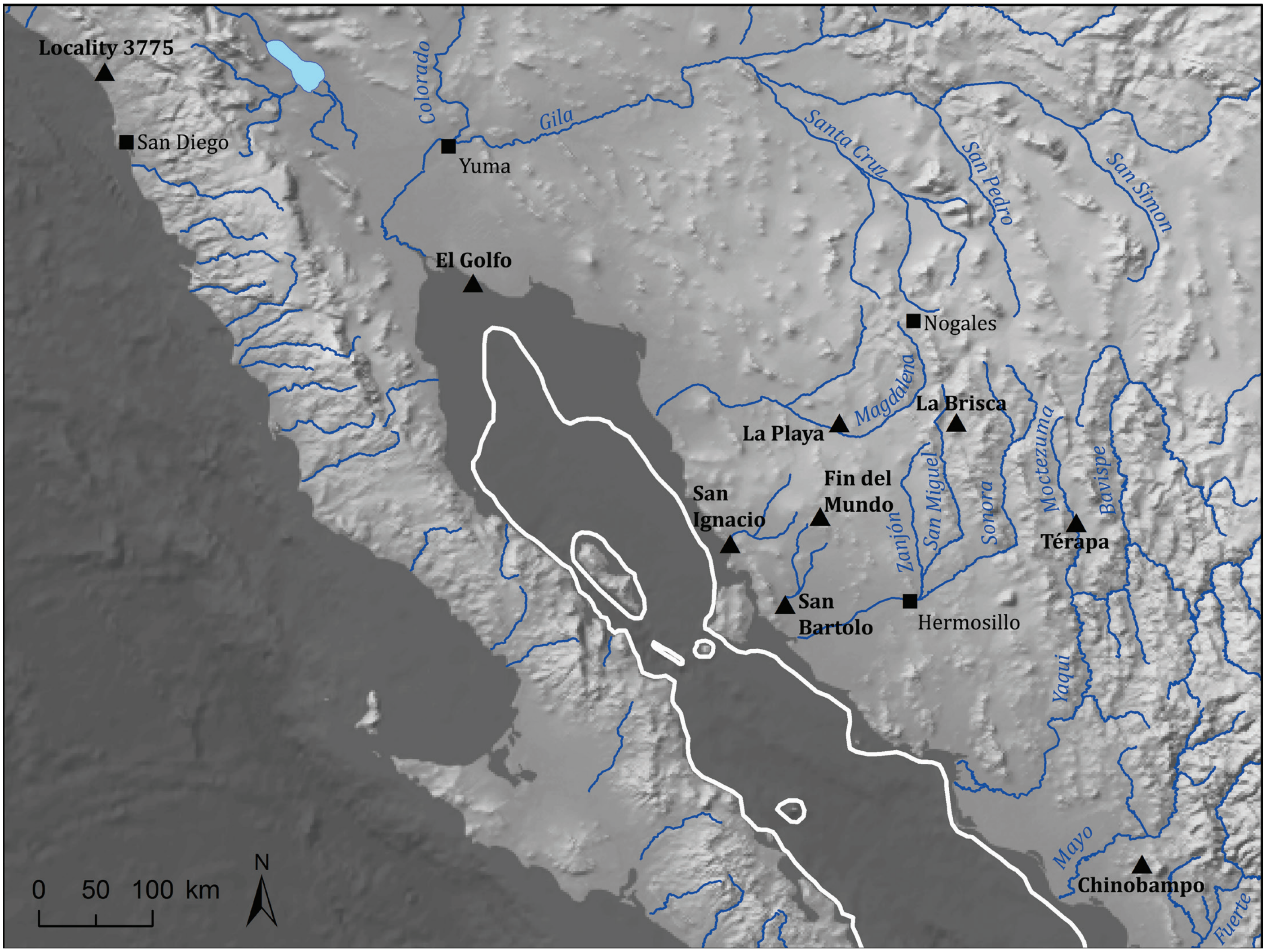

Figure 3. Map of northwestern México and southwestern United States, showing key cities for landmarks (solid square) and key paleontological sites mentioned in the text (solid triangles). Major river valleys indicated and labeled. Glacial maximum shoreline indicated by white line, based on bathymetry. The US/Mexico border is approximated by the location of San Diego, Yuma and Nogales. Map courtesy of Matthew C. Pailes, Department of Anthropology, University of Oklahoma.

Chronology: Unfortunately, none of the recovered fossils provide clear biochronological control concerning the age of the enclosing strata. Although no remains of *Bison* (an "index" fossil for the Rancholabrean NALMA) were recovered from these strata, there are a number of extinct mammalian taxa that typically occur in Rancholabrean age faunas of southern California (e.g., *Mammut americanum*, *Megalonyx jeffersonii*), or only in the Rancholabrean (*Nothrotheriops shastensis*). Further, fossils of *Bison latifrons* have been recovered from potentially correlative strata located in the San Luis Rey River Valley, approximately 18 km upstream from the Town Center North fossil localities (Deméré et al. 2013). Considering the fauna and strata together suggests that deposition of the Town Center North Pleistocene stratigraphic sequence occurred during an interglacial interval and most likely during the early Rancholabrean MIS 5 interglacial (~130 ka to 80 ka).

SYSTEMATIC PALEONTOLOGY

RODENTIA Bowdich, 1821
CAVIOIDEA Gray, 1821
CAVIIDAE Fisher, 1817
HYDROCHOERINAE Gray 1825
Hydrochoerus Brisson, 1762
Hydrochoerus hesperotiganites sp. nov.
Figures 2, 5, 6, 7
3D Animated Rendering

Holotype: SDSNH 50000, a nearly complete skull lacking mandible.

Type locality and horizon: SDSNH Locality 3775, San Diego County, California, USA. The fauna and stratigraphy together suggest that deposition occurred during an interglacial interval and most likely during the early Rancholabrean MIS 5 interglacial (~130 ka to 80 ka).

Table 1. Faunal lists for the three depositional units producing fossils

Lower Lacustrine Unit	Upper Lacustrine Unit (basal sandstone)	Upper Lacustrine Unit (mudstone/siltstone)
	Mollusca	Mollusca
	Gastropoda	Gastropoda
	Physa sp.	*Physa* sp.
	Fossaria sp.	
	Gyraulus sp.	
	Pelecypoda	Pelecypoda
	Anodonta sp.	*Anodonta* sp.
Vertebrata	Vertebrata	Vertebrata
	Osteichthyes	Osteichthyes
	Mugil sp. cf. *M. cephalus*	*Mugil* sp. cf. *M. cephalus*
	Gila sp.	*Gasterosteus* sp.
	Gasterosteus sp.	Gobiidae
	Amphibia	
	Bufo sp.	
	Chelonia	
	Actinemys marmorata	
	Squamata	
	Thamnophis sp.	
	Colubridae	
	Aves	
	Aechmophorus occidentalis	
	Podilymbus podiceps	
	Podiceps parvus	
	Pelecanus erythrorhynchus	
	Aythya affinis	
	Bucephala albeola fossilis	
	Oxyura jamaicensis	
	Rallus limicola	
	Fulica americana	
	Phalaropus lobatus	
	Callipepla californica	
	Geococyx californicus	
	Aphelocoma californica	
	Vireo sp.	
	T*oxostoma redivivum*	
	Agelaius phoeniceus	
	Meospiza sp. cf. *M. melodi*	
Mammalia	Mammalia	Mammalia
Hydrochoerus hesperotiganites	Talpidae	*Equus* sp.
cf. *Stockoceros* sp.	*Sylvilagus* sp. cf. *S. auduboni*	
	Thomomys sp.	
	Peromyscys sp.	
	Microtus sp. cf. *M. californicus*	
	Urocyon cinereoargenteus	Plantae
	Tapirus sp.	Tracheophyta
	Equus sp.	*Quercus* sp.
	Mammut americanum	*Platanus* sp.
	Megalonyx jeffersonii	
	Nothrotheriops shastensis	

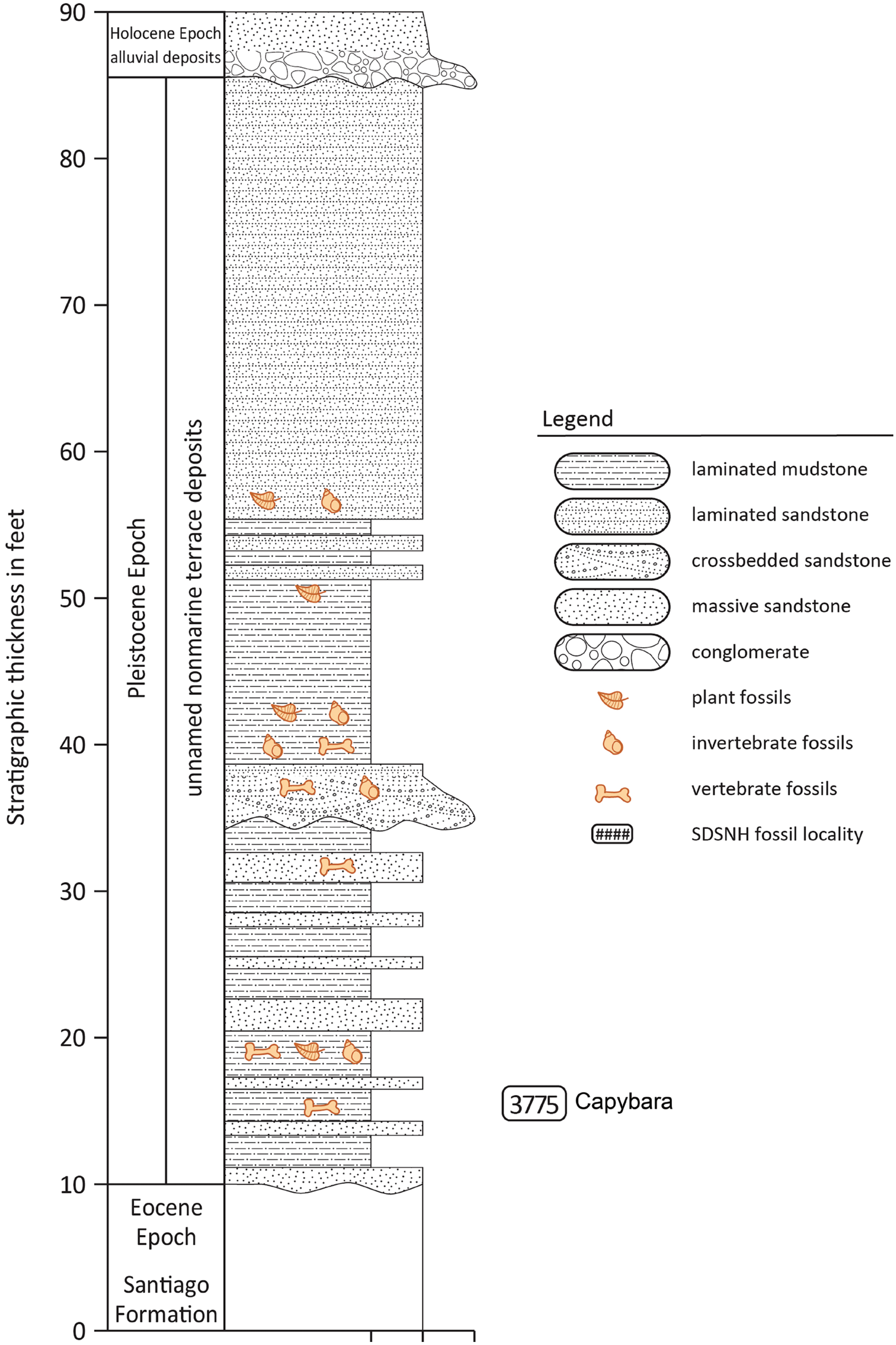

Figure 4. Stratigraphic section for SDSNH locality 3775 Oceanside, San Diego County, California, USA.

