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Megalonychid Sloths from the Early Late Hemphillian (Late Miocene), Curré Formation, San Gerardo de Limoncito, Costa Rica

Perezosos Megalonychidos del Hemphilliano Tardío Temprano (Mioceno Tardío), Formación Curré, San Gerardo de Limoncito, Costa Rica

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ABSTRACT: A reevaluation of the late Miocene (early late Hemphillian) megalonychid fossils found at San Gerardo de Limoncito, Coto Brus Valley, Costa Rica is presented. These specimens which had previously been referred to *Pliometanastes* cf. *P. protistus*, based on a partial mandible and associated teeth material are now considered to belong to the genus *Zacatzontli*, previously only known from the late Miocene of Mexico and here reported for the first time from Costa Rica. The material is considered to be a new species of *Zacatzontli* based on a comparison with the type and other members of the Megalonychidae from the Hemphillian of North America as *Zacatzontli tecolotlanensis*, *Pliometanastes protistus* and *Megalonyx* spp.

Keywords: Xenarthra; Megalonychidae; *Zacatzontli*; Late Miocene: Curré Formation; San Gerardo de Limoncito; Costa Rica.

RESUMEN: Se reevalúan los fósiles de Megalonychidae del Mioceno Tardío (Hemphilliano Tardío Temprano) de Costa Rica, procedentes de la localidad San Gerardo de Limoncito, Valle de Coto Brus. Los restos fósiles fueron inicialmente referidos a *Pliometanastes* cf. *P. protistus* con base en el material dental y mandibular. Estos son ahora asignados al género *Zacatzontli*, previamente conocido para el Mioceno tardío de México y que ahora se registra por primera vez para Costa Rica en América Central. El material es considerado como una nueva especie de *Zacatzontli*, basado en la comparación con otros Megalonychidae del Hemphilliano de América del Norte como *Zacatzontli tecolotlanensis*, *Pliometanastes protistus* and *Megalonyx* spp.

Palabras clave: Xenarthra; Megalonychidae; *Zacatzontli*; Mioceno Tardío; Formación Curré; San Gerardo de Limoncito; Costa Rica.

Introduction

The Megalonychidae is a distinctive family of sloths within the Order Xenarthra, which originated in South America. The earliest record of the Megalonychidae in South America comes from the late Oligocene (Deseadan, South American Mammal Age, SALMA, ca. 29-21 Ma) represented by a single taxon, *Deseadognathus riggsi* (Carlini & Scillato-Yane, 2004). However, a proximal femur referred to this family is also known from the early Oligocene of Puerto Rico (MacPhee & Iturralde-Vinent, 1995) suggesting the family had an earlier origin in South America which has not yet been documented. A record from the early Miocene, ca. 18.5 – 15.5 Ma of Cuba (MacPhee & Iturralde-Vinent, 1994, 1995; MacPhee et al., 2003) supports the idea that members of the family were good dispersers especially into the Antillean Islands, including the Greater, Lesser and Netherland Antilles, probably through GAARlandia (MacPhee & Iturralde-Vinent, 1995). The Cuban and Puerto Rican records indicate that megalonychid sloths had become established on multiple Caribbean Islands prior to their appearance in North America in the late Miocene (Hemphillian, North American Mammal "Age", NALMA), and survived there until the early Holocene (Steadman et al., 2005).

No megalonychids have been reported from the Colhuehuapian SALMA and it is not until the Early Miocene (Santacrucian SALMA Age, 17.5 – 16.3 Ma), that the family is again known based on the genera, *Eucholoeops* and *Megalonychotherium* (Bargo et al., 2012). The family is never diverse during most of the early Miocene, although multiple taxa have been described from the late Miocene Ituzaingó Formation of Entre Ríos Province, Argentina (Brandoni, 2011). Known taxonomic diversity is limited in the Pliocene but there is an increase in the number of genera during the Pleistocene, based on recently described new taxa from Brazil, Venezuela, and Mexico, complementing the previously known Antillean taxa.

A further indication of the beginning of increased taxonomic diversity within the family in South America is also seen in the Late Miocene formations (Huayquerian SALMA, 9-11 Ma) in the Urumaco desert in Venezuela. The evidence, although limited, suggests there are two different lineages within the Megalonychidae, one associated with the clade that dispersed into the Antilles (*Urumacocnus*) and another associated with the clade which dispersed into North America through Central America (*Pattersonocnus*) (Rincón et al., 2019).

Both before and after the formation of a land connection between North and South America, Central America served as the primary dispersal route between North and South America during the early stages of the Great American Biotic Interchange (GABI). However, there are very few records of members of the Megalonychidae of any age in Central America. Among the earliest records are a few remains of Megalonychidae from the Late Miocene of Costa Rica previously assigned to *Pliometanastes* cf. *P. protistus*, the southernmost record of that genus (Valerio & Laurito, 2014; Laurito & Valerio, 2012) and the focus of this study, and *Meizonyx salvadorensis* and *Megalonyx obtusidens*, from the Pleistocene of El Salvador (Webb & Perrigo, 1985).

