

Description of the *Nechoerus* specimens from the late Pleistocene (Rancholabrean) of Chiapas, and comments on the taxonomic identity of the fossil capybaras from other Mexican localities

Descripción de especímenes de Nechoerus del Pleistoceno (Rancholabreano) tardío de Chiapas, y comentarios sobre la taxonomía de los capibaras fósiles de otras localidades mexicanas

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ABSTRACT

The capybara *Nechoerus aesopi* is an extinct giant rodent that inhabited North, Central, and South America during the Rancholabrean/Lujanian (late Pleistocene). In Mexico, only *N. aesopi* has been reported from Tlapacoya, Mexico State; Chapala lake, Jalisco; and La Cinta-Portalitos, on the border of Michoacán and Guanajuato. Here, we describe *N. aesopi* remains from the late Pleistocene at Los Mangos locality, Villaflores municipality, Chiapas, Mexico. In addition, the capybara material from Jalisco and Puebla, referred as *Hydrochoerus* sp. and *Nechoerus* sp., respectively, is reexamined. The mandibular and dental morphological characteristics and measurements of the specimens examined from Jalisco and Puebla allow this material to be referred as *N. aesopi*. The definitive identification of this species broadens its spacial range in North America.

Keywords: Capybara, *Nechoerus*, *Hydrochoerus*, taxonomy, Pleistocene, Mexico.

RESUMEN

El capibara *Nechoerus aesopi* es un roedor gigante extinto que habitó Norte, Centro y Sudamérica durante el Rancholabreano/Lujaniano (Pleistoceno tardío). En México, sólo *N. aesopi* ha sido reportado para Tlapacoya, Estado de México; el lago de Chapala, Jalisco y La Cinta-Portalitos, en los límites de Michoacán-Guanajuato. Aquí describimos los restos de *N. aesopi* encontrados en los sedimentos del Pleistoceno tardío que afloran en la localidad Los Mangos, en el Municipio de Villaflores, Chiapas, México. También, reexaminamos el material de capibaras de Jalisco y Puebla (referido como *Hydrochoerus* sp. y *Nechoerus* sp., respectivamente). Las características morfológicas mandibulares y dentales, así como las medidas de los especímenes examinados de Jalisco y Puebla permiten referirlos también como *N. aesopi*. La identificación definitiva de esta especie amplía su rango geográfico en América del Norte.

Palabras clave: Capibara, *Nechoerus*, *Hydrochoerus*, taxonomía, Pleistoceno, México.

1. Introduction

The capybaras (Rodentia: Caviidae: Hydrochoerinae) are large rodents that lived in North and South America from the Miocene to the recent. Only two genera are known from the late Pleistocene, *Hydrochoerus* and *Nechoerus* (Kurtén and Anderson, 1980). *Hydrochoerus* is represented by two living species: *H. hydrochaeris* and *H. isthmius*. Today, *Hydrochoerus hydrochaeris* inhabits Venezuela, Brazil, Paraguay, Uruguay, and eastern Colombia. It also inhabits the Amazon basin of Ecuador, Peru, and Bolivia, as well as northeastern to southern Argentina (Mones and Ojasti, 1986). The species has a late Pleistocene fossil record from Curaçao, Uruguay, Brazil, and Argentina (Mones, 1991; Kerber and Ribeiro, 2011) and *Hydrochoerus isthmius* inhabits Panama, western Colombia, and western Venezuela (Woods and Kilpatrick, 2005) and does not have a fossil record. Only two species of *Hydrochoerus* are represented in the fossil record: *H. ballesterensis* from late Pliocene to early Pleistocene of the Villa Ballester, Argentina (Mones, 1991), and *H. gaylordi* from late Pliocene to early Pleistocene of Grenadines Bank, island of Grenada, Lesser Antilles island-arc (MacPhee *et al.*, 2000).

Nechoerus is an extinct genus closely related to *Hydrochoerus* (Vucetich *et al.*, 2014), with a fossil record throughout the late Pliocene to the late Pleistocene of North and South America (Mones, 1991). *Nechoerus* was erected by Hay (1926) for the species *Hydrochoerus pinckneyi*, which he described based on a single M3 (third upper molar) from the Pleistocene of South Carolina (Hay, 1923).

Currently, six species are recognized: (i) *Nechoerus occidentalis* from Blancan-Irvingtonian (late Pliocene–early Pleistocene) of Sonora and Jalisco (Carranza-Castañeda, 2016); (ii) *N. cordobai* from Blancan III (early Pliocene) of Guanajuato (Carranza-Castañeda, 2016), referred as *Phugatherium dichroplax* by Vucetich *et al.* (2015); (iii) *N. tarijensis* from Ensenadian (middle Pleistocene) of Tarija,

Bolivia; (iv) *N. fontanai* from late Pliocene to early Pleistocene of Villa Ballester, Buenos Aires, Argentina (although Mones [1991] considered it a *nomen dubium*); (v) *N. sulcidens* from the Lujanian (late Pleistocene) of Brazil and Uruguay; and (vi) *N. aesopi* from the Rancholabrean/Lujanian (late Pleistocene) of North, Central, and South America (Mones, 1991; Lucas *et al.*, 2008). Occasionally, *N. pinckneyi* from South Carolina, USA (Hay, 1923, 1926) has been considered valid by some authors (*e.g.*, Álvarez, 1969; Kurtén and Anderson, 1980; Rufolo, 1998; Carranza-Castañeda, 2016), but it was considered a synonymy of *N. aesopi* by Mones (1991), because both taxa came from the same locality.

The only North American Rancholabrean species, *N. aesopi*, has been described in Mexico from Tlapacoya, Mexico State (referred to as *N. pinckneyi*; Álvarez, 1969); La Cinta-Portalitos locality, on the border of Michoacán and Guanajuato; and Chapala lake, Jalisco (Lucas, 2008; Eng-Ponce, 2018). Other records of the genus include *N. cordobai* from the Blancan to Irvingtonian of Guanajuato (Carranza-Castañeda and Miller, 1988), and *N. occidentalis* from Irvingtonian of Jalisco and Sonora (Carranza-Castañeda *et al.*, 1981; Shaw, 1981; Shaw and McDonald, 1987; Carranza-Castañeda, 2016). In addition, specimens referred to *Hydrochoerus* from the late Pleistocene of Media Luna lagoon, San Luis Potosí; Térapa, Sonora; Chapala lake, Jalisco; and Valsequillo, Puebla (Hernández-Junquera, 1977; Pichardo, 1997; Mead *et al.*, 2006; Carranza-Castañeda, 2016), and indeterminate hydrochoerids from Los Tanques, Zacatecas (Lozano-Ramos *et al.*, 2006) have been reported. The fossil record of capybaras in Mexico is poorly known. Therefore, the aim of this work is to formally describe the capybaras specimens recovered from Chiapas state, adding the first locality with these rodents in south-southeastern Mexico. We also comment on the taxonomic identity of the late Pleistocene capybara specimens from other localities in Mexico.