Etymology: The specific epithet is from the Greek 'hesperos', meaning western, and the Greek 'tiganites', meaning pancake, in reference to its geographic location as the northwestern-most occurrence of a capybara in North America, as well as the crushed condition of the holotype.

Diagnosis: A hydrochoerine caviid rodent referred to *Hydrochoerus* because it has an anteriorly grooved upper incisor (I1) with faint striations within and lateral to the groove and an M3 with a Bi-Lobed First Prism (BLFP) followed by 12 independent prisms. It differs from other described species of *Hydrochoerus* in its larger size, wider skull roof, more robust zygomatic process of the maxilla, and more robust descending zygomatic process of the lacrimal. In the otic region, the anteromedial part of the petrosal reaches and overlaps the alisphenoid; in the extant species *H. hydrochaeris* the anterolateral process of the petrosal does not reach the alisphenoid because the rostral process of the malleus separates the two.

DESCRIPTION

Skull

SDSNH 50000 is a nearly complete, although badly crushed skull (Figs. 2, 5, 6, 7; link to 3D scan). To better reference the position of the structures described, as well as the direction and extent of distortion during crushing, we established the dorsal midline of the skull (Fig. 5A) as a line passing through the midline of the nasal bones and the midline of the occipital bone. Ventrally we established the midline as a line passing between the nasals, and the midline of the basisphenoid and basioccipital (Fig. 5C). Neither line is entirely straight, nor are the two lines congruent, due to the differential distortion of the ventral versus the dorsal aspect of the skull.

Dorsal view: In dorsal view (Fig. 5A, B), the skull seems relatively undeformed; the long axis of the specimen as preserved approximates the sagittal axis of the skull. The nasal, frontal, parietal, and occipital bones are present although fragmented. The condition of the naso-frontal and fronto-parietal sutures suggests that they were unfused; the parietal-occipital suture is clearly unfused. The left and right nasal bones are present, although only the right preserves the anterior margin. The maximum length of the right nasal is 87.8 mm. The maximum width of the left nasal is 30.0 mm and the right nasal, 30.7 mm. The left premaxilla is represented by two unattached fragments preserving portions of the incisor alveolus. The upper incisor can be accurately placed in anatomical position between these fragments, allowing visualization of the form of the left premaxilla. The dorsal premaxilla fragment preserves the ventrolateral margin of the external nares and a portion of the sharply defined nasal process of the premaxilla. The ventral premaxilla fragment preserves the medial surface of the intrapremaxillary suture, the anterolateral margin of the incisive foramen, and the ventrolateral external surface. Portions of the right maxilla are visible in dorsal view but badly fragmented. However, enough is preserved to allow the infraorbital canal to be visualized. As viewed anteriorly, the canal opening has the form of an acute triangle about 34.9 mm wide at the base. The preserved height of the canal is 46.3 mm, but this represents only the dorsomedial height of the canal as measured on the lacrimal and not the maximum height as measured on the maxilla.

The frontals are badly fragmented; the right frontal more so than the left. Neither the fronto-nasal nor the fronto-parietal sutures are clearly visible; we interpret them as unfused, given the unfused condition of other cranial sutures. However, this cannot be determined definitively given the damaged nature of the specimen. The fronto-squamosal sutures are also unfused, as evidenced by the mortised sutural surface on the ascending processes of the squamosals that are elevated above the diagenetically depressed frontals. The dorsal surface of the frontals is planar and marked along the position of the completely fused interfrontal suture by several minute foramina. A slight sagittal ridge occurs behind the posterior-most foramen and extends 32.8 mm to the broken posterior margin. A portion of the right lacrimal is present, where it remains in articulation with the ascending process of the maxilla.

The dorsal surface of the fused parietals is also relatively planar and does not appear to slope ventrally towards its contact with the occipital, although this is difficult to judge given the crushed condition of the skull. There is no indication that an inter-parietal was present. Anteriorly, the lateral edges of the dorsal parietal table are bounded by sharply defined, medially convex parasagittal ridges, that mark the juncture of the lateral and horizontal surfaces of the parietal. These features have been referred to as the sagittal crest by Simpson (1930), although they are not a true sagittal crest, as they never unite at the midline. This same feature has also been termed the temporal line in suid crania (e.g., Doley et al. 2018). Hulbert et al. (2009) described a similar feature in *Tapirus polkensis* (Tapiridae), terming them parasagittal ridges; we follow this terminology. The parasagittal ridge extends from the occipito-parietal suture towards the fronto-parietal suture at the postorbital projection of the frontal. The posterior portion of each parasagittal ridge is sharply marked and produced into a ridge not more than 1 mm in height above the dorsal table. As the ridge extends further anteriorly toward the postorbital projection, it becomes lower and broader until it nearly disappears. The parasagittal ridges never unite to form a true sagittal crest; their closest approximation to each other is located 10.1 mm anterior to the occipito-parietal suture. The posterior width of the dorsal surface of the parietal table at its narrowest is 23.5 mm. The parasagittal ridges are continu-

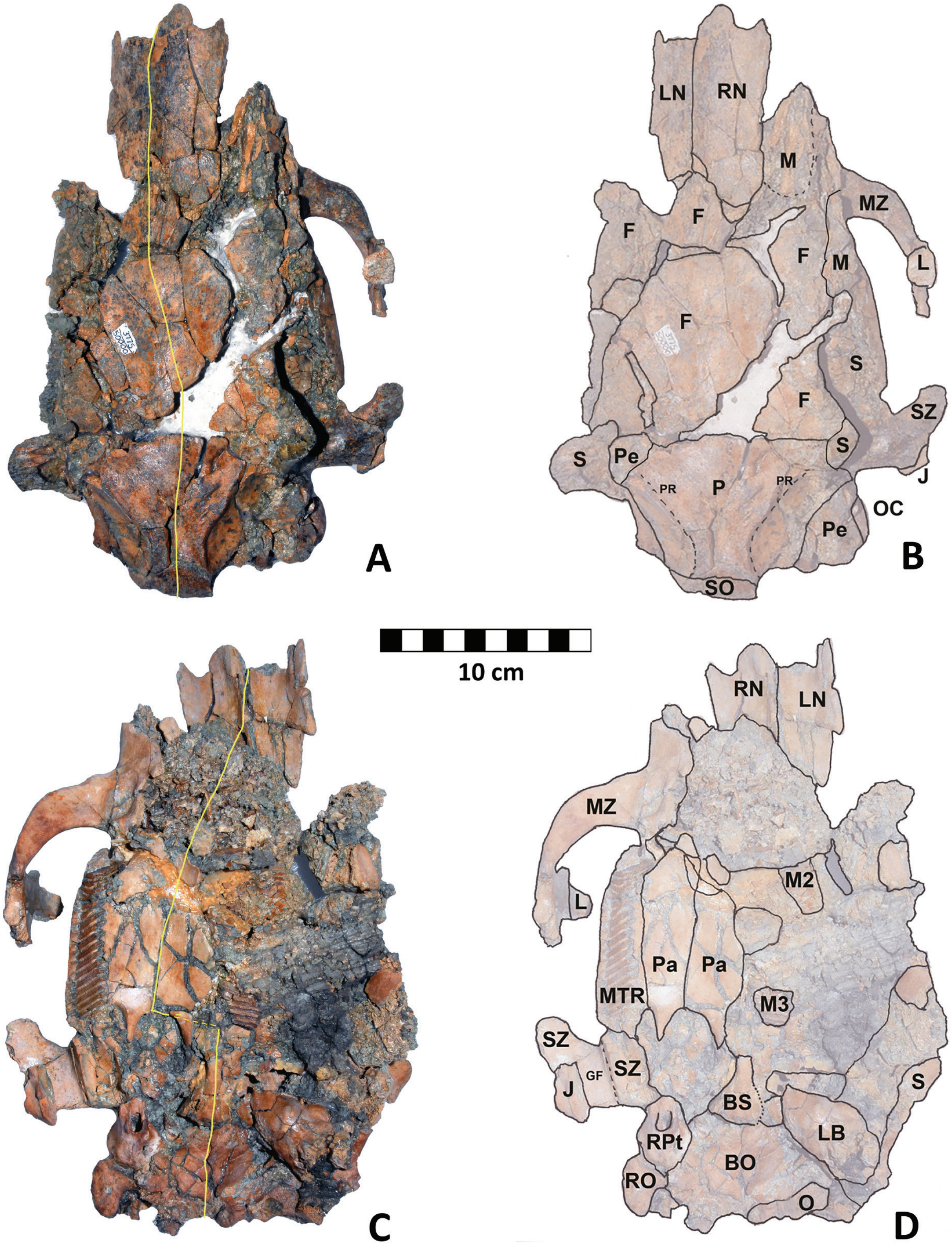

Figure 5. SDSNH 50000. A, B: dorsal view; C, D: ventral view. In B and D, the boundaries of the bones are approximations, as the crushed condition of the skull prevented determining actual suture lines in many cases. Abbreviations: BO, basioccipital; BS, basisphenoid; F, frontal; GF, glenoid fossa; J, jugal; L, lachrymal; LB, left auditory bulla; LN, left nasal; M, maxilla; MTR, maxillary tooth row; MZ, zygomatic process of maxilla; M2, fragment of second upper molar; M3, fragment of third upper molar; O, occipital; OC, occipital condyle; P, parietal; Pa, palatine; Pe, petrosal; PR, parasagittal ridge; RN, right nasal; RO, right occipital condyle; RPt, right petrosal; S, squamosal; SO, supraoccipital; SZ, zygomatic process of squamosal. Unlabeled areas are either fragments of bone which could not be allocated to a specific element, areas of crushed and comminuted bone, matrix, or are gaps between bones where fragments have separated or are missing.