The North American temperate record of Megalonychidae is restricted to two genera, *Pliometanastes* from early to late Hemphillian, and *Megalonyx* from the late Hemphillian to the late Pleistocene (Hirschfeld & Webb, 1968). The earliest record of *Pliometanastes* with an associated date is from the Siphon Canal locality in California at 8.19 ± .16 Ma. These taxa document the first dispersal event of any Megalonychidae or Xenarthra out of South America to North America. A second dispersal event of sloths in the later Hemphillian is also suggested by the mylodont, *Thinobadistes*, which also first occurs in the Hh3 late Hemphillian (McDonald & Naples, 2008).

Recently, the Pleistocene diversity of the Megalonychidae in the tropical part of southern Mexico has been increased considerably with the description of new taxa; *Xibalbaonyx oviceps*, *Xibalbaonyx microcaninus*, *Xibalbaonyx exinferis*, *Nohochichak xibalbahkah*, *Meizonyx salvadorensis* and one taxon from the Late Miocene, *Zacatzontli tecolotlanensis*, (McDonald et al., 2020; McDonald & Carranza-Castaneda, 2017; Stinnesbeck et al., 2017; Stinnesbeck et al., 2018; Stinnesbeck et al., 2020).

The diversity of megalonychids remains low throughout their presence in North America from the beginning of the middle Hemphillian with one genus and two species, *Pliometanastes protistus* and ?*Pliometanastes galushai*, followed by the late Hemphillian *Megalonyx mathisi*, and *M. curvidens* followed by a series of chronospecies; *M. leptostomus* (Blancan, NALMA), *M. wheatleyi* (Irvingtonian, NALMA), and *M. jeffersonii* (late Irvingtonian and Rancholabrean, NALMA) (McDonald, 1977).

Hirschfeld (1981) concluded that *Pliometanastes* is the ancestor to *Megalonyx*, but based on the new Miocene taxa in Venezuela it is possible they are sister taxa independently derived from a pre-Hemphillian megalonychid and represent two distinct dispersal events into North America (Rincón et al., 2019).

Within the Megalonychidae from the late Miocene to Pleistocene there are no genera in common between North and South America, except for the new remains recently found in northern South America, Venezuela, which have been assigned to aff. *Xibalbaonyx*. *Xibalbaonyx* was first reported from Mexico, and its possible record in Venezuela indicates that it is the first intertropical Megalonychidae in the Americas (Rincón et al., 2021). While the earliest megalonychid outside of South America, *Pliometanastes*, is known from both North and Central America, it has not yet been found in South America. This raises the question as to whether it originated in South America and dispersed into North America, or whether it has an earlier ancestor in North America and evolved there. Hirschfeld & Webb (1968) suggest that *Pliometanastes* is derived from the *Pliomorphus-Ortotherium* complex known from Argentina (see Brandoni 2010, 2011 for a taxonomic review). But these taxa are only known from Argentina and have not yet been found in northern South America, a distance of 4000 km. Outside of the records in Argentina and Venezuela there is essentially no record of the family for the Miocene or Pliocene elsewhere in South America. While there are a few records of megalonychids from the Middle Miocene of La Venta and Coyaima, Colombia they are not sufficiently complete to permit either a generic or specific determination (Hirschfeld, 1981). The two genera from the Miocene Urumaco Formation in Venezuela are based on postcranial material which limits a refined determination of the relationship of *Urumacocnus urbanii* and *Pattersonocnus diazgameroi* to other megalonychid taxa that are based on cranial and dental material (Rincón et al., 2019).

The discovery of *Zacatzontli tecolotlanensis*, from the late Miocene of Mexico (McDonald & Carranza-Castañeda, 2017) has increased the diversity of megalonychids known from the Miocene of North America and suggests a reexamination is needed of the number of dispersal events of members of this family and a reevaluation of the systematic relationships of Miocene members of the family in North, Central and South America. This includes a reexamination of Megalonychidae material assigned to *Pliometanastes* cf. *P. protistus*, from the Curré Formation, Coto Brus Valley, San Gerardo de Limoncito, Costa Rica and newly discovered megalonychid specimens from this locality, which is the goal of this paper.

Geological Synopsis

The remains of the new species of Megalonychidae described in this article, come from an outcrop of conglomerates in the vicinity of the town of San Gerardo de Limoncito, Coto Brus Valley, Costa Rica (Fig. 1). This sedimentary unit is located at the top of the Curré Formation and these conglomeratic lenses have been interpreted as part of a subaquatic fan delta facies, indicating the transition of typical facies indicative of inner neritic platforms to sub-littoral and estuarine coastal environments (Fig. 2) (see Laurito & Valerio, 2010 and Rincón, Valerio & Laurito, 2020 for a more detailed description of the geology).

Repositories and institutional abbreviations.— CFM, Museo Nacional de Costa Rica, Colección de Fósiles; UF, Florida Museum of Natural History.

mf- lower molariform followed by a number indicating position.

Systematic paleontology

Order Xenarthra Cope, 1889
Suborder Pilosa Flower, 1883
Family Megalonychidae Gervais, 1855
Genus *Zacatzontli* McDonald & Carranza-Castañeda, 2017
Zacatzontli cotobrusensis nov. sp.