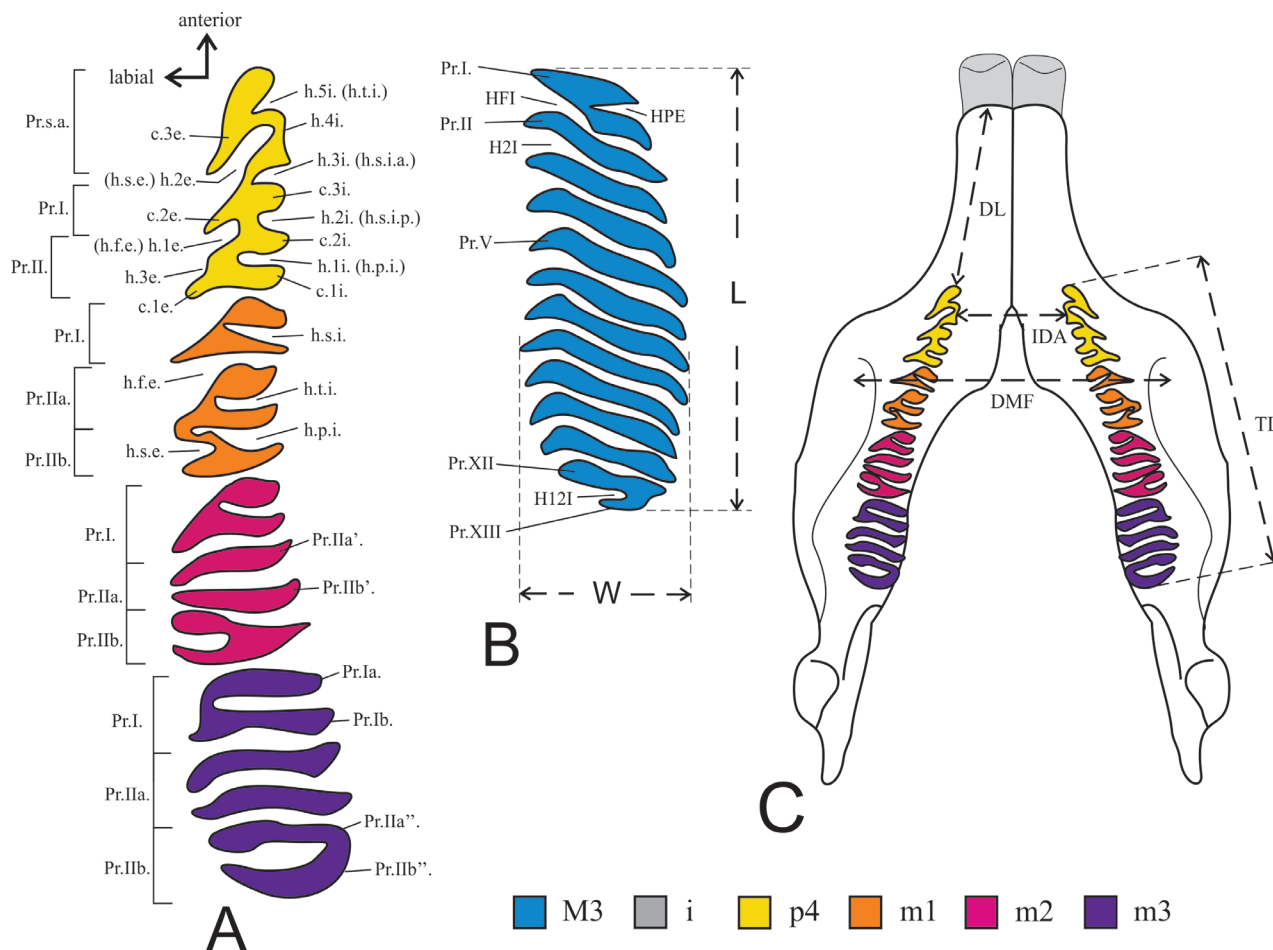


Figure 2 Nomenclature of the lower (A) and upper teeth (B), modified from Mones (1991), and some mandible measurements (C) taken from Carranza-Castañeda (2016). Dental abbreviations: i, lower incisor; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3: third lower molar; M3, third upper molar; h.1-5i., first-fifth internal fissure; h.1-3e., first-third external fissure; c.1-3e., first-third external column; c.1-3i., first-third internal column; h.s.e., secondary external fissure; h.f.e., fundamental external fissure; h.t.i., tertiary internal fissure; h.s.i., secondary internal fissure; h.s.i.a., anterior secondary internal fissure; h.s.i.p., principal secondary internal fissure; h.p.i., primary internal fissure; HFI, fundamental internal fissure; H2-12I, second-twelfth internal fissure; HPE, principal external fissure; Pr.I, first prism; Pr.II, second prism; Pr.V, fifth prism; Pr.XII, twelfth prism; Pr.XIII, thirteenth prism; Pr.s.a., secondary anterior prism of p4; Pr.Ia-Pr.Ia', anterior plate of first prism; Pr.Ib-Pr.Ib', posterior plate of first prism; Pr.IIa-Pr.IIa', anterior plate of second prism; Pr.IIb-Pr.IIb', posterior plate of second prism. Measurements abbreviation: L, length; W, width; DL, diastema length; TL, toothrow length; IDA, internal distance between the alveoli of p4; DMF, distance of the masseteric fossa through the Pr.I of the m1.

incisives preserved; IHNFG-4873, left hemi-mandible with an incisor, p4 and m1; IHNFG-5760, occipital part of the skull; and IHNFG-5761, a pelvic girdle. Specimens were recovered using the traditional vertebrate paleontology methods, and cleaned with needles, airscribe, and soft bristle brushes to remove sediment. The broken parts were joined with commercial glue insoluble to water, and the fissures were filled with epoxy clay. Specimens are housed at Paleontological

Collection of the Paleontological Museum “Eliseo Palacios Aguilera”, Secretaría de Medio Ambiente e Historia Natural, Chiapas, Mexico.

3.2. NOMENCLATURE

We use the nomenclature for upper and lower dentition of capybaras (Figure 2) proposed by Mones (1975a, 1991), adapted and used by other authors (e.g. Kerber and Ribeiro, 2011; Vucetich

et al., 2015; Carranza-Castañeda, 2016). Upper and lower dentition are identified by uppercase and lowercase letters, respectively (*e.g.*, M1, m1). For the cranial, mandibular and postcranial elements the nomenclature was based on König and Liebich (2007), Bode *et al.* (2013) and Brombini *et al.* (2018). In the text, we employ the name *Nechoerus cordobai* because it is the first name used in the original description (see Carranza-Castañeda and Miller, 1988). Carranza-Castañeda (2016) used the name *N. cordobae* and did not explain the reason for the change of the taxonomic name, and there is no previous work where modifications in the nomenclature are discussed.