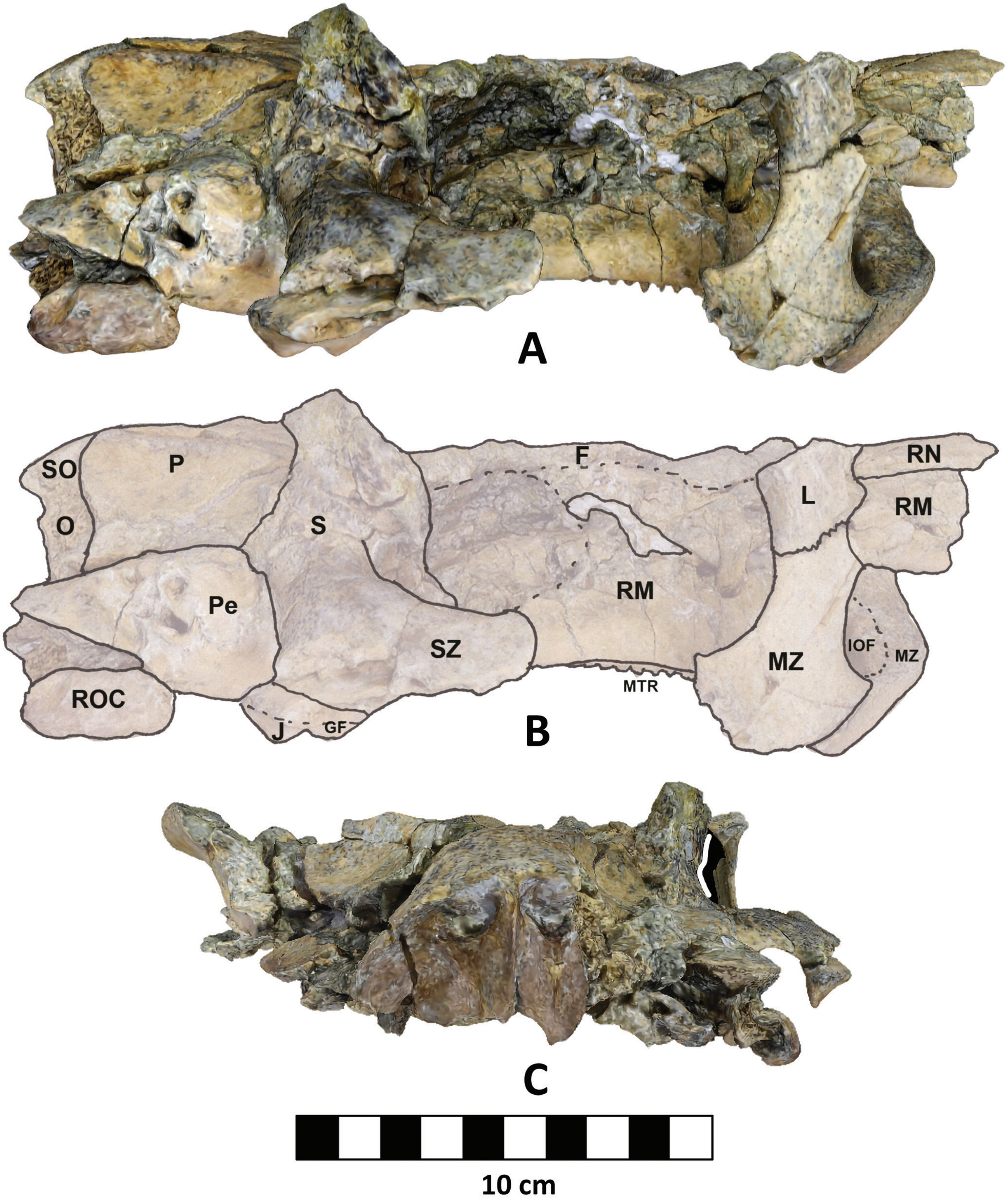

Figure 6. SDSNH 50000. A & B, lateral view; C, posterior view. In B, the boundaries of the bones are approximations, as the crushed condition of the skull prevented determining actual suture lines in many cases. Abbreviations: F, frontal; GF, glenoid fossa; J, jugal; L, lachrymal; MTR, maxillary tooth row; MZ, zygomatic process of maxilla; O, occipital; P, parietal; Pe, petrosal; RM, right maxilla; RN, right nasal; ROC, right occipital condyle; RPt, right petrosal; S, squamosal; SO, supraoccipital; SZ, zygomatic process of squamosal. Unlabeled areas are either fragments of bone which could not be allocated to a specific element, areas of crushed and comminuted bone, and matrix, or are gaps between bones where fragments have separated or are missing.

ous with the temporal crests marking the lateral edges of the posterior facing portion of the supraoccipital and occipital. The temporal crests appear to be continuous with the posterior edge of the paracondylar process as far as can be seen on the portion of the process preserved on the right side.

There is no indication of a supraoccipital-occipital suture; we interpret the suture to be completely ossified in contrast with the suture between the supraoccipital and the parietal which appears to be unfused. In posterior view, the dorsal margin of the occipital forms the nuchal crest, which is broadly rounded and evenly curved laterally and ventrally. Immediately below the nuchal crest, there is a small deep depression on either side of the vertical median crest of the supraoccipital. A second pair of shallower but larger depressions is present on the supraoccipital immediately above and lateral to the midline of the foramen magnum. The occipital is preserved, although the elongated paracondylar processes have been separated from the skull and cannot be reattached because of missing pieces. The right paracondylar process is more complete than the left and is relatively robust. We interpret the supraoccipital—paraoccipital suture as unfused. The dorsal margin of the foramen magnum is preserved, having a small, inverted V-shaped notch at its apex.

Lateral view: In lateral view (Fig. 6 A, B), the skull shows the crushed condition, with the right squamosal pushed up above the parietal table, and overriding parts of both the frontal and parietal. The zygomatic arch comprises the laterally and posteriorly directed zygomatic process of the maxilla, the jugal, and the laterally and anteriorly directed zygomatic process of the squamosal. The lateral zygomatic processes of both squamosals are preserved, while only the zygomatic process of the right maxilla is present. The zygomatic process of the left maxilla is missing, as is the left jugal (Fig. 6A). The anterior body of the right jugal remains attached to the posteriorly directed zygomatic process of the maxilla (not visible in Fig. 6 A, B). A small fragment of the posterior portion of the right jugal is preserved where it overlaps the anterior part of the zygomatic process of the squamosal, forming the mandibular fossa.

Ventral view: The ventral aspect of the skull (Fig. 5C, D) is more deformed than the dorsal, with the left side more distorted, fragmented, and more widely disarticulated than the right. The somewhat fractured palate is preserved with the individual fragments separated from each other by narrow bands of matrix. The entire palate, along with both tooth rows, is shifted to the right of the midline as defined by the basioccipital and basisphenoid, but is nearly complete. The right M2 and M3 are well preserved. The LM3 is represented by the posterior-most 4 prisms. Fragments of what is likely the LM1 and/or LM2 are present anterior to the remnants of the LM3 (Fig. 5C, D). The posterior portion of the palate has a rounded U-shaped posterior margin demarcating the nasal choanae.The pterygoid processes are relatively long and narrow. The suture between the palatal bone and the palatal portion of the maxillary bones is not visible. The area of the ventral exposure of the premaxillae and maxillae is largely missing and filled with matrix; the palatine fissure is not visible.

The basisphenoid is well preserved, as is the anterior half of the basioccipital. We are unable to determine whether the suture between the two bones is present and open, or if the bones were fused in life but are now broken. It is likely that, given the size of this individual, the suture was fused, as the basicranial sutures in modern capybara are all fused by 4 years of age, while many of the cranial sutures persist throughout the life of the individual (Ojasti 1973, 2011; Gorosabel et al. 2017). The paracondylar process is present on the right side but largely missing on the left, where only a small fragment of the dorsal-most part of the process remains.

The mandibular fossa for the articulation of the lower jaw is preserved on the right side. As in all hydrochoerines, the squamosal and the jugal participate in the formation of this fossa. The fossa is roofed dorsally by the zygomatic process

Figure 7. *Hydrochoerus hesperotiganites* SDSNH 50000 Right otic region of skull. Anterior toward top.

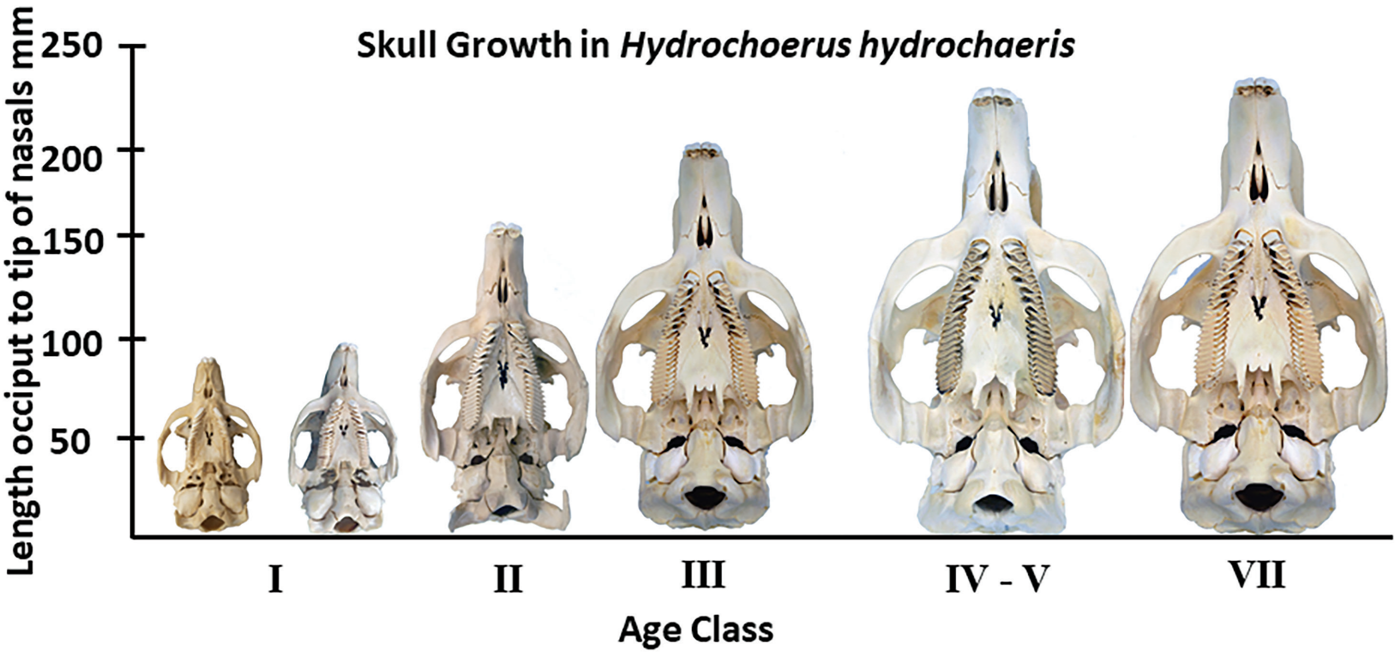

Figure 8. Skull growth in *Hydrochoerus hydrochaeris*. Specimens are, from left to right: MSCC 456, MSCC 457, MSCC 463, MSCC 461, MSCC 462, MSCC 460.

of the squamosal, which has a ridge produced ventrally forming the medial wall of the mandibular fossa. The posterior end of the jugal has a ridge produced ventrally which forms the lateral wall of the mandibular fossa. The two ridges serve to prevent any side-to-side movement of the mandible and limit its motion to the fore and aft movement characterizing propalinal mastication (Ahearn 1981).