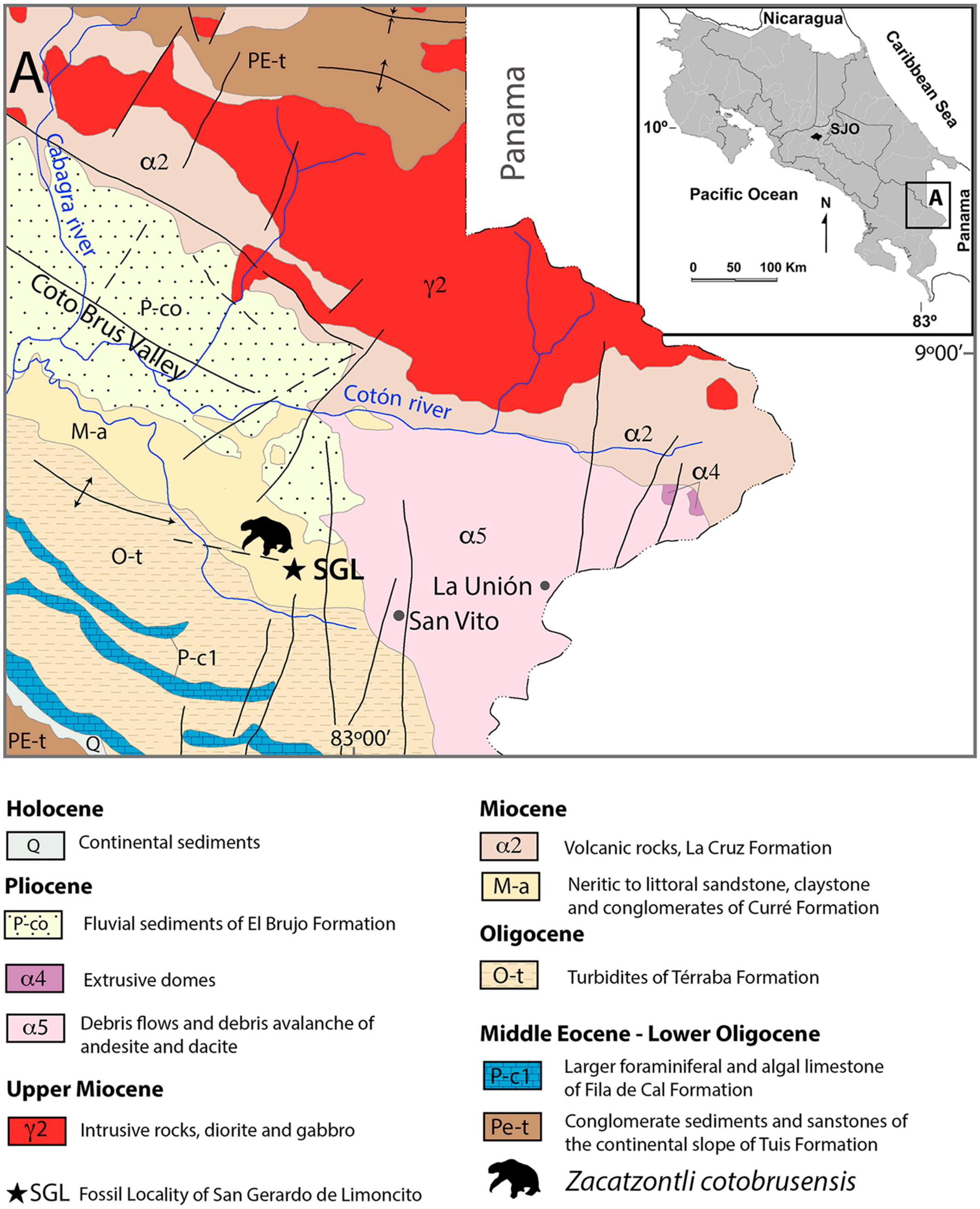
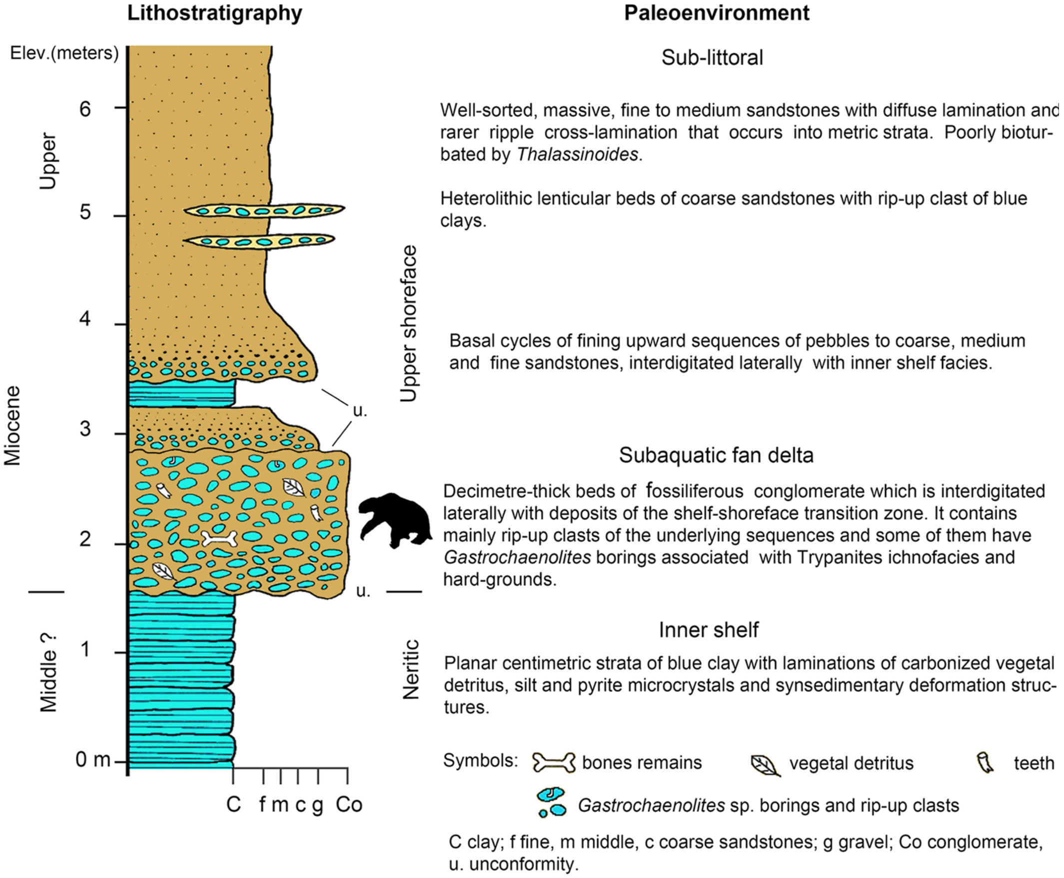