3.3. MEASUREMENTS AND PHOTOGRAPHS

The measurements were obtained with a digital caliper with 0.01 mm accuracy following Mones (1991) and Carranza-Castañeda (2016), as shown in Figure 2. The measurements of *Nechoerus pinckneyi*, *N. aesopi* (mean), *N. sulcidens* (mean), *N. tarijensis* (mean), *N. cordobai*, *N. occidentalis*, and *Hydrochoerus hydrochaeris* used for comparison were obtained from the literature (Carranza-Castañeda and Miller, 1988; Mones, 1991; Sanders, 2002; Kerber and Ribeiro, 2011; Carranza-Castañeda, 2016). The measurements of *N. occidentalis* from Sonora were obtained from the figures presented in Carranza-Castañeda (2016) using ImageJ software (Rasband, 2012). The comparative bivariate plots were elaborated in JMP version 8 (SAS, 2008), using the measurements of Appendix 1 and 2 (Supplementary Material).

The photographs were taken with a digital camera Canon XS, using a lightbox and indirect lighting. Later, the images were processed in Adobe Illustrator to erase the background. The final figures were made in CorelDraw X8.

3.4. INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; AWC, Arizona Western College, Arizona, USA; IHNFG, Instituto de Historia

Natural, Fósil Geográfico, Chiapas, Mexico (historically is the acronym for the Paleontological Collection of the Secretaría de Medio Ambiente e Historia Natural, Chiapas, Mexico); INAH, Instituto Nacional de Antropología e Historia, Ciudad de Mexico, Mexico; MCN-D, Museu de Ciências da Pontificia Universidade Católica do Rio Grande do Sul, Uruguaiana, Brazil; MCN-PV, Coleção de Paleovertebrados do Museu de Ciências da Pontificia Universidade Católica do Rio Grande do Sul, Uruguaiana, Brazil; MCPV, Museu de Ciências da Pontificia Universidade Católica do Rio Grande do Sul, Uruguaiana, Brazil; MCPV-PV, Coleção de Paleovertebrados do Museu de Ciências da Pontificia Universidade Católica do Rio Grande do Sul, Uruguaiana, Brazil; MCPV-M, Coleção de Mastozoologia do Museu de Ciências da Pontificia Universidade Católica do Rio Grande do Sul, Uruguaiana, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MPGJ, Museo de Paleontología Geociencias, Querétaro, Mexico; TMM, Jackson School of Geosciences, Vertebrate Paleontology Laboratory, The University of Texas at Austin, Texas, USA.

4. Results

4.1. SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Orden RODENTIA Bowdich, 1821
 Infraorder Hystricognathi Tullberg, 1899
 Family Caviidae Fischer, 1817 *sensu* Waterhouse, 1839
 Subfamily Hydrochoerinae (Gray, 1825) Gill, 1872

Genus *Nechoerus* Hay, 1926
Nechoerus aesopi (Leidy, 1853)

Holotype. Fragment of the incisive (position indeterminate), described as *Oromys aesopi*, collected by Prof. Holmes on the Ashley River, Charleston, South Carolina, USA (Leidy, 1853). Housed at the AMNH under the catalog number FM 485.

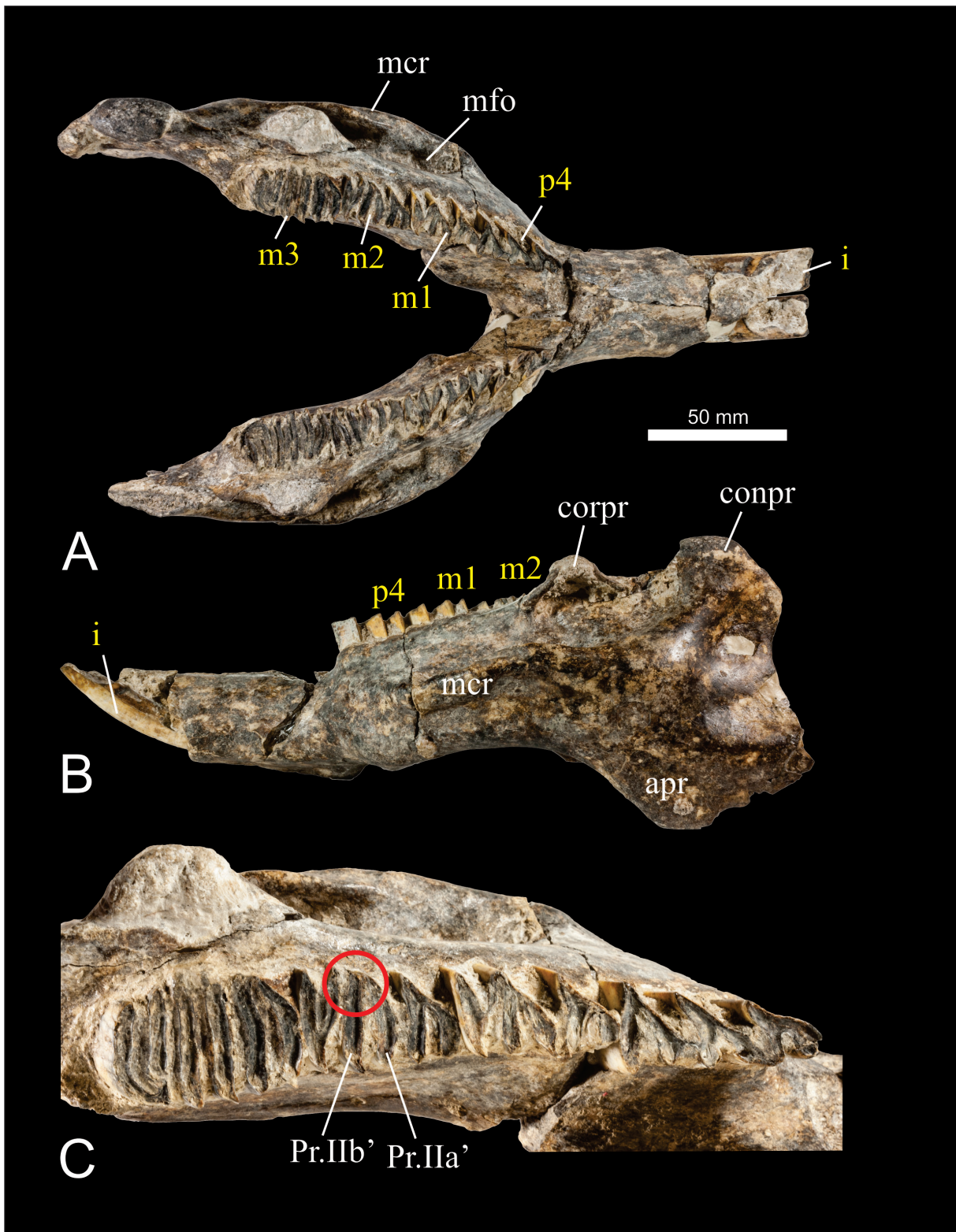


Figure 3 IHNFG-4866, nearly complete mandible from Los Mangos locality, Villaflores, Chiapas, in occlusal (A) and left lateral (B) view. Detail of the left tooththrow in occlusal view (C); the red circle indicates the unusual union between the Pr.IIa' and Pr.IIb'. Abbreviations: apr, angular process; conpr, condylar process; corpr, coronoid process; mcr, masseteric crest; mfo, masseteric fossa. Dental abbreviations as in Figure 2.