The otic region is variably preserved (Fig. 7). On the left side, the auditory bulla is complete, although fractured. The right bulla is lacking, exposing the petrosal, which is unbroken. Anteriorly, the lateral margin of the petrosal lies against the squamosal, reaching and overlapping the alisphenoid. Medial to the anterolateral-most part of the petrosal lies the rostral process of the malleus. There is a space between the alisphenoid and the petrosal between the two anterior processes of the petrosal, which forms the pyriform fenestra. Posterior and slightly medial to the pyriform fenestra is what we interpret to be either the oval window or the stapedius fossa or both. The anteromedial part of the petrosal reaches and overlaps the alisphenoid; in the extant species *H. hydrochaeris* the anterolateral process of the petrosal does not reach the alisphenoid because the rostral process of the malleus separates the two completely.

Table 2. Skull measurements (in mm) of hydrochoerine specimens

	Hydrochoerus hesperotiganites SDSNH MSCC 50000	*Hydrochoerus hydrochaeris* MSCC 460	*Neochoerus aesopi* MSCC 575
Length of Skull Nasal to Occipital	250.3	230.2	—
Length of R Nasal	85.5	90.2	—
Width of R Nasal	33.5	27.3	—
Length of Frontal, approximate[1]	102.1	91.6	121.2
Length of Parietals	53.9	59.0	65.8
Posterior Width of Parietal Table	45.6	26.0	34.1
Anterior Width of Parietal Table	76.4	76.8	108.6
Length of Occipital	18.5	21.3	28.1
Width of Occipital, estimated[2]	45.1	56.3	73.2
Depth of Occipital excluding notch	31.7	31.9	42.1

[1] Approximate measurement due to uncertainty of exact position of suture.

[2] Estimated using bilateral symmetry where one side is complete and the other incomplete.

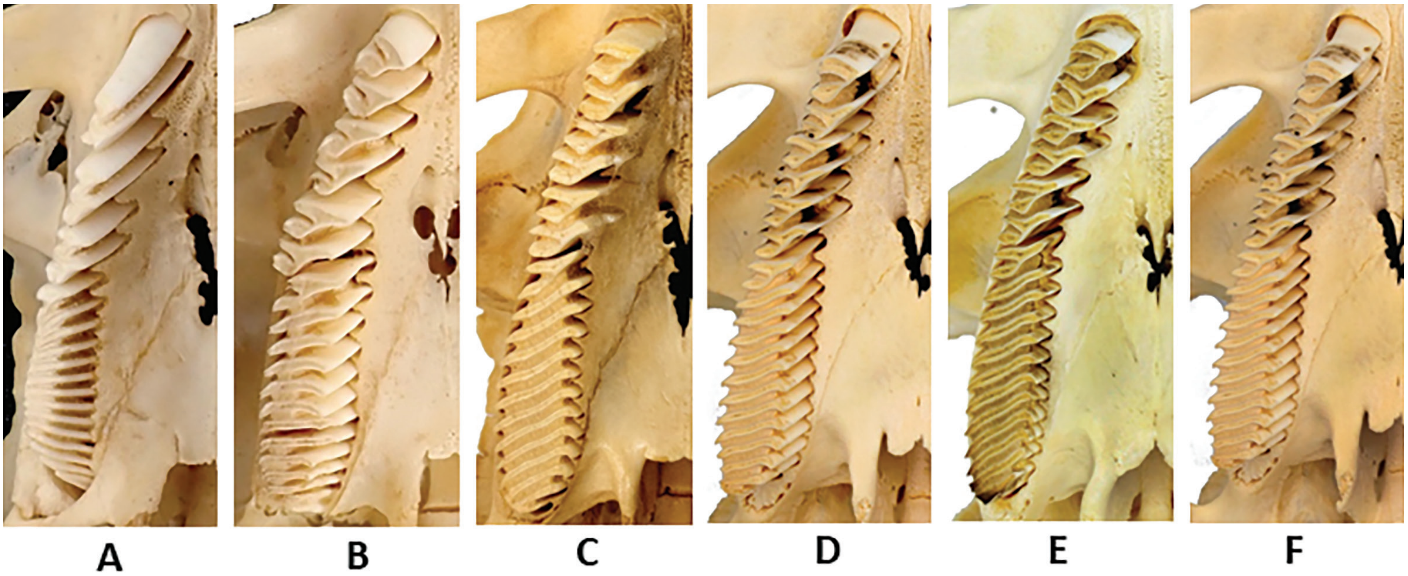

Figure 9. Ontogenetic series of right mandibular tooth rows in *Hydrochoerus hydrochaeris*. A, Age Class I with no wear on anterior teeth (MSCC 456); B, Age Class I with wear on all teeth (MSCC 457); C, Age Class II (MSCC 463); D, Age Class III (MSCC 461); E, Age Class IV – V (MSCC 4620; F, Age Class VII (MSCC 460). Measurements of the upper third molar (M3) are provided in Table 5.

Mones (1974) described and beautifully illustrated the auditory region of the extant *Hydrochoerus hydrochaeris*. His drawings (Mones 1974:figs.3–22) of the auditory region of neonate, juvenile, and adult specimens match closely the specimens in our ontogenetic series (Fig. 8). Given that the auditory region is well preserved in SDSNH 50000, it is possible that there may be generically diagnostic characters present. We are unable to compare this with *Neochoerus*, since a comparably detailed description of the auditory region for *Neochoerus* has not been published.

Relatively few accurate measurements can be taken of SDSNH 50000 because of the crushed condition of the skull; those which can be either directly measured or approximated are provided in Table 2.

Dentition: SDSNH 50000 possesses three teeth that are well enough preserved to provide adequate description of the dentition. The RM2 and RM3 (Fig. 2) are preserved in their entirety. The RM3 has sunk into its alveolus due to compaction with its occlusal surface resting ~4 mm below the lateral rim of the maxilla. The incomplete left upper incisor (I1) is preserved with a partial premaxilla (Fig. 10B), which cannot be attached to the skull because of missing pieces.

The RM3 measures 49.6 mm in the anteroposterior length and 15.7 mm in maximum transverse width. There are 12 enamel prisms posterior to the BLFP, which has one enamel column on the lingual side of the tooth, and 2 columns on the buccal side separated by a distinct Hendedura Primera Externa (HPE, Fig. 2). The BLFP has been described as "V-shaped" (Ahearn 1981:64), or "Y-shaped" (Kerber and Ribeiro 2011:7); we follow Perez et al. (2017) and describe it as bi-lobed. While prism counts of the M3 have figured prominently in the literature and have been used as diagnostic at both the specific and generic level for hydrochoerids, the method of counting prisms and reporting those counts has varied considerably among the various authors, who were not always specific about the method used (Ahearn 1981; Mones 1991). For the purpose of this paper, we count, and report, the number of independent (free) enamel prisms (laminae) posterior to the BLFP as illustrated in Figure 2. The posterior prism sometimes has a tiny additional prism joined to it on the buccal side; we count them as two independent prisms following Mones (1991). Thus, our count is one less than reported by those authors who counted BLFP as a single prism (Ahearn 1981; Mones 1991). The RM3 of SDSNH 50000 has 12 enamel prisms posterior to the BLFP (Fig. 2).

M2 measures 12.6 mm anteroposteriorly and 10.0 mm in maximum transverse width at the second prism. The M1 and M2 are so nearly identical in *Neochoerus* and *Hydrochoerus* that they are not usually separated out in discussions of isolated teeth. In *Hydrochoerus* and *Neochoerus*, M1 and M2 are composed of two prisms, both in a V-shape open buccally and joined lingually. We follow Mones (1991) in counting the two lamina which make up each prism as a single prism, even where they lose their connection during wear. The re-entrant between the two lamina of each prism is termed the HPE (Hendedura Primera Externa) for the anterior prism I and the HSE (Hendadura Secundaria Externa) for the posterior Prism II (after Mones 1991, in turn based upon Rusconi (1939) and Kraglievich (1941) (Fig. 2).

Table 3: Tooth measurements (in mm) of SDSNH 50000

Anterior-Posterior Length of RM2	12.60
Medial-Lateral Width of RM2	10.03
Anterior-Posterior Length of RM3	49.60
Medial-Lateral Width of RM3	15.70
Width of Upper L Incisor	13.90
Anterior-Posterior Depth of Upper L incisor	9.72

In SDSNH 50000 the connections between the laminae making up each prism have been lost, likely due to wear, extending the HPE and HSE across the entire width of the tooth. Albright et al. (2019) figure a left M2 from an individual of uncertain age from the Cooper River in South Carolina that they refer to *Neochoerus pinckneyi* which has the laminae of both prisms joined lingually. Unfortunately, they do not provide measurements of this tooth. Mones (1991) provides drawings of M2 in *Hydrochoerus hydrochaeris* at birth, 4 weeks, 6 weeks, and adult; all have the laminae of both prisms joined lingually.