Fig. 1: Geographic location of study area and geological map of the San Gerardo de Limoncito area, modified from Denyer & Alvarado (2007).

Synonymy

Pliometanastes cf. *P. protistus* in Laurito & Valerio (2012), page. 97, figures 2 and 3
Pliometanastes protistus Valerio & Laurito (2014), page. 160, Fig. 2



Well-sorted, massive, fine to medium sandstones with diffuse lamination and rarer ripple cross-lamination that occurs into metric strata. Poorly bioturbated by *Thalassinoides*.

Heterolithic lenticular beds of coarse sandstones with rip-up clast of blue clays.

Basal cycles of fining upward sequences of pebbles to coarse, medium and fine sandstones, interdigitated laterally with inner shelf facies.

Decimetre-thick beds of fossiliferous conglomerate which is interdigitated laterally with deposits of the shelf-shoreface transition zone. It contains mainly rip-up clasts of the underlying sequences and some of them have *Gastrochaenolites* borings associated with Trypanites ichnofacies and hard-grounds.

Planar centimetric strata of blue clay with laminations of carbonized vegetal detritus, silt and pyrite microcrystals and synsedimentary deformation structures.

C clay; f fine, m middle, c coarse sandstones; g gravel; Co conglomerate, u. unconformity.

Fig. 2: Stratigraphic column and sedimentological interpretation of the locality of San Gerardo de Limoncito, Costa Rica (Laurito & Valerio, 2010) where *Zacatzontli cotobrusensis* nov. sp. was found.

Type specimen.— CFM-2916, posterior fragment of a left mandible with mf2-mf3, lacking the superior half of the ascending ramus, and the anterior part of the mandible (Fig. 3).

Referred material.— CFM-2917, first upper molariform, CFM-1000, second or third upper molariform (figure 4).

Etymology.— Geographic in reference to the Coto Brus Valley, Costa Rica where the specimen was found.

Type locality.— San Gerardo de Limoncito, Coto Brus Valley, Costa Rica with a geographical location: 8º51'19.6" N and 83º04'51.9" W at 760 m above sea level (figure 1).

Age.— early Late Hemphillian (Hh3) (Late Miocene), Curré Formation, Strontium Age (^{87}Sr/^{86}Sr) 5.80 Ma +/- 0.60/-0.80 (Rincón et al., 2020).

Diagnosis.— Small species of Megalonychidae similar in size to *Zacatzontli tecolotlanensis*; in lateral view the postero-external foramen of the mandibular canal is located at the posterior margin of the mf3, and is more posteriorly positioned than in *Pliometanastes protistus* where it is midway between the mesial and distal sides of the mf3, or *Zacatzontli tecolotlanensis*, where it is at the anterior part of mf3; the ventral margin of the horizontal ramus is only slightly convex below the molariforms, so it differs from *Pliometanastes* where this is prominent or *Zacatzontli tecolotlanensis* where the ventral margin is flat and lacks this convex shape; the angle between the dorsal margin of the horizontal ramus and the base of the vertical ramus of the mandible is higher than in *Zacatzontli tecolotlanensis*; the mf3 is almost hidden by the anterior margin of the ascending ramus, so it differs from *Pliometanastes protistus* or *Zacatzontli tecolotlanensis* where the last molariform is partially visible in lateral view.