Synonymy. *Oromys aesopi* (Leidy, 1853); *Hydrochoerus aesopi* (Leidy, 1856); *Hydrochoerus magnus* (Gervais and Ameghino, 1880); *Hydrochoerus robustus* (Leidy, 1887); *Hydrochoerus holmesi* (Simpson, 1928); *Neochoerus magnus* (Kraglievich, 1930); *Neochoerus robustus* (Kraglievich, 1930); *Prohydrochoerus sirasakae* (Spillmann, 1941); *Protohydrochoerus schirasakae* [sic] (Spillmann, 1948); *Neochoerus* (*Neochoerus*) *sirasakae* (Hoffstetter, 1952); *Neochoerus sirasakae* (Mones, 1975b); *Neochoerus pinckneyi* (Mones, 1991).

4.2. DESCRIPTION

IHNFG-4866 is a nearly complete mandible. However, the right condylar and angular process are missing (Figures 3A and 3B). Both tooth rows are complete and included the p4-m3. The diastema length (DL) is shorter (nearly 90 mm) than the toothrow length (TL: 100.5 mm in the left toothrow, 110 mm in the right toothrow). The internal distance between the alveoli of the p4 (IDA) in its lingual portion is 34 mm. The masseteric crest is robust and more retracted than in *Hydrochoerus hydrochaeris* and begins below the Pr.I (first prism) of p4. The masseteric fossa in the two portions of the mandible is located below the Pr.I of the m1 and the distance of the masseteric fossa (DMF) through the Pr.I of the m1 is 97 mm.

Like in all rodents, the lower incisors lack enamel in their lingual portion (Hillson, 2005). They are robust and have an anteromedial canal with longitudinal grooves in the labial portion. The alveolus of the incisors extends below the h.s.i. (secondary internal fissure) of the m1. Both p4 show the Pr.s.a. (secondary anterior prism), Pr.I and Pr.II are joined by a small enamel bridge. The h.4i. (fourth internal fissure) is not present and the h.2e. (second external fissure) extends to more than 90% of the total width of the prism. The junction of Pr.I and Pr.II is flanked by h.1e. (first external fissure) in the labial portion and in the lingual portion by the h.s.i.p. (principal secondary internal fissure) leaving a narrow enamel bridge. The Pr.s.a. has a Y shape like the Pr.I, while Pr.II

has a V shape. The length of the p4 is greater than the length of the m2, this feature is characteristic of *N. aesopi* (Mones, 1991).

The m1 presents the Pr.IIa joined to Pr.IIb in the labial portion by a thin bridge of enamel; the h.p.i. (primary internal fissure) is deep, exceeding 90% of the width of the prisms but does not separate them. The Pr.I and Pr.IIb are Y shape, while the Pr.IIa are V shape. Both m2 possess complete Pr.Ia and Pr.IIb. On the left molar the h.t.i. (tertiary internal fissure) does not divide the Pr.IIa into Pr.IIa' (anterior plate of the second prism) and Pr.IIb' (posterior plate of the second prism) and maintain the union of the enamel bridge in the labial portion (Figure 3C). This feature has been observed in juveniles and young adults of *H. hydrochaeris*, but it is a rare feature in adults (Mones, 1975a) and cannot be seen in the right m2 because that area is damaged. The right m3 has the Pr.I divided into two plates; the Pr.IIb has an abnormal widening making the h.s.e. shorter. The left m3 has a complete Pr.I; the h.s.i. exceeds 90% of the total width and the h.s.e. is deep, exceeding 90% of the width of the molar. The complete prisms have a V shape.

IHNFG-4865 is a right maxillary fragment with the M3 (Figure 4A). It is composed of 16 prisms of which Pr.I is incomplete in its mesial portion and Pr.XVI is represented only by a fragment of enamel laminae. The length of the M3 is 59.12 mm and the width is 20.67 mm. The prisms in the mesial portion are robust and tend to thin out at their distal portion.

IHNFG-4873 corresponds to the anterior portion of the left hemimandible of a juvenile with incisor, p4, m1, and an associated unidentified upper molar fragment (Figures 4B and 4C). The specimen preserves the distal portion of the masseteric crest and the masseteric fossa is located below the Pr.II of m1. It retains most of the incisor, which presents the anteromedial groove and poorly marked longitudinal striations. The p4 shows the Pr.s.a. and Pr.I in Y shape while Pr.II has V shape. The Pr.s.a. is similar to the adult