The incomplete left I1 (Fig. 10B) has a curvilinear length of 51.00 mm (as measured along the anterior enamel margin), a width of 13.90 mm, and a depth of 9.72 mm distally, with a width of 14.24 mm and a depth of 9.77 mm proximally. It has a wide, shallow groove on the anterior enamel covered surface. Visible in incident light are fine longitudinal striations, both within the groove and lateral to it; no sharply marked longitudinal ridges are present. The root end of the tooth has a damaged but open pulp cavity. When fitting the partial tooth to the isolated ventral and dorsal portions of the left premaxilla, it is clear that the preserved portion of the incisor was unerupted and entirely within the incisor alveolus. Dental measurements are provided in Table 3.

TAXONOMIC ASSIGNMENT

Identifying North American Pleistocene capybara fossils has long been a contentious undertaking (Ahearn 1981; Mones 1991; Vucetich et al. 2015; Carranza-Castañeda 2016). In the past, taxonomic assessment has relied primarily on three morphological features, one on the mandible, one on the skull, and one on the upper and lower incisors. The masseteric ridge of the mandible has been used to separate *Neochoerus* (originally including *N. dichroplax*, now assigned to the genus *Phugatherium*) from *Hydrochoerus*. In *Neochoerus* (less *N. dichroplax*), the masseteric ridge begins lateral to the middle of the last prism (PIII) of p4, according to Ahearn (1981), while in *Hydrochoerus*, the masseteric ridge begins lateral to the middle prism (PII). Since SDSNH 50000 lacks the lower jaws, it cannot be allocated to either genus based on characters of the lower jaw.

The upper and lower incisors of both genera have a wide anteromedial longitudinal groove on the enamel surface of the tooth. *Hydrochoerus* was diagnosed by Ahearn (1981) as grooved but lacking ridging on the enamel surface, while *Neochoerus* has both the groove and ridged enamel (Fig. 10). Based on our examination of six extant *Hydrochoerus hydrochaeris*, this character needs slight revision. Careful examination of those six specimens in incident light reveals that faint longitudinal striations are visible both within the groove and to the lateral and medial side of the groove (Fig. 10C). We propose changing the character state seen in *Neochoerus* to "pronounced ridging" of the enamel. SDSNH 50000 is grooved, and lacks the pronounced ridging seen in *Neochoerus*, but does have faint striations visible, as in *Hydrochoerus* (Fig. 9C). Thus, SDSNH 50000 is referrable to *Hydrochoerus* based in part on this character of the upper incisor.

The character most often used to allocate specimens to hydrochoerine genera has been the M3, specifically the number of enamel prisms present. Dental characters have been discounted by some workers who note that size and occlusal pattern change markedly through ontogeny (Prado et al. 1998; Vucetich et al. 2005). Additionally, confusion has been caused by the different methods employed to count the number of prisms as noted above. Ahearn (1981:62) characterizes the genus *Neochoerus* as having an M3 "…composed of an anterior Prism with a V-shaped cross-section followed by 13 to 16 separate laminae." following the BLFP, while *Hydrochoerus* has 11 or 12 separate lamina. According to Ahearn (1981:62), *Neochoerus pinckneyi* has an M3 "…composed of seventeen prisms (laminae)". We interpret this to mean that it has a BLFP and 16 independent laminae.

Table 4 presents descriptions of M3 as used by Ahearn (1981), Mones (1991) and Vucetich et al. (2015) to characterize the genera and species of North American hydrochoerines. We interpret the terminology of both Ahearn (1981) and Mones (1991) based on their written descriptions as well as the illustrations they provided. It should be noted that the low prism count for *Neochoerus* reported by Ahearn (1981) and Mones (1991) is due to the inclusion of South American species of *Neochoerus*, particularly *N. tarijensis* and *N sulcidens*. No North American specimens of *Neochoerus* have been reported with fewer than 15 post-BLFP prisms. The Central American skulls of *Neochoerus* examined by us directly or in photographic images also have 15 or more post-BLFP prisms. A more complete review of the South American species is needed to determine their status. We here consider 15 or more post-BLFP prisms as diagnostic for North American species of *Neochoerus*.

Several authors have remarked that tooth morphology, including size, prism counts, and occlusal pattern, vary

Table 4. Description of M3 in hydrochoerines by previous authors and as used in this study.

Taxon	Ahearn 1981	Mones 1991	Vucetich 2015	This study
Hydrochoerus	BLFP + 11-12	BLFP + 9 - 13	—	BLFP + 10 - 13
H. hydrochaeris	BLFP + 11-12	BLFP + 10 - 13	—	—
H. holmesi	BLFP + 11-12	—	—	—
Neochoerus	BLFP + 13 -16	BLFP + 12 - 16	—	BLFP + 15- 161
N. dichroplax	BLFP + 14 -15	BLFP + 15	—	—
N. pinckneyi	BLFP + 16	—	—	—
N. aesopi	—	BLFP + 15 - 16	—	BLFP + 15 - 16
*N. tarijensis*2	—	BLFP + 13 - 14	—	—
*N. sulcidens*2	—	BLFP + 12 - 13	—	—
Phugatherium	—	—	BLFP + 14 -18	BLFP + 14 - 18
*P. cataclisticum*2	—	—	BLFP + 16 - 18	—
P. dichroplax	—	—	—	BLFP + 15

[1] Excludes South American species
[2] Indicates South American species

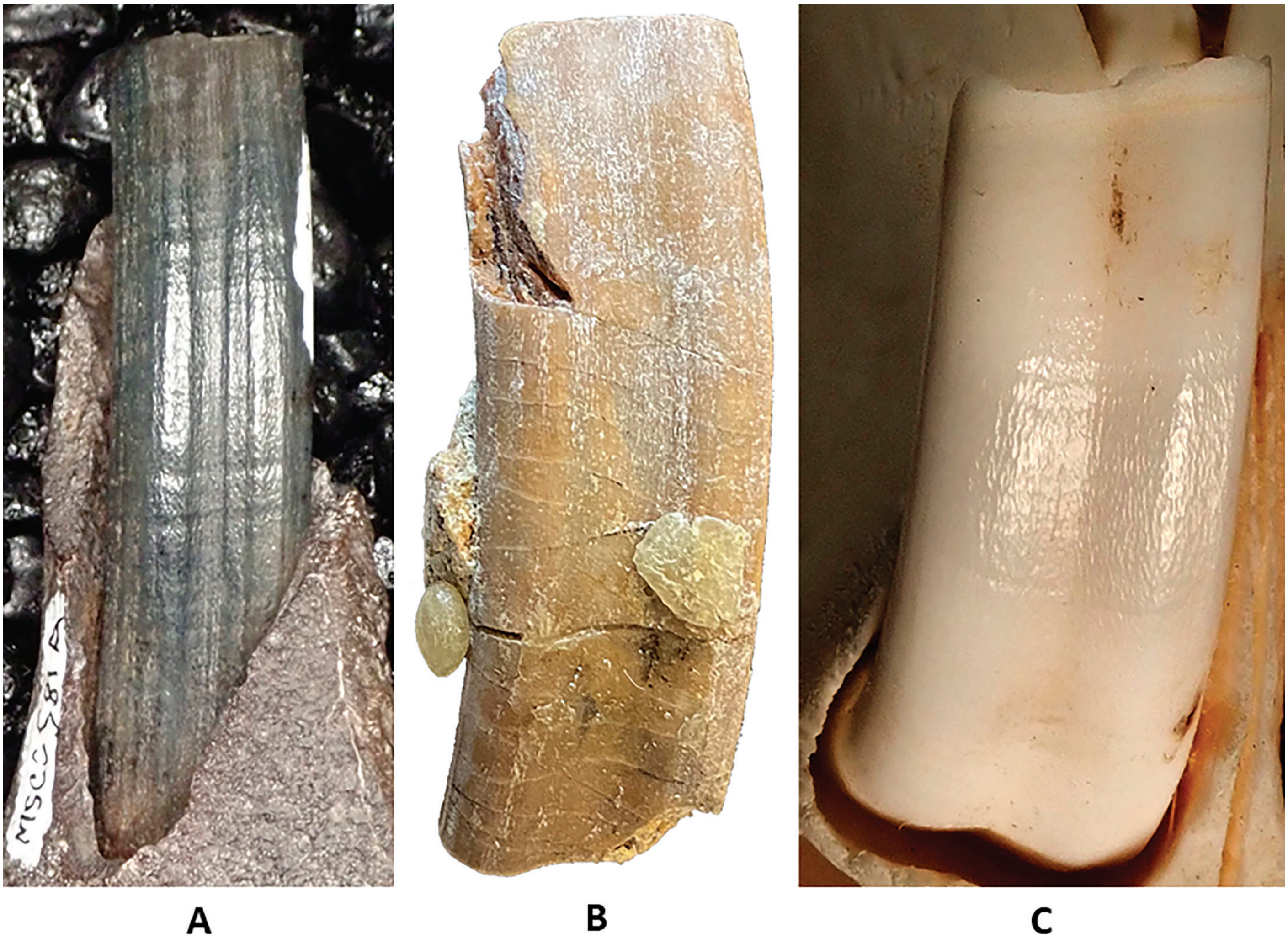

Figure 10. Anterior enamel surface of incisors. A, *Neochoerus aesopi*, MSCC 581, Florida; B, *Hydrochoerus hesperotiganites*, SDSNH 50000, California; ,. *Hydrochoerus hydrochaeris*, MSCC 461, zoo specimen.

Table 5. Ontogenetic series of *Hydrochoerus hydrochaeris* M3s.

Specimen Number	Age Class	Calendar Age	Post- BLFP Independent Prisms	Length of M3 (mm)	Width of M3 (mm)
MSCC 456	I	0-4 months	13	13.5	3.5
MSCC 457	I	0-4 months	12	15.9	5.6
MSCC 463	II	4 –12 months	11	30.4	12.0
MSCC 461	III	1 – 1.5 years	12	35.1	12.9
MSCC 462	IV-V	1.5 – 2 years	11	43.3	15.8
MSCC 460	VII	4 years and up	12	48.2	17.2

Table 6. M3 prism counts in *Hydrochoerus hydrochaeris*, data from Mones (1991); N = 57.

Number of prisms	Number of Post-BLFP Prisms	Count in sample	% of sample
11	10	1	1.8
12	11	20	34.9
13	12	34	59.4
14	13	2	3.7

ontogenetically, and thus should not be given much taxonomic weight (Prado et al. 1998; Vucetich et al. 2005). Mones (1991:fig. 7) illustrated the ontogenetic changes in M3 of extant *Hydrochoerus hydrochaeris*.