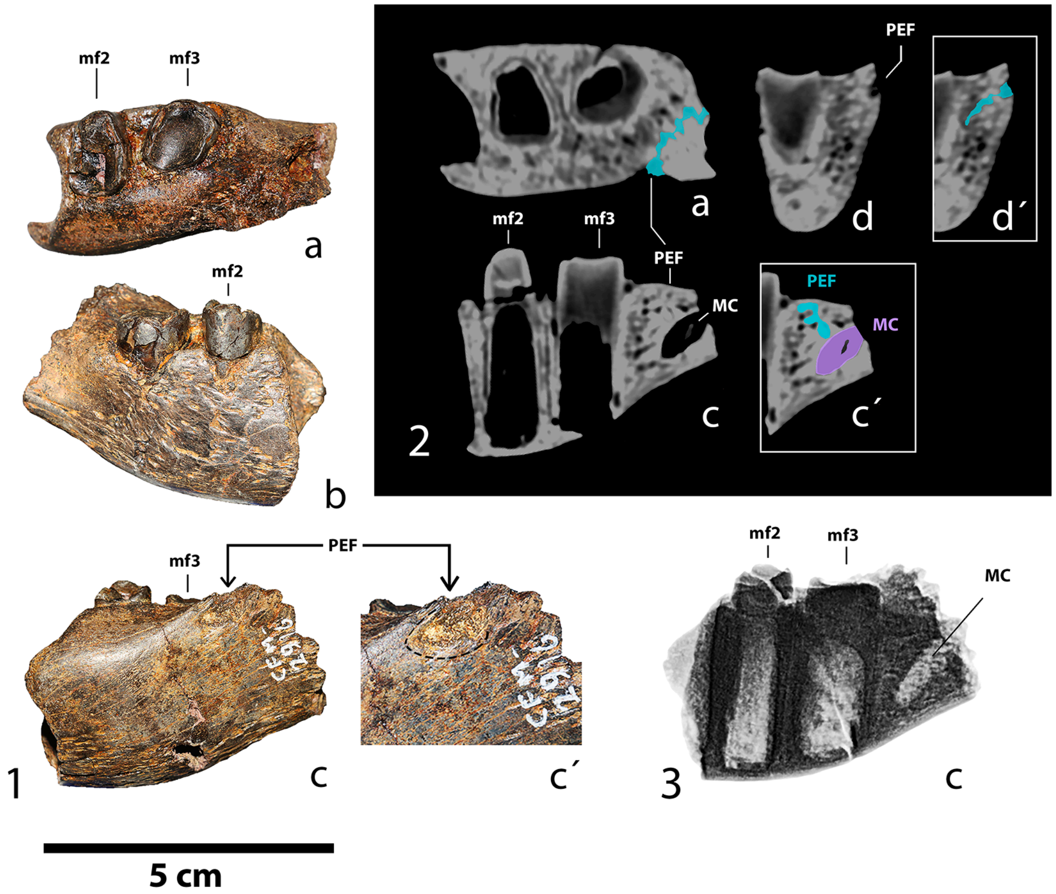


Fig. 3: *Zacatzontli cotobrusensis* n. sp. (CFM2916): 1. Mandible in 2. Computerized Axial Tomography images and 3. X-Ray image; in a. occlusal view, b. lateral lingual view, c. lateral vestibular view and d. transvere section. In 2c and 3c are through the sagittal plane of the alveoli and show the PEF (posteroexternal mandibular foramen), and (2) anterior view. In 1c´, 2d´ and 2a the PEF and MC (mandibular canal) is highlighted.

Description and comparison.— The mandible (CFM-2916) is from an adult as the sides of the molariforms are parallel and lack the conical shape present in juvenile sloths. Its size is much smaller than known adults of *Pliometanastes protistus* and is closer in size to *Zacatzontli tecolotlanensis* (Table 1, Fig. 5).

The posterolateral foramen of the mandibular canal is positioned just anterior to the mf3 in *Zacatzontli tecolotlanensis*, while in *Pliometanastes protistus*, *Megalonyx* curvidens and *Eucholoeops* ingens it is located at the mid-point anteroposterior to the mf3. Valerio & Laurito (2014) described the posteroexternal foramen (PEF) of the mandibular canal in CFM-2916 as at the same level as the anterior part of the mf3, however, we observe that the PEF in *Zacatzontli cotobrusensis* (CFM-2916) is positioned at the most posterior part of mf3, so it differs from *Pliometanastes* where it is at the middle of mf3 and *Zacatzontli tecolotlanensis* where it is well anterior to the mf3. In *Zacatzontli cotobrusensis* (CFM-2916) the PEF is below the lateral dorsal margin of the alveolus or the ascending ramus of the mandible, and is not as dorso-lateral as in *Megalonyx*, *Pliometanastes*, or *Eucholoeops*.

The posteroexternal foramen of the mandibular canal in *Zacatzontli tecolotlanensis* is positioned on the lateral side of the horizontal ramus opposite the mesial margin of the lower third molariform and the anterior margin and base of the coronoid process (Fig. 4). Its position differs from *Pliometanastes* and *Megalonyx*, where it opens anterodorsally and not laterally (McDonald & Carranza-Castañeda, 2017). In *Zacatzontli cotobrusensis* (CFM-2916) the posteroexternal foramen of the mandibular canal opens laterally on the horizontal ramus.