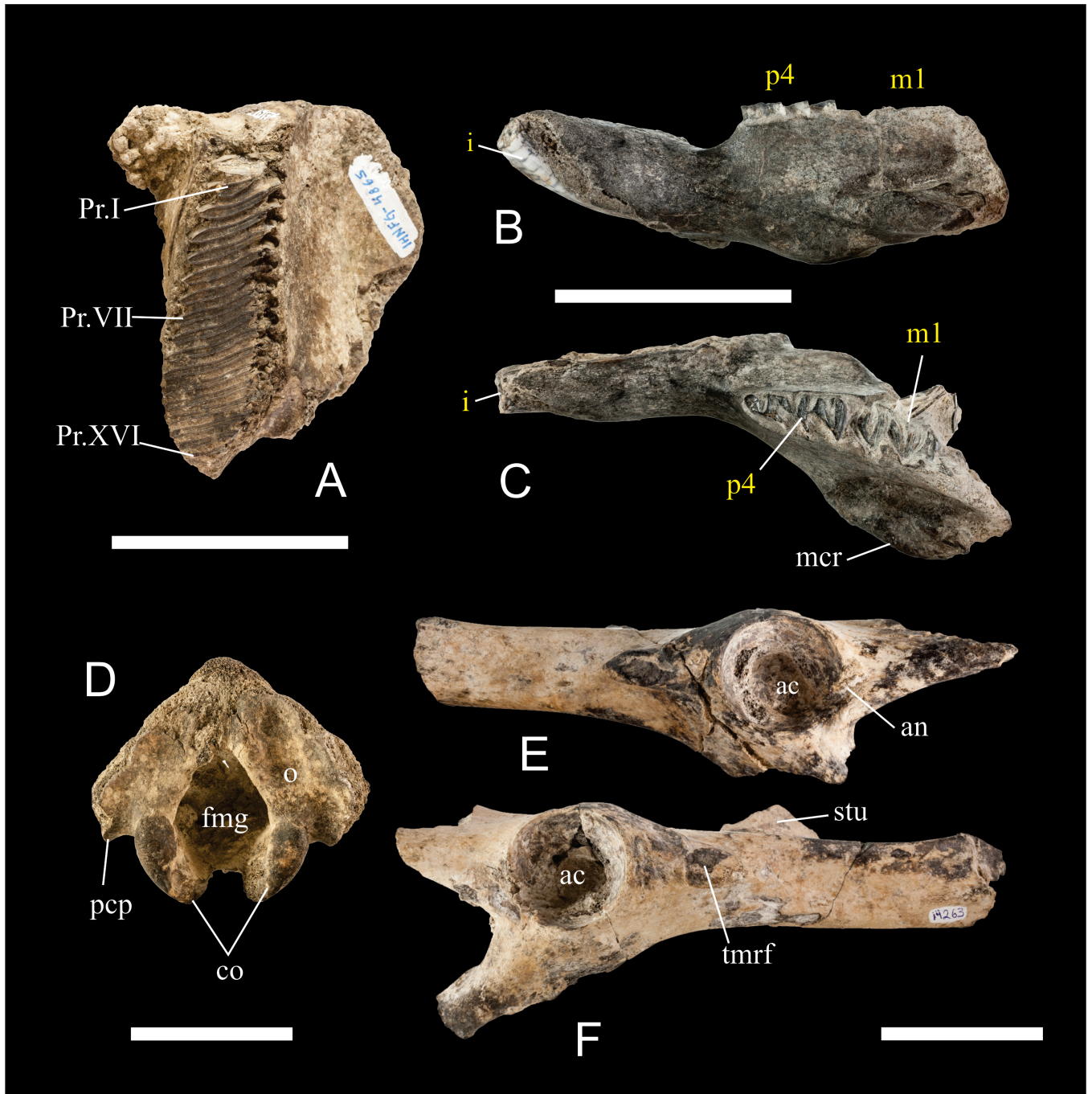


Figure 4 Dental, cranial and postcranial material of *Nechoerus aesopi* from Los Mangos locality, Villaflores, Chiapas. IHNFG-4865, right M3 in occlusal view (A); IHNFG-4873, left hemimandible in lateral (B) and occlusal (C) views; IHNFG-5760, parietal (D); IHNFG-5761, pelvic girdle (E and F). Bar scale in all cases equal to 50 mm. Abbreviations: ac, acetabulum; an, acetabular notch; co, condyle; fmg, foramen magnum; mcr, masseteric crest; o, occipital bone; pcp, paracondylar process; stu, sacral tuberosity; tmrf, tuberosity for the m. rectus femoris. Dental abbreviations as in Figure 2.

specimen with the exception of the h.5i. (fifth internal fissure), which is deeper. The h.4i. is little marked and, like the adult, the union between Pr.I and Pr.II is very thin. Only the shape of the prisms can be observed in the m1 and, unlike the adult specimen, the Pr.I and Pr.IIa have a V shape and Pr.IIb has a Y shape.

IHNFG-5760 is an occipital portion of the skull (Figure 4D) and is similar to the occipital of *Hydrochoerus hydrochaeris*. The occipital bone is almost flat, with a smooth depression in each side of the foramen magnum. The condyles are thin and border the lower part of the foramen magnum. The foramen magnum is oval in shape. The paracondylar processes are small and are at the level of the upper end of the occipital condyle.

IHNFG-5761 is a pelvic girdle partially conserved and resembles the pelvis of the extant capybara *H. hydrochaeris*. In ventral view, the hip bones are elongated and narrow and with an Y shape. The ilium is straight. The distal part of both ilium is missing but it is notorious that the ilium wing lay in a sagittal plane. The upper side of the body of the right ilium preserves the proximal part of the sacral tuberosity, which is thin in lateral-medial direction. The body of the ilium bears a prominent tuberosity for the *m. rectus femoris*. Only the iliopubic eminence of the ilium is preserved. The pubis is not preserved and is only observed as part of the branch of the pubis. The acetabulum is deep and circular in shape, with a smooth acetabular notch located in the posterior margin (Figure 4E).

5. Discussion

5.1. TAXONOMIC ASSESSMENT

The *Nechoerus* genus can be distinguished from the close relative *Hydrochoerus* by the following: *Nechoerus* is almost twice as large; the rostrum is longer; the anterior portion of the zygomatic arc is more rounded and oriented backward; the anterorbital bar and lacrimal are more robust; the skull roof is wider; the supraoccipital is wider and more

excavated; the masseteric crest is retracted; the coronoid process is greatly reduced; and the M3 has 14 to 17 prisms, while *Hydrochoerus* has 12–13 prisms (Mones, 1991; Flynn, 2008). In the mandible IHNFG-4866, the masseteric crest is retracted and the coronoid process is slightly elevated, while in the M3 IHNFG-4865 16 prisms are observed. In addition, the measurements of IHNFG-4865 and IHNFG-4866 fall within the observed range of *Nechoerus* (Figures 5A and 5B). All these characteristics allow us to assign the fossil material from Chiapas to the genus *Nechoerus*.

The North American species in the genus *Nechoerus* can be differentiated by its size and dental morphology. In the oldest species, *N. cordobai* and *N. occidentalis*, the central laminas of the M3 bear small invaginations in the labial side (Carranza-Castañeda and Miller, 1988; Carranza-Castañeda, 2016), called extraordinary external fissures (Mones, 1991). Apparently, this feature is a primitive dental character in the capybaras, because it is also present in the M3 of the Pliocene taxa *Phugatherium*, “*Chapalmatherium*” and *Hydrochoeropsis* (Deschamps *et al.*, 2013; Vucetich *et al.*, 2014). This dental morphological characteristic is not present in the M3 of *N. aesopi*.

Another difference between *N. cordobai*, *N. occidentalis*, and *N. aesopi* is observed in the DL. The DL in *N. cordobai* and *N. occidentalis* is between 60 and 70 mm, while in *N. aesopi* it is 70–90 mm. In specimen IHNFG-4865, the M3 does not have the extraordinary external fissures on the laminas like *N. aesopi*. In the same way, the mandible of IHNFG-4866 has a DL of 90.05 mm, longer than the DL of *N. cordobai* and *N. occidentalis*, falling into the range of *N. aesopi*.

5.2. HYDROCHOERUS IN MEXICO?

Material of capybaras from Chapala lake, Jalisco; Terapa, Sonora; Media Luna lagoon, San Luis Potosí; and Valsequillo, Puebla, have been referred to *Hydrochoerus* (Álvarez, 1971; Hernández-Junquera, 1977; Pichardo, 1997; Mead *et al.*, 2006; Carranza-Castañeda, 2016).