In order to further evaluate the usefulness of prism counts as a taxonomic character, we examined an ontogenetic series of six modern skulls of *Hydrochoerus hydrochaeris* (Figs. 8, 9), ranging in age from about 4 months (Age Class I) to 4+ years (Age Class VII) based on the scheme of Ojasti (1973, 2011) as utilized by Gorosabel et al. (2017). Counts of the independent prisms posterior to the BLFP and the length and width of the M3 are presented in Table 5. Figure 9 shows enlarged views of the individual tooth rows; Figure 8 shows the 6 skulls to scale to illustrate skull growth. As can be seen from this relatively small sample, the number of independent prisms ranges from 11 to 13 but is not correlated with

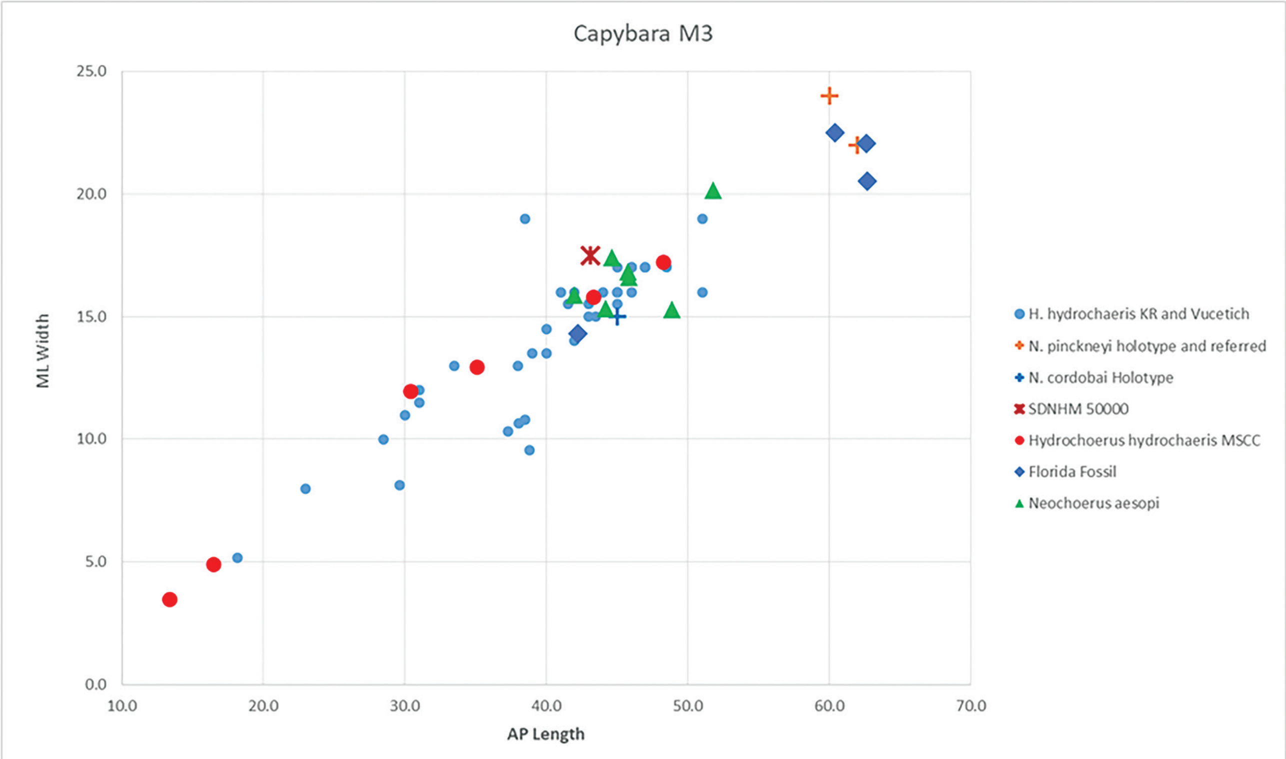

Figure 11. Bivariate plot of M3 measurements of capybaras.

ontogeny. Mones (1991) reported on a sample of 57 M3s of *Hydrochoerus hydrochaeris* from Uruguay. Table 6 summarizes those counts and their percentage in the entire sample. Additional data on the M3 of extant *Hydrochoerus hydrochaeris* were published by Hooijer (1959) who measured a series of 20 capybara skulls in the Leiden Museum, recording the length of the M3 and the basilar length of the skull. We have plotted his data, with the data from our 6 specimens, in Figure 12. It is clear from this plot that the length of M3 increases throughout ontogeny.

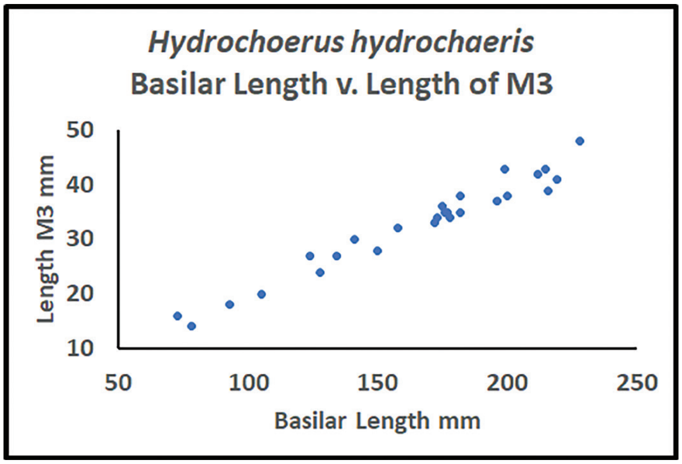

Figure 12. Bivariate plot of the length of M3 plotted against the basilar length of the skull. Data from a sample of extant H. hydrochaeris in Hooijer (1959) and from our sample of extant *H. hydrochaeris* (Tab. 5). N=26.

Gorosabel et al. (2017) examined 250 skulls collected in northern Argentina, stating that the skulls corresponding to different age categories exhibited the same number of prisms. It is unclear whether they intended to indicate that the entire sample has the same number of prisms, or that each age category has the same range of plate counts. However, either interpretation suggests that variation in prism count in the teeth of extant *Hydrochoerus hydrochaeris* is unrelated to ontogenetic age. Aeschbach et al. (2016) examined the growth of the cheek teeth in their samples of 117 *H. hydrochaeris* and *H. isthmus* and concluded that the number of prisms did not change through post-natal ontogeny. These data all indicate that the changes in occlusal pattern occur within the first 3 to 4 months; and that after that time, the occlusal pattern, particularly the prism count, is remarkably stable.

Other characters have been utilized to differentiate *Hydrochoerus* from *Neochoerus*. We note here that all specimens we were able to find in the literature that have been referred to *Neochoerus pinckneyi* are exceedingly large. Figure 11 presents a bivariate plot of the length and width of the upper third molar (M3) based on measurements in Kerber and Ribiero (2011), Vucetich et al. (2005), Carranza-Castaneda and Miller (1988), Hay (1923) and our own measurements. It is curious that no smaller specimens have been assigned to that taxon. In contrast, smaller specimens have been assigned to both *Neochoerus aesopi* and *Hydrochoerus holmesi*. Ahearn (1981) considered *H. holmesi* to be a *nomen dubium* but noted that the ridged incisor of the type might indicate a small or juvenile *Neochoerus* (in which she also included *N. dichroplax*). Mones (1991) included both *H. holmesi* and *N. pinckneyi* in *Neochoerus aesopi*. Baskin et al. (2020) considered *H. holmesi* to be a junior synonym of *N. aesopi*. These authors recognized just one species of *Neochoerus* from the late Blancan through the late Rancholabrean of North America, *Neochoerus aesopi*. Given the existence of juvenile specimens of both *Neochoerus* and *Hydrochoerus,* it seems unlikely that only fully adult *Neochoerus pinckneyi* have been found. We are not convinced by the arguments of Mones (1991), accepted by most recent authors, that all of the specimens of *N. pinckneyi* referred by him to *N. aesopi* are correctly allocated, particularly those dating to the Blancan NALMA. Given the significant range in size of the three species allocated to *Hydrochoerus*, the most parsimonious interpretation, and the one followed here, is that the specimens identified as *H. holmesi* in the bivariate plot of Ahearn (1981), and those described by others as *N. aesopi* (Baskin et al. 2020; Carbot-Chanona et al. 2020) are simply younger conspecifics of the large, presumably fully adult individuals identified as *Neochoerus pinckneyi*. This confusion is exacerbated by the difficulty in aging capybara specimens independent of tooth size. Nevertheless, we advocate for a more thorough study of this problem that includes Florida Blancan and Irvingtonian samples.

Another potentially diagnostic character was first described by Simpson (1930:9) involving the skull roof.

"It is the skull roof that most obviously distinguishes fossil and recent animals. The frontal region on the fossil is very broad and nearly flat. The sagittal crests on the parietals narrow very rapidly: at the postorbital processes they are nearly twice as wide as in *Hydrochoerus*, while at the contact with the supraoccipital (or interparietal?) they are of almost the exact same width as in the latter. The roof of the parietals is not arched and does not curve downward posteriorly but continues the plane of the frontals and rises to a point at the supraoccipital suture. The interparietal part of the supraoccipital is relatively longer in the fossil, and the occiput relatively higher."

Mones (1991:39, translation by RSW) included characters of the skull roof in his generic diagnoses of *Hydrochoerus* and *Neochoerus*:

> [*Hydrochoerus* with] "… face relatively shorter than *Neochoerus*, with the skull roof proportionally shorter at the level of the frontals and nasals, and slightly

> descending towards the occiput; thinner anteorbital bar and less robust lacrimal; supraoccipital narrower and less excavated.
>
> [*Neochoerus* differs] "… from *Hydrochoerus* in: size one third to two times larger; proportionally longer face; anterior portion of the zygomatic arch more rounded and directed backwards, less transverse; more robust anteorbital bar and lacrimal; skull roof very broad, proportionally wider through the nasals and frontals, with these proportionally shorter and the parietals longer, occiput less convergent dorsally, supraoccipital wider and relatively more excavated; …" (Mones 1991:49)

Interpreting this character complex is somewhat subjective in SDSNH 50000 since the skull has been extensively crushed dorso-ventrally. In addition, Mones (1991) included "*Neochoerus dichroplax*" in his diagnosis of the genus in which he discussed only dental characters, so we are unable to determine how the rest of his diagnosis for the genus would be affected by the reallocation of *N. dichroplax* to the genus *Phugatherium* (Vucetich et al. 2015). SDSNH 50000 is somewhat larger than the largest of the modern *Hydrochoerus hydrochaeris* specimens available to us (MSCC 460). The skull length, measured from the posterior edge of the occipital to the anterior end of the nasals is 9% larger than MSCC 460 (250.3 mm, versus 230.2 mm). Other measurements vary from smaller to larger in SDSNH 50000 than MSCC 460 (Table 2), but how much of this is due to the distortion in the fossil is unclear. SDSNH 50000 is clearly somewhat larger than our largest modern specimen, MSCC 460, but nowhere near the 33-50% larger condition described by Mones (1991) for *Neochoerus*. The parietals and frontals appear broader in SDSNH 50000 than in modern *Hydrochoerus*. In addition, the supraoccipital of SDSNH 50000 is broader and gently rounded laterally and ventrally, as opposed to MSCC 460, where the supraoccipital is higher, less broad and has a straighter slope laterally. Our ontogenetic sample of modern *H. hydrochaeris* shows that the supraoccipital does not unite with the occipitals until Age Class IV where it is partly, but not completely, fused. In Age Class VII no suture is visible.