Measurements (in

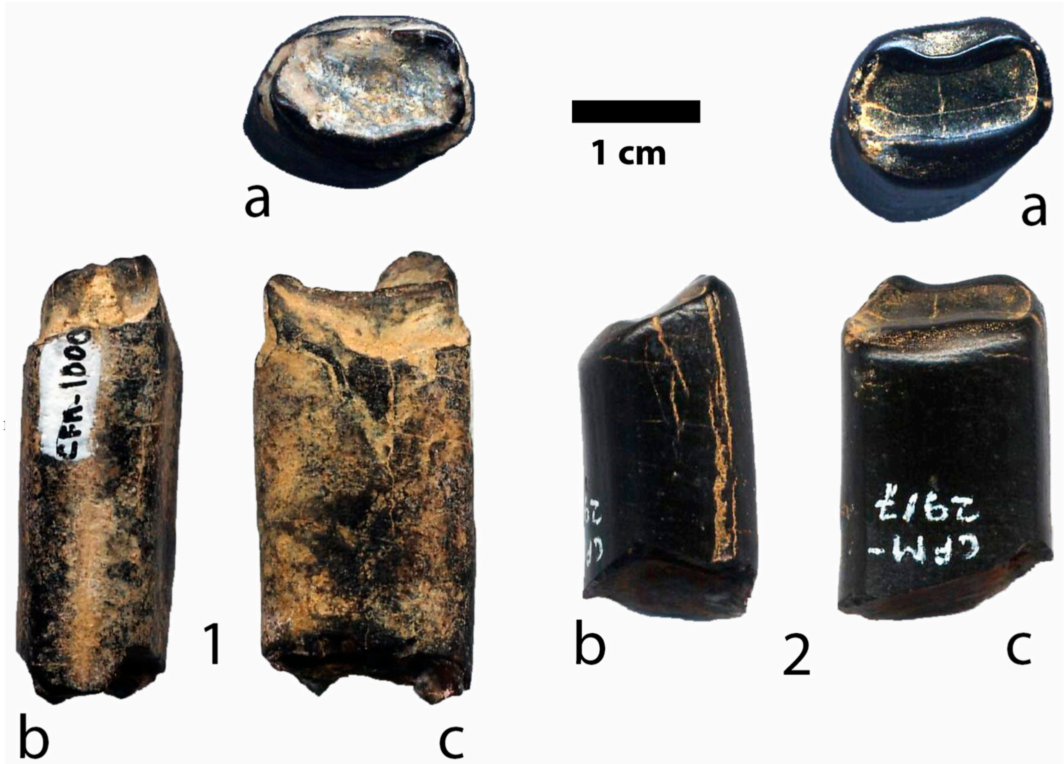


Fig. 4: *Zacatzontli cotobrusensis* n. sp.: the CFM-1000 corresponds to a second or third upper molariform and CFM-2917 that corresponds to a first upper molariform in a. occlusal, b. lingual and c. distal views.

The other feature that seems to distinguish *Zacatzontli cotobrusensis* (CFM-2916) from *Pliometanastes protistus* is that in lateral view, the mf3 is hidden by the anterior margin of the base of the ascending ramus, while in *Pliometanastes protistus* most of the mf3 is visible in lateral view. The anterior margin of the ascending ramus contacts the horizonal ramus near the posterior margin of the mf3. Extrapolating from the small amount of the ascending ramus preserved in *Zacatzontli cotobrusensis*, it appears the slope of the anterior margin of the ascending ramus is around 45 degrees, whereas in *Pliometanastes protistus* it is steeper at around 60 degrees.

The transition between the horizontal ramus of the mandible (CFM-2916) and the angular process is more gradual than in any other member of the Megalonychidae. In all other taxa in North American the transition is a virtually a step.

The dentition in ?*Pliometanastes galushai* is smaller than *Zacatzontli cotobrusensis* (Table 1, Fig. 5).

The mandibular insertion of the buccinatorius muscle in ?*P. galushai* is narrow buccally as in *Pliometanastes protistus* and differs from *Z. cotobrusensis* where the mandibular insertion of the buccinatorius muscle is wider buccally as in *Zacatzontli tecolotlanensis*.

The only difference in the dentition between ?*P. galushai* and *P. protistus* is that in ?*P. galushai* in occlusal view the shape of the mf1 and mf2 are subrectangular in shape, and in *P. protistus* the mf1, and mf2 are sub trapezoidal in shape (Hirschfeld & Webb, 1968).

Zacatzontli tecolotlanensis and *Z. cotobrusensis* differ from *P. protistus* as the ventral expansion below the mandibular body is not as great as in *P. protistus*. The small amount of expansion present is also smaller and less developed than in *Meizonyx salvadorensis*, *Nohochichak xibalbahkah*, *Xibalbaonyx oviceps*, *Xibalbaonyx exinferis*, *Xibalbaonyx microcaninus*, *Megalonyx obtusidens*, *Megalonyx jeffersonii*, or *Megalonyx curvidens*, where the mandibular expansion is robust and very well developed.