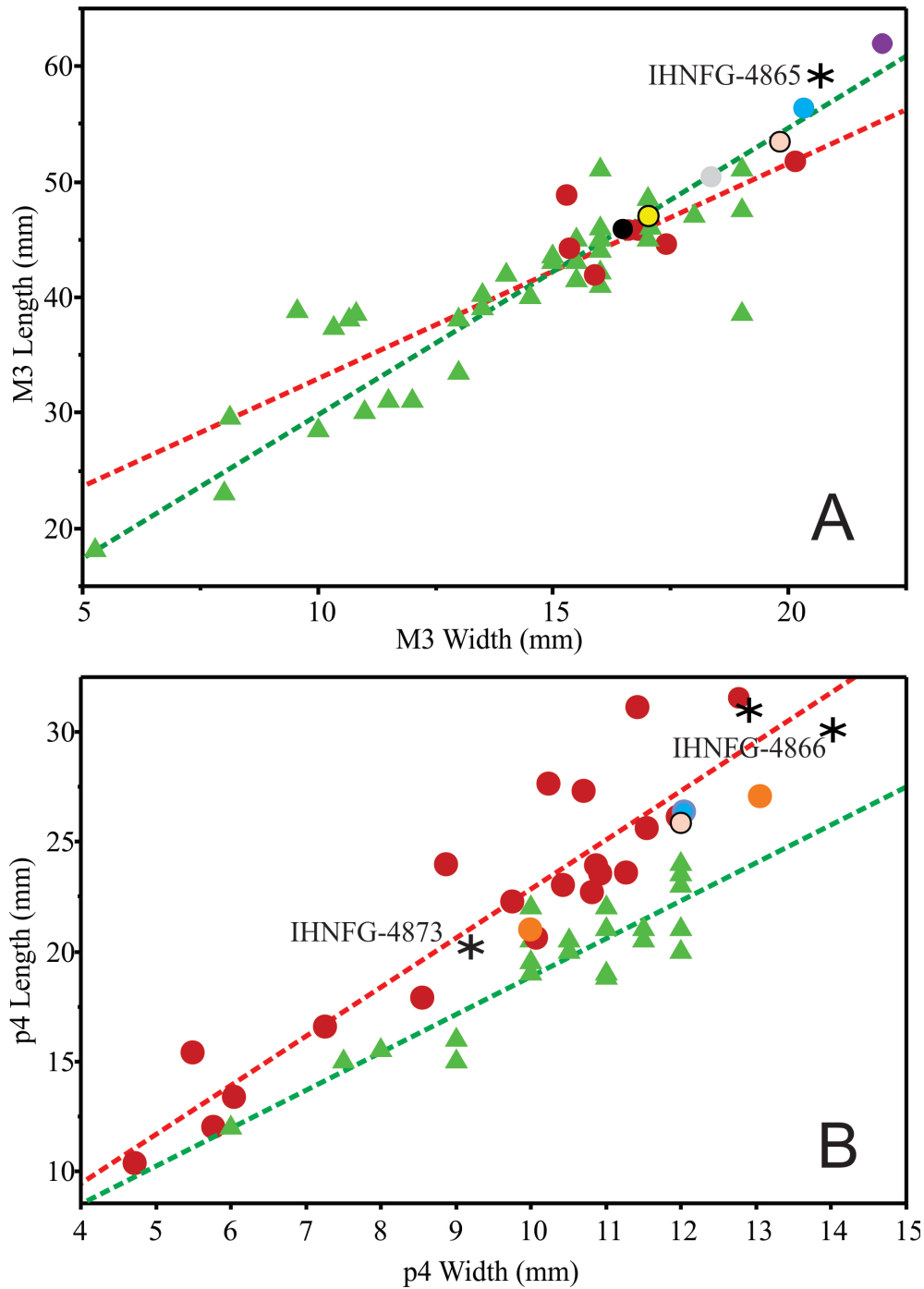


Figure 5 Bivariate plot of M3 and p4 measurements. Black asterisks: *Neochoerus aesopi* from Villaflores, Chiapas; red dots: *N. aesopi* from Chapala Lake, Jalisco (INAH, Mexico City, not catalogued); black dot: *N. aesopi* from Valsequillo, Puebla (INAH CDMX, “66-I; Y-I”); purple dot: *N. pinckneyi* (= *N. aesopi*, Sanders, 2002); blue dots: *N. aesopi* mean (Mones, 1991); pink dots: *N. sulcidens* mean (Mones, 1991); gray dot: *N. tarijensis* mean (Mones, 1991); yellow dot: *N. cordobai* (Carranza-Castañeda and Miller, 1988); orange dots: *N. occidentalis* (Carranza-Castañeda, 2016); green triangles: *Hydrochoerus hydrochaeris* (Kerber and Ribeiro, 2011). Red lines: trend of the genus *Neochoerus*; green lines: trend of the genus *Hydrochoerus*.

5.2.1. SPECIMENS FROM CHAPALA LAKE

Álvarez (1971) referred the specimens from Chapala lake as *Hydrochoerus*. Recently, Carranza-Castañeda (2016) reviewed this material and mentioned that some specimens have characteristics of *Hydrochoerus*, and referred the specimens labeled with the numbers 78 and 126 as *Hydrochoerus* sp. (fig. 9, p. 310). Nevertheless, a review of these specimens from Chapala (housed at the Laboratorio de Arqueozoología, INAH), by one of the authors (JEP) showed that these specimens have the *Neochoerus* mandibular characteristics mentioned by Mones (1991) that allows the differentiation of *Neochoerus* from *Hydrochoerus*. Such differences are more evident in the DL and the TL. In *H. hydrochaeris* the range of the DL is 35–52.1 mm, while in *H. isthmus* it is 34.6–41.7 mm (Mones, 1991). In *Neochoerus* the DL has a longer range (60–90 mm).

In the same way, in the *Neochoerus* species, the TL range is between 90 and 112 mm (*N. cordobai* = 112 mm, *N. aesopi* = 90–110 mm, *N. sulcidens* = 102.6 mm, *N. tarijensis* = 101 mm), while in *Hydrochoerus* the TL range is 61.5–91.4 mm (*H. hydrochaeris* = 64–91.4 mm, *H. isthmus* = 61.5–71.5 mm) (Mones, 1991). Specimen 78 from Chapala has a DL of 71.97 mm and a TL of 99.26 mm, measurements within the range of *Neochoerus*. Additionally, the masseteric crest begins between the Pr.s.a and the Pr.I (like in *Neochoerus*), while in *Hydrochoerus* it begins in the anterior part of the Pr.s.a. On the other hand, specimen 126 has a DL of 40.3 mm and a TL of 89.87 mm, measurements within the range of *Hydrochoerus*. However, the p4 length is greater than the m2 length, and the masseteric crest begins in the posterior part of the Pr.s.a, characteristics of *N. aesopi* (Mones, 1991). The DL and TL measurements of the specimen are indicative of one young individual.

The M3 also exhibits differences between *Neochoerus* and *Hydrochoerus*. Although the general morphology is similar, the number of prisms varies. In *Neochoerus*, the number of prisms is 14 to 17, while in *Hydrochoerus* it is 12 to 13 (Mones, 1991;

Flynn, 2008). In some individuals from Chapala, the M3 has 14 prisms (also mentioned by Carranza-Castañeda, 2016), which allows assigning the specimens to *Neochoerus*. The size of the M3 in some specimens from Chapala falls into the range of *Hydrochoerus*, whereas the taxonomic assignation to *Neochoerus* or *Hydrochoerus* is difficult (Figure 5A).