Since we cannot reliably separate the effect of distortion and the difference in size in skull roof proportions, we are not confident that this character complex is well-enough defined to be considered in our taxonomic assignment.

Considering all the above, SDSNH 50000 can confidently be allocated to *Hydrochoerus*, based on the morphology of M3 and I1 as described. The fact that the skull is somewhat larger, and the likelihood that the skull roof is relatively broader in SDSNH 50000 than in living *H. hydrochaeris* indicates its specific distinctiveness from the extant *H. hydrochaeris*, as does the more robust zygomatic process of the maxilla and descending zygomatic process of the lacrimal. Characteristics of the otic region are also different from those in extant *Hydrochoerus*, although the true taxonomic significance of these differences cannot be meaningfully evaluated until descriptions of this area in other hydrochoerines are available. Although we cannot adequately quantify the difference in the breadth of the skull because it is crushed and distorted, the other differences are clearly defined and justify the establishment of the new species *Hydrochoerus hesperotiganites*.

BIOGEOGRAPHY

Capybaras (Caviidae: Hydrochoerinae) and the porcupine *Erethizon* (Erethizontidae) are the only two groups of South American caviomorph rodents that reached temperate North America in the late Pliocene to early Pleistocene (late Blancan and early Irvingtonian) phase of the Great American Biotic Interchange (GABI) (Frazier 1981; Morgan 2005, 2008; Woodburne 2010; Vucetich et al. 2015). This later phase of the GABI began in the early Pliocene about 5 Ma with the final connection of North America and South America at the Isthmus of Panama (O'Dea et al. 2016). During an earlier phase of the GABI in the late Miocene (early Hemphillian NALMA, ~9 Ma), two genera of ground sloths in the families Megalonychidae and Mylodontidae apparently reached North America by overwater dispersal from South America (Morgan 2005; 2008). Although our paper describing a new species of the extant genus *Hydrochoerus* from the late Pleistocene is not the appropriate place for a detailed discussion of the biogeography and systematics of capybaras associated with the late Pliocene and early Pleistocene phase of the GABI, it is nevertheless important to establish the evolutionary history of *Hydrochoerus* and other hydrochoerines in North America.

Three genera of capybaras, the extinct *Neochoerus* and *Phugatherium* and the extant *Hydrochoerus*, have been reported from the North American fossil record (Ahearn 1981; Mones 1991; Morgan 2005, 2008; Vucetich et al. 2015). *Phugatherium* was named from the Pliocene of Argentina and is represented in North America by the species *P. dichroplax* (Vucetich et al., 2015), originally described as *Neochoerus dichroplax* from three late Blancan faunas in the southern USA, 111 Ranch (= Dry Mountain) in Arizona (type locality) and two sites in southern Florida (Ahearn and Lance 1980). Morgan and Hulbert (1995) and Hulbert (2010) reported several additional late Blancan records of *N.* (= *P.*) *dichroplax* from Florida. The earliest well-dated capybara from North America is *N. cordobai* from the early Blancan (~3.6 Ma) of central México (Carranza-Castañeda and Miller 1988). Although Vucetich et al. (2015) synonymized *N. cordobai* with the late Blancan (~2.5–2.7 Ma) *N. dichroplax* from the southern USA, Carranza-Castañeda (2016) recognized *N. cordobai* as a valid species of *Neochoerus* and also described a new species *N. occidentalis* from several late Blancan and early Irvingtonian faunas in México. *Neochoerus* (not including *Phugatherium* but including most previous North American records of *Hydrochoerus*—see below) first appeared in either the early Blancan of México or the late Blancan of Florida and South Carolina (Ahearn 1981; Morgan 2005; Vucetich et al. 2015; Carranza-Castañeda 2016; Albright et al. 2019). Several of these North American Blancan capybaras appear to be older than the oldest records of *Neochoerus* from South America (Vucetich et al. 2015). That begs the question—did *Neochoerus* evolve in South America and disperse to North America in the Pliocene as a participant in the GABI, or did *Neochoerus* evolve in North America from *Phugatherium dichroplax* or a species closely related to *N. cordobai*? An answer to this question will require more detailed systematic studies of North American Blancan capybaras, which is beyond the scope of this paper.

More relevant to our current study is the status of fossil capybaras from North America previously referred to the living genus *Hydrochoerus*. Simpson (1928) described an extinct species of *Hydrochoerus*, *H. holmesi*, from the late Pleistocene (Rancholabrean) Sabertooth Cave in Florida. Many other Florida fossil capybaras have since been referred to *H. holmesi*, including specimens as old as late Blancan (Ahearn 1981; Morgan 2005). However, the taxonomic studies we follow here (e.g., Mones 1991; Baskin et al. 2020) transferred *H. holmesi* to *Neochoerus* and have also synonymized this species with *N. aesopi*, in which they also included *N. pinckneyi*. Although these authors proposed that *N. aesopi* occurred over a time period of nearly 2 million years, from the late Blancan to the late Rancholabrean, it is worth noting that few Rancholabrean species of North American mammals have chronologic ranges that extend back into the Blancan (Kurtén and Anderson, 1980). Furthermore, Vucetich et al. (2015:325) stated "…extinct species [of capybaras] had short stratigraphic ranges (partly because of their physiological requirements) and relatively wide geographic ranges, rendering them useful as biostratigraphic tools…". Most late Blancan and Irvingtonian samples of *Neochoerus* from the southeastern United States, in particular Florida, have not been studied in detail and may represent a species of *Neochoerus* distinct from *N. aesopi* (= *N. pinckneyi* = *H. holmesi*).

In summary, it appears that all previous fossil records of capybaras from North America represent one of two extinct genera, *Neochoerus* or *Phugatherium*. These records span the time period from the late Pliocene (~3.6 Ma) of central México to the late Pleistocene of the southeastern United States and Central America, with *Phugatherium* known only from the Blancan and Neochoerus occurring in the Blancan, Irvingtonian and Rancholabrean. Following the current taxonomy, with referral of *Hydrochoerus holmesi* to *Neochoerus aesopi* (Mones 1991; Baskin et al. 2020), none of the previously described North American capybaras belong to the extant genus *Hydrochoerus*. Consequently, the new species described here, *H. hesperotiganites*, from the Rancholabrean of southern California appears to be the only valid fossil record of *Hydrochoerus* from North America, causing us to rethink the biogeography of this genus. With the northern-most range extension of the living capybara *H. isthmius* in eastern Panama, there appears to be no record of *Hydrochoerus*, living or fossil, between Panama and southern California.

Determining which species of capybara crossed the Panamanian Land Bridge, and when, as well as what route they took in their dispersal northwards into North America would naturally begin, of course, with Central America and southern México. However, the fossil record of capybaras is extremely limited for Central America, with just five records (one unpublished), all probably, but not certainly, of Pleistocene age. Importantly, all are identified as *Neochoerus* rather than *Hydrochoerus*. The unpublished record is from Guatemala, in the American Museum of Natural History (FM 94034; RSW notes), the other in the Paleontological Museum in Estanzuela, Guatemala (PV-H-45; McDonald and Davila A 2017; H.G. McDonald, personal communication). Judging from the available photographs, both specimens appear to be *Neochoerus*, as they have M3s with 15 independent prisms following the BLFP. The published records include one each in San Salvador (Webb and Perrigo 1984), Nicaragua (Leidy 1887; Lucas et al. 2008), Honduras (Ahearn 1981; Webb and Perrigo 1984) and Guatemala (Lucas et al. 2021; McDonald and Davila A 2017; H.G. McDonald, personal communication). All four were identified as *Neochoerus* and dated as late Pleistocene. McDonald and Davila A (2010) map the occurrence of *Mammuthus columbi* in Central America; all known occurrences are confined to the Pacific lowlands of El Salvador, Honduras, Nicaragua, and Costa Rica. This suggests that the corridor for southward dispersal (and presumably northward as well) was along the Pacific Coast. Alternate explanations could be that there has been less paleontological exploration along the Atlantic coast and the interior highlands; or that an Atlantic dispersal corridor lies east of the present shoreline and was submerged by rising sea levels after the last glacial high sea level. Certainly, intensive exploration of the interior and the Atlantic coast areas is desirable.

The only record of Rancholabrean capybaras from southern México is that reported by Carbot-Chanona et al. (2020) from Chiapas and discussed below. Given the paucity of records of capybaras in Central America and southern México, we will confine our analysis and speculations primarily to central and northern México and to the southwestern United States.

Late Pleistocene (Rancholabrean) records of capybaras from central and northern México include abundant material from Lake Chapala, Jalisco, which has been referred to *Hydrochoerus magnus* (Peters 1951), *Hydrochoerus* (Alvarez 1971), *Neochoerus* (Carranza-Castañeda and Miller 1988), *Neochoerus* ?*pinckneyi* (Rufolo 1998), *Neochoerus aesopi* (Mones 1991), *Neochoerus aesopi* (Lucas 2008) and *Hydrochoerus* sp. (Carranza-Castañeda 2016). Carbot-Chanona et al. (2020) after a careful review of the material, rejected the presence of *Hydrochoerus* in the Lake Chapala fauna, assigning the Lake Chapala capybara to *Neochoerus aesopi*.

Fossil capybara has been reported from the Rancholabrean site of Térapa, Sonora, in the Rio Moctezuma drainage. Initially referred to *Hydrochoerus* sp. by Mead et al. (2006) and later as Hydrochoeridae indeterminate (Nunez et al. 2010), the Térapa material was referred to *Neochoerus aesopi* by Carbot-Chanona et al. (2020), even though they did not examine the fossils and no illustrations have been published. These fossils are currently under study by the authors.