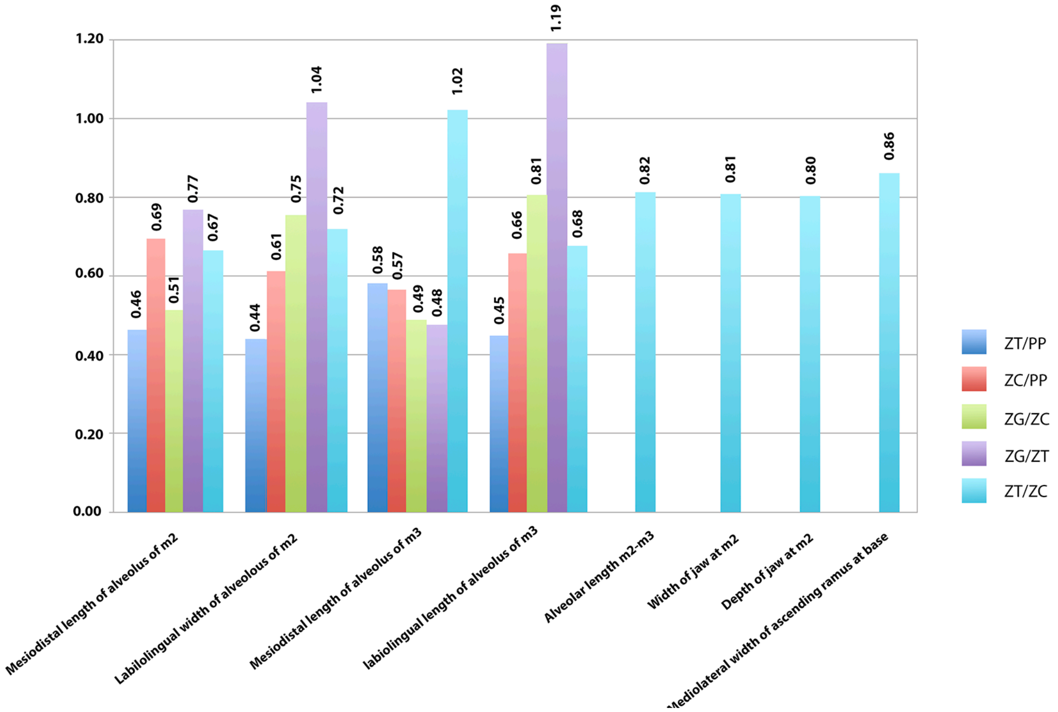


Fig. 5: Measurement ratios among some Megalonychidae, ZT (*Zacatzontli tecolotlanensis*); ZC (*Zacatzontli cotobrusensis* n. sp.); PP (*Pliometanastes protistus*); PG (?*Pliometanastes galushai*).

In *Zacatzontli cotobrusensis* the bulge formed by the lateral expansion of the horizontal ramus is at the level of mf2 but is less developed, so differs from *Z. tecolotlanensis* where that bulge is very well developed.

Discussion

While the incompleteness of the mandible prevents a more extensive analysis, the differences described are sufficient for us to infer that ?*P. galushai*, *P. protistus*, *Zacatzontli tecolotlanensis*, and *Zacatzontli cotobrusensis* n. sp. are different taxa.

Valerio & Laurito (2014) described the associated mf2 and mf3 (CFM-2916) as sub-rectangular in occlusal shape. However, based on a reexamination of these two teeth we consider the occlusal shape to be more sub-trapezoidal, with the mf3 slightly narrower than the mf2. The labial side of the mf2 is convex and wider than the lingual side of the tooth, and narrower and more convex than lingual side, which gives the tooth a trapezoidal shape in occlusal view, which is better described as being a sub-trapezoidal shape of the occlusal view for the mf2.

Laurito & Valerio (2012) also described an isolated mf1 (CFM-2917) and mf3 (CFM-1000). In the Megalonychidae the lower molariforms are more curved along their long axis while the upper molariforms are straighter. Given that the specimens CFM-2917 and CFM-1000 are straight along the apico-basal axis we consider them both to be upper molariforms and as the occlusal shape of CFM-2917 is strongly trapezoidal we consider it to be an upper first molariform (MF1), and CFM-1000 probably is the second or third upper molariform (MF3).

The type specimen of ?*Pliometanastes galushai* (FAM 77811) has been considered a subadult individual based on the slight taper of the molariforms and by the porous nature of the bone of the mandibular body (Hirschfeld & Webb, 1968).

Table 1

Measurements (in millimeters) of teeth of some North and Central American Megalonychidae.