However, the variation in the size of the teeth of capybaras is a consequence of age, which does not affect significantly the morphological characteristics (Vucetich *et al.*, 2005). Therefore, the small size of some individuals is the result of age, and not due to specific differentiation.

The bivariate plot of the p4 (Figure 5B) shows that the size of this molar is more informative and a better indicator for *Neochoerus* to *Hydrochoerus* differentiation, although it is the most morphologically variable tooth (Álvarez, 1971).

Finally, the presence of *Hydrochoerus* in Chapala lake is rejected, because the coexistence of two or more species with the same ecological requirements within the same area is not possible.

5.2.2. THE CAPYBARA FROM VALSEQUILLO, PUEBLA

Hydrochoerus remains have been reported from Valsequillo, Puebla (Pichardo, 1997). However, these remains have not been illustrated. Later, Pérez-Crespo *et al.* (2014, 2019) mentioned the presence of *Neochoerus* sp. in Valsequillo. However, they are not specific on the basis of the taxonomic assignment.

The examination of the incomplete skull from Valsequillo (housed at Laboratorio de Arqueozoología, INAH, labeled with the number “66-I; Y-I”) allow us to assign this specimen to *Neochoerus aesopi*. The taxonomic assignation is based on the morphological characteristics of the skull and the M3. The skull roof is wider than *Hydrochoerus*, with the supraoccipital wider and more excavated; lacrimal more robust and higher, and the M3 with 15 laminae, and these without extraordinary external fissures. The size of M3 indicates that this specimen is from a juvenile (Figure 5A).

5.2.3. HYDROCHOERUS FROM TÉRAPA AND MEDIA

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Fossil remains of capybaras from Térapa have been referred to *Hydrochoerus* sp. (Mead *et al.*, 2006) and Hydrochoeridae indeterminate (Nunez *et al.*, 2010). However, this material has never been described or illustrated. Unfortunately, the repository of these fossils is not mentioned and therefore a revision is not possible. Further, the fossil of capybaras from Media Luna lagoon, San Luis Potosí, assigned as *Hydrochoerus* sp. (Hernández-Junquera, 1977), was never formally deposited in a museum and is now missing (Ferrusquía-Villafranca, 2018, pers. com.). Nevertheless, we do believe that the capybaras from Térapa and Media Luna lagoon are *Nechoerus*, and, considering the temporal range (late Pleistocene, Rancholabrean) assigned for both faunas, it is possible to refer this material as *N. aesopi*.

Such affirmation is based upon two assumptions: (1) Mones (1984) considered that the reports of *Hydrochoerus* in North America are misidentifications of *Nechoerus*, and (2) the review of the specimens from Chapala and Valsequillo, identified as *Hydrochoerus*, showed that they are actually *Nechoerus*.

5.3. PALEOECOLOGICAL SIGNIFICANCE

The paleoecological aspects of the extinct capybaras have been inferred by comparison with the extant species of *Hydrochoerus*. Recent capybaras are semiaquatic and live within lowlands habitats in the proximity of water, like forested riverbanks, former riverbeds, brackish wetlands, and mangrove swamps (Mones and Ojasti, 1986).

Fossil capybaras are usually recovered from fluvial, lacustrine or swampy deposits (Vucetich *et al.*, 2013), so the lifestyle related to water is supported. Therefore, the presence of *Nechoerus aesopi* in Los Mangos locality indicates the existence of permanent water bodies in the area during the late Pleistocene, which is consistent with the lithology

of the outcrops in the study locality. The feeding habits of *Nechoerus* can also be inferred through comparison with feeding habits of *H. hydrochaeris*.

Hydrochoerus hydrochaeris consumes grasses, aquatic plants, and occasionally bark, stems, and leaves (Ojasti, 1973). Recent observations show that *H. hydrochaeris* has preference for *Hymenachne amplexicaulis* (an aquatic grass) during the wet season, and feeds on *Eleocharis interstincta* (a reed) and *Paratheria prostrata* (a grass) during the dry season (Barreto and Quintana, 2013).

Based on the feeding habits of *H. hydrochaeris*, it is possible to infer that *N. aesopi* from Los Mangos locality fed on different types of grasses, reeds, and shrubbery. This assumption is supported by the microwear and stable isotopes analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ on *N. aesopi* from La Cinta-Portalitos, Michoacán-Guanajuato and Valsequillo, Puebla, and shows that some individuals have a mixed feeder diet based on C3/C4 plants and other individuals were C4 grazers (Pérez-Crespo *et al.*, 2014; Eng-Ponce *et al.*, 2017; Eng-Ponce, 2018). These data are similar to that obtained from *N. tarijensis* from Bolivia, species referred to as a C3/C4 mixed feeder (MacFaden and Shockey, 1997).

6. Conclusions

The formal description of the capybara fossil remains from Villaflores, Chiapas, allows us to confirm the specific taxonomy assignation as *Nechoerus aesopi*, which adds a new locality for this taxon in Mexico. It also documents the southernmost record, until now, for North America, and increases the spatial range of *Nechoerus* in the late Pleistocene.

The historical presence of *Hydrochoerus* in Chapala lake, Jalisco, and Valsequillo, Puebla, is rejected based upon the review of the specimens housed in Laboratorio de Arqueozoología, INAH, and confirms that the only species present in both areas is *Nechoerus aesopi*. In the same way, we refer

the capybaras from Térapa and Media Luna lagoon as *N. aesopi*. The presence of *N. aesopi* from Sonora to Chiapas allows us to hypothesize that this was the only capybara species present in the late Pleistocene of Mexico.

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Appendix 1. Dental measurements of *Neochoerus* and *Hydrochoerus* species.