A fossil capybara from Media Luna lagoon, San Luis Potosi, described by Hernandez-Junquera (1977) as *Hydrochoerus* sp. was, as Carbot-Chanona et al. (2020) noted, never deposited in a museum and is now presumed lost. While they refer that missing material to *Neochoerus aesopi*, we prefer to leave it as Hydrochoerinae indeterminate. Further south in México, fossil capybaras have been reported from the late Pleistocene site of Valsequillo, Puebla, as *Hydrochoerus* by Pichardo (1997), and as *Neochoerus* sp. by Perez-Crespo et al. (2014, 2017). Carbot-Chanona et al. (2020) examined some of this material (an incomplete skull) and documented the morphological features which allow it to be assigned to *Neochoerus aesopi*. Carbot-Chanona et al. (2020) describe significant well preserved capybara material from the late Pleistocene (Rancholabrean) Los Mangos locality in Chiapas, allocating it to *Neochoerus aesopi*. *Hydrochoerus* is represented in the fossil record of South America (Mones 1991) but not in Central America; this may be the result of the paucity of well investigated sites in Central America.

We are thus left with no confirmed recent or late Pleistocene record of *Hydrochoerus* between eastern Panama and the San Luis Rey River in southern California, a distance of about 6,000 km (3,730 miles). The previous northwestern-most record for a Pleistocene capybara is the latest Blancan or early Irvingtonian record of *Neochoerus occidentalis* from El Golfo, Sonora (Croxen et al. 2007; Carranza- Castañeda 2016) and the late Blancan record of *Phugatherium dichroplax* from 111 Ranch in Arizona (Ahearn and Lance 1980; Galusha et al. 1984; Tomida 1987). Capybaras appear in the Rancholabrean of northern Sonora at Térapa, 180 kilometers (112 miles) south of the México / USA border. There is no Rancholabrean record of any capybara in Arizona, New Mexico, or in western Texas.

Ceballos et al. (2010) defined seven corridors through which mammals moved in and out of México to establish their present distribution. Two of those routes, the Sonora – Central American Lowlands along the Pacific Coast of México and the Tamaulipas – Central America Gulf Lowlands along the Gulf of México, are relevant to our discussion of capybara dispersal into northern México and the United States.

Florida has the most diverse Plio-Pleistocene Interchange mammalian fauna in temperate North America with more than ten species (Morgan 2005), including two genera of capybaras, *Phugatherium* and *Neochoerus* (Ahearn and Lance 1980; Vucetich et al. 2015). Mammals that participated in the Plio-Pleistocene phase of the GABI first appeared in Florida in the early Pleistocene (late Blancan; about 2.5 Ma), including *Phugatherium dichroplax*. Webb (1974, 1978) proposed that the Florida Interchange fauna used a dispersal route he called the 'Gulf Coast Savanna Corridor' (GCSC), equivalent to and an extension of the Tamaulipas – Central America Gulf Lowlands corridor of Ceballos et al. (2010:fig. 6, corridor 6) and corresponding to the coastal plain of the Gulf of México from southern México to Florida. A northern extension of this corridor existed along the southeastern Atlantic Coastal Plain, allowing the northward dispersal of several members of the GABI fauna into Georgia and South Carolina, including the capybara *Neochoerus aesopi* (Sanders 2002; Albright et al. 2019). Morgan and Emslie (2010) proposed that the GCSC was active throughout the Pleistocene, serving as a pathway for certain tropical species of mammals, as well as birds, to disperse from Central America around the Gulf of México to tropical/subtropical habitats in the Florida peninsula. The Gulf Coastal Plain of Texas was part of the GCSC, supporting a diverse GABI mammal fauna in the late Pleistocene, including *N. aesopi* (Baskin and Thomas 2007; Baskin et al. 2020).

Confining our considerations to northern México and the southwestern United States, we can envision several potential routes for the dispersal of capybaras from central and southern México. These routes fall within the northern-most portions of the western-most corridor defined by Ceballos et al. (2010:fig. 6, corridor 7) for México: the Sonora – Central American Lowlands along the Pacific Coast of México.

Two major routes are potentially available. *Hydrochoerus* could have followed a coastal route from further south in México northward along the coasts of Sinaloa and Sonora to the mouth of the Colorado River where they would have travelled inland into California and potentially made their way westward through the Salton depression and thence north along the Whitewater River drainage, finally reaching the San Luis Rey River in San Diego County. There are difficulties in envisioning this route, particularly once capybaras had reached the Colorado River, as there are stretches where overland dispersal would have been necessary and permanent sources of water scarce or unknown.

A second route also starts with capybaras moving north along the coasts of Sinaloa and Sonora, but then entering the major north or northeast flowing drainages which enter the Gulf of California, particularly the Rio Fuerte, Rio Mayo, Rio Yaqui, and the Rio Sonora (Fig. 3). We know that capybaras did travel north along the Rio Yaqui, and into the Rio Moctezuma, a distance of 350 km (220 miles) where they reached the site of Térapa in eastern Sonora (Mead et al. 2006) accompanied by crocodiles, to within 180 km (110 miles) of the México/USA border. It is easy to envisage them traveling further north into the San Simon drainage and thence to the Gila River, from where they could have reached downstream to the Colorado River and into California. Just such a route may well have been available for more than 2.5 million years, and used by the two previous lineages to disperse into northwestern México and the American Southwest: *Phugatherium dichroplax* appears in the latest Blancan in the San Simon drainage in Arizona in the 111 Ranch fauna during a short interval just below the Gauss/Matuyama Boundary, 2.58 Ma (Ahearn and Lance 1980; Galusha et al. 1984; Tomida 1987) and *Neochoerus occidentalis* into northwestern Sonora near the mouth of the Colorado River in the El Golfo fauna of latest Blancan or earliest Irvingtonian age (Carranza-Castañeda 2016). Whatever the identity of the Térapa capybara, it also followed this route in the Rancholabrean some 40–42 ka (Mead et al. 2006; Bright et al. 2010; Short et al. 2021). Until the discovery of SDSNH 50000 in San Diego County, we had no evidence that capybaras had penetrated into, or perhaps survived in, the Rancholabrean of New Mexico, Arizona, or California.

The Rio Yaqui is not the northern-most drainage which animals with southern affinities have taken to extend their distribution northwards. Remains of the Sabinal Frog (*Leptodactylus melanonotus*) were recovered from Rancho La Brisca, in the Rio Sonora drainage, some 240 km (150 miles) north of their present distribution on the Rio Yaqui (Van Devender et al. 1985). A record of the Sabinal Frog from near Hermosillo, also in the Rio Sonora drainage, is mentioned by Van Devender et al. (1985) and by Rorabaugh and Lemos-Espinal (2016), who also mention an unconfirmed sight record near Moctezuma on the Rio Yaqui drainage. It is reasonable to suggest that other taxa with southern affinities might have utilized the Rio Sonora and other drainages to disperse north.

What are we to make of this paucity of capybara remains in the Rancholabrean fossil record in Sonora, Baja California, Western Texas, New Mexico, and Arizona, with only a single record in Térapa, Sonora? Were capybaras rare or otherwise absent? We suggest that several factors are responsible. First and foremost, very few late Pleistocene sites in Sonora have been intensively sampled, with adequate efforts for the recovery of microfauna. Térapa and Rancho La Brisca are, to our knowledge, the only two sites where micromesh screen washing has been employed and reported. No capybara was recovered from Rancho La Brisca (Van Devender et al. 1985). White et al. (2010) documented 60 sites known to have produced Pleistocene (Irvingtonian and Rancholabrean) fossils in Sonora. Several of these sites have the potential to produce significant faunal remains if intensively sampled; for example, Chinobampo, in the Río Mayo drainage appears to have been formed in much the same way as Térapa, with a classic Rancholabrean fauna including *Bison*, *Equus*, and *Glyptotherium*. However, Chinobampo may date somewhat later than does Térapa, given the purported presence of human skeletal material in association with the Rancholabrean faunal remains (White et al. 2010).

The mouths of the rivers emptying into the Gulf of California in Sinaloa and southern Sonora have thorn scrub habitats and tend to be associated with more or less extensive growth of mangrove trees today. The northern-most mangrove swamp on the Sonoran side of the Gulf of California is the one located just south of Cerro Tepopa at the Sargento Estuary. There is an extinct estuary further north at the mouth of the Rio San Ignacio just south of the Comcaac village of Desemboque de los Seris. There is then a gap of some 50 km (30 miles) where another extinct estuary is located at Puerto Libertad. The areas around all three of these estuaries (Punta Sargento, Rio San Ignacio, and Puerto Libertad) should be carefully examined to see if fossil-bearing sediments can be located. Bathymetric data in the vicinity of these localities suggest that the glacial maximum shorelines would not have been far from the present-day shoreline, so the chance of significant deposits being preserved, and accessible, is much greater than father north, where the glacial maximum shoreline was distinctly farther from the present-day shoreline (Fig. 3).

It is possible that the San Diego County record of *Hydrochoerus* came north along the coast of México, then along the Pacific coast of Baja California prior to the separation of Baja from mainland México and the formation of the Gulf of California, and into what is now California. Geologic evidence, however, suggests that the Gulf of California began to appear as early as about 10 Ma as Baja California rifted north and west from mainland México towards its present position (Dolby et al. 2015). The Gulf of California was nearly at its present length but narrower, by 6 Ma (Dolby et al. 2015). This is well before any record of capybaras in México at about 3.3–3.8 Ma (Carranza-Castañeda 2016). The opening of the Gulf of California increased summer monsoonal rainfall in mainland Sonora and Sinaloa, marking a northern expansion of humid, subtropical thorn forest vegetation along the coasts of Sinaloa and Sonora (Chapin 2008), which would have provided an ideal corridor along which taxa with southern affinities, such as capybaras, crocodiles, glyptodonts, and pampatheres could have dispersed. This further supports our contention that it is along the Gulf of California coasts of Sinaloa and Sonora where evidence of the dispersal of *Hydrochoerus* northward should be sought if the coastal dispersal route, rather than an interior route, was involved in capybaras reaching coastal southern California in the late Pleistocene.

CONCLUSIONS

Hydrochoerus hesperotiganites represents a new species of capybara from San Diego County, California USA. The new species is the only confirmed record of fossil *Hydrochoerus* in North America and is the northwestern-most record in North America during the Rancholabrean.

Future areas of work should include the search for fossil *Hydrochoerus* along the coast of northwestern Mexico. Descriptions of the auditory region, particularly of *Neochoerus*, are needed. A larger sample of extant capybaras needs to be examined in detail, especially of the smaller species, *H. isthmius*, which comprises the geographically closest population of *Hydrochoerus* to the new California species, and presumably to any as yet undiscovered geographically intermediate forms in Central America.

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