Measurements	*Zacatzontli tecolotlanensis* MPG 1312G	*Zacatzontli cotobrusensis* n. sp. CFM-2916	*Pliometanastes protistus* UCMP 97371	?*Pliometanastes galushai* FAM 77811
Mesiodistal length of alveolus of m2	6.90	10.33	14.90	5.30
Labiolingual width of alveolus of m2	9.60	13.34	21.80	10.00
Mesiodistal length of alveolus of m3	11.10	10.85	19.10	5.30
Labiolingual width of alveolus of m3	8.40	12.41	18.80	10.00
Alveolar length m2-m3	20.50	25.10	-	-
Width of jaw at m2	18.40	22.80	-	-
Depth of jaw at m2	26.20	32.60	-	-
Mediolateral width of ascending ramus at base	10.00	11.60	-	-

Valerio & Laurito (2014) also considered the small size of ?*P. galushai* as indicative of a subadult individual. Because of the small size of the mandible (CFM-2916) they concluded that the mandible from Costa Rica belonged to a subadult individual too. However, on reexamination of the mandible CFM-2916, we did not see any indication of porous bone on the mandibular body similar to that present in ?*P. galushai*, or any indication of tapering in the molariforms (figures 2-2, 3-3). Additionally the molariforms have a very well-developed occlusal surface with a small mesial and distal ridge, both with wear facets anterior and posteriorly, and a small valley or basin between the ridges, typical of the dentition in adult individuals.

Another characteristic is that the base of the lower molariforms has the same length mesiodistally as the occlusal surface, resulting in a rectangular shaped teeth in lateral view (Fig. 3-2C; Fig. 4), characteristic of adult individuals. In young individuals the mesiodistal and labial-lingual dimensions of the molariform base are greater than these same measurements of the occlusal surface resulting in a conical shape in lateral view. This characteristic has been reported in other sloths such as *Nothrotheriops shastensis*, where the molariforms in juveniles are conical in shape in lateral view (Naples, 1990).

For these reasons we consider the type specimen of *Zacatzontli cotobrusensis* (CFM- 2916) to be an adult individual of a small taxon.

Given the greater similarities between the mandible (CFM-2916) from Costa Rica with *Zacatzontli tecolotlanensis* than any of the other late Miocene North American megalonychids based on its lack of a ventral expansion of the mandible, the mandibular insertion of buccinatorius muscle that is wider buccally, and its overall size, we assign the mandible (CFM-2916) from Costa Rica to the genus *Zacatzontli*. However, as a number of other characters do not exactly match with *Zacatzontli tecolotlanensis* from Mexico such as the position of the posteroexternal foramen of the mandibular canal on the mandibular body or mf3; the slight development of the convexity of the ventral margin of the horizontal ramus below the molariforms which in *Zacatzontli tecolotlanensis* is flat or absent; the angle between the dorsal line of horizontal ramus and the base of the vertical ramus of the mandible is higher than in *Zacatzontli tecolotlanensis*; and the the mf3 is almost hidden by the ascending ramus, differing from *Zacatzontli tecolotlanensis* where the last molariform is partially visible in lateral view these differences distinguish the two taxa from each other. While the mandible (CFM-2916) from Costa Rica can be assigned to *Zacatzontli*, we consider the observed differences to permit its assignment to a separate species for which we propose the name *Zacatzontli cotobrusensis*.

The astragalus of a Megalonychidae indeterminate CFM-2645 from Coto Brus Valley

Laurito & Valerio (2012) described a megalonychid astragalus (CFM-2645) from the Coto Brus Valley, Costa Rica, which was also referred to *Pliometanastes* cf. *Pliometanastes protistus* based on the association with the megalonychid molariforms, CFM-2917 and CFM-1000. Their description of the specimen included dimensions of the astragalus that are slightly greater than those reported by Hirschfeld & Webb (1968) for *P. protistus*. Laurito & Valerio (2012) assigned the astragalus CFM-2645 to *Pliometanastes* cf. *Pliometanastes protistus*, because it could not be differentiated from specimens of *Pliometanastes protistus* from Florida except by the dimensions of the astragalus CFM-2645.

We observe that the Costa Rican megalonychid astragalus CFM-2645 is certainly slightly smaller than *Pliometanastes protistus*, based on the measurements in Laurito & Valerio, 2012 (Cuadro 1) and Hirschfeld & Webb, 1968 (Table 13, p. 268).

Additionally, there are features of the astragalus (CFM-2645) that differ from *Pliometanastes protistus*. The angle formed by the posterior border of the astragalus, and internal (mesial) border is 135º in the Costa Rica specimen, while in *Pliometanastes protistus* (UF 9440) it is 120º, and in *Pliometanastes protistus* (UF 95400) it is 114º, a difference of 15º to 21º. Also, the proportion in relationship between the maximum length and the maximum width of the articular surface for the tibia, in CFM-2645 is 56.6% of the length of the astragalus, while in *P. protistus* (UF9440) it is 71%, and in *P. protistus* (UF95400) it is 81%, a difference of 14.4 and 24.4% in the width of the surface for the tibial articulation. The articular surface for the tibia in CFM-2645 is basically flat and lacks the medial grove as in *P. protistus* where it is present but weakly developed, or in *Megalonyx* which has a well-developed medial grove running anteroposteriorly on the articular surface for the tibia. The navicular facet in CFM-2645 is separated from the astragal body by a neck and is positioned more internally (mesial) in relation to the astragalar body, while in *P. protistus*, the navicular facet is located more antero-internal in relation to the astragalar