Taxon	Collection number	p4 width (mm)	p4 length (mm)	m1 width (mm)	m1 length (mm)	m2 width (mm)	m2 length (mm)	m3 width (mm)	m3 length (mm)	Source	Notes
<i>Neochoerus aesopi</i>	IHNFG-4866	12.91	30.98	12.27	24.4	16.65	24.7	20.63	30.98	this work	Right tooth row
<i>Neochoerus aesopi</i>	IHNFG-4866	14.02	30.1	13.01	23.57	17.65	23.26	21.51	28.25	this work	Left tooth row
<i>Neochoerus aesopi</i>	IHNFG-4875	9.2	20.21	10.09	17.16	-	-	-	-	this work	Juvenile specimen
<i>Neochoerus aesopi</i>	Without number	12.03	26.38	12.95	24.82	20.33	24.52	17.2	29.15	Mones (1991)	Mean
<i>Neochoerus aesopi</i>	99	7.26	16.57	-	-	-	-	-	-	INAH Mexico City	
<i>Neochoerus aesopi</i>	100	8.55	17.92	-	-	-	-	-	-	INAH Mexico City	
<i>Neochoerus aesopi</i>	101	12.77	31.54	-	-	-	-	-	-	INAH Mexico City	
<i>Neochoerus aesopi</i>	102	11.42	31.14	-	-	-	-	-	-	INAH Mexico City	
<i>Neochoerus aesopi</i>	103	10.7	27.32	-	-	-	-	-	-	INAH Mexico City	
<i>Neochoerus aesopi</i>	105	11.95	26.13	-	-	-	-	-	-	INAH Mexico City	
<i>Neochoerus aesopi</i>	249	-	-	-	-	-	-	18.24	26.29	INAH Mexico City	
<i>Neochoerus aesopi</i>	259	-	-	-	-	-	-	19.39	26.95	INAH Mexico City	
<i>Neochoerus aesopi</i>	273	-	-	-	-	-	-	18.73	28.67	INAH Mexico City	
<i>Neochoerus aesopi</i>	PN-08	-	-	-	-	-	-	17.47	23.79	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-09	11.27	23.59	11.8	21.13	15.95	23.25	18.93	28.85	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-10	10.86	23.91	11.66	21.96	15.62	22.92	17.65	24.5	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-11	11.54	25.65	12.11	21.49	18	24.21	20.84	27.14	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-12	10.23	27.66	10.97	23.07	15.09	22.01	17.71	26.8	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-13	10.81	22.69	11.46	20.69	15.13	22.08	18.19	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-14	9.75	22.28	10.78	17.7	13.59	20.65	16.77	23.54	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-15	8.87	23.99	12.04	21.06	-	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-16	10.07	20.62	-	-	-	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-17	10.92	23.55	11.91	19.75	11.72	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-18	10.42	23.06	10.84	18.61	14.07	20.05	16.12	25.39	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-19	5.76	12.02	6.64	11.32	-	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-20	4.72	10.36	-	-	-	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-21	5.49	15.41	-	-	-	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus aesopi</i>	PN-22	6.04	13.37	-	-	-	-	-	-	INAH Mexico City	Not catalogued, PN = provisional number
<i>Neochoerus pinckneyi</i>	941 DP	-	-	-	-	16	24.2	-	-	INAH Mexico City	DP= Departamento de Prehistoria (Prehistory Department; Álvarez, 1969)
<i>Neochoerus tarijensis</i>	Without number	-	23.56	-	21.86	-	22.9	-	32.9	Mones (1991)	Mean
<i>Neochoerus sulcidens</i>	Without number	12	25.87	13.4	21.3	17.5	25	21.4	30.5	Mones (1991)	Mean
<i>Neochoerus occidentalis</i>	MPGJ 2968	10	21	11	19	-	-	-	-	Carranza-Castañeda (2016)	
<i>Neochoerus occidentalis</i>	AWC 20369	13.2	26.9	14.1	23.1	16.5	23.6	-	-	Carranza-Castañeda (2016)	
<i>Neochoerus cordobai</i>	IGM 5836	14*	28*	13	26	14	28	22	30	Carranza-Castañeda and Miller (1988)	
<i>Neochoerus cordobai</i>	IGCU 5658	-	-	12	21	13	23	17	26	Carranza-Castañeda and Miller (1988)	
<i>Hydrochoerus hydrochaeris</i>	MCPU-PV-047	11.5	20.5	11	17.5	18.5	20	15	24	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCPU-M-041	11	22	12	20	15	20	16	23	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-PV 9573	10.5	20.5	11.5	18.5	13	20	16	24.5	Kerver and Ribiero (2011)	Fossil specimen
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2727	12	23.5	13	20	15	20	16	24	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3221	12	21	12.5	19	13.5	20	15.5	24	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2830	12	23	12	20	16.5	22	17.5	23	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2652	10	22	11	18.5	15	22.2	17	26.5	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2721	10	21	11	19	12	20	15	24	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 1691	10	20.5	11	20	14	18	15	22	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3222	12	24	25	21	16	22.5	18	26	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2812	10	19	11	17	13	18	14	22	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 1639	12	20	12.5	16.5	12.5	17	14	19	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3207	10	19.5	11.5	17.5	14	19	15.5	24	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3217	11	19	22	16.19	22	18.5	15	21	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2679	10	21	11	19	12	20	15	24	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3205	11	21	12	19	14	17	15	23	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3206	10.5	20	10	16	11	17.5	15	23.5	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3234	10.5	20	10	16	13.5	18	15	23	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3223	12	23	12.5	20.5	15	21.5	17	25	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3026	11	18.8	11	17	12.5	18	19	19	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3208	9	15	10	14.5	12	15	12	17	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3219	9	16	10	13.5	12	14	12	17	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2320	8	15.5	10	14	11	14	11	17.5	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3218	7.5	15	9	13	9.5	12	10	16	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 1766	6	12	6	10	7	11	8	14	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-D-0350	11.5	21	14	18.5	20	22.5	15	22	Kerver and Ribiero (2011)	

Appendix 2. Mandibular measurements of *Neochoerus* and *Hydrochoerus* species.

Taxon	Collection number	p4-m3 length (mm)	Diastema length (mm)	Source	Notes
<i>Neochoerus aesopi</i>	IHNFG-4866 (right)	110	90.05	this work	Right tooth row
<i>Neochoerus aesopi</i>	IHNFG-4866 (left)	100.5	90.05	this work	Left tooth row
<i>Neochoerus aesopi</i>	78 (INAH Jalisco)	99.26	71.97	Carranza-Castañeda (2016)	Measurements obtained with ImageJ
<i>Neochoerus aesopi</i>	126 (INAH Jalisco)	89.87	40.3	Carranza-Castañeda (2016)	Measurements obtained with ImageJ
<i>Neochoerus pinckneyi</i>	-	110	-	Carranza-Castañeda y Miller (1988)	
<i>Neochoerus cordobai</i>	IGM 5836	112	-	Carranza-Castañeda y Miller (1988)	
<i>Neochoerus occidentalis</i>	MPGJ 2968	-	69.98	Carranza-Castañeda (2016)	
<i>Neochoerus occidentalis</i>	AWC 20369	-	60.19	Carranza-Castañeda (2016)	Approximate measurement because the diastema is incomplete
<i>Hydrochoerus isthmius</i>	-	65.18	38.55	Mones (1991)	Mean
<i>Hydrochoerus hydrochaeris</i>	-	80.85	44.52	Mones (1991)	Mean
<i>Hydrochoerus hydrochaeris</i>	MCN-PV 9573	86	-	Kerver and Ribiero (2011)	Fossil specimen
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2727	86	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3221	79	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCPU-047	80.5	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2830	90	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2652	89	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2721	78	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 1691	80	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3222	90	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2812	75	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCPU-041	84	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 1639	75.9	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3207	76.5	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3217	76	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2679	78	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3205	78	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-D-0350	80	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3206	75	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3234	75	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3223	84.5	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3026	72	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3208	61	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3219	61	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 2320	59.8	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 3218	54	-	Kerver and Ribiero (2011)	
<i>Hydrochoerus hydrochaeris</i>	MCN-M 1766	48.5	-	Kerver and Ribiero (2011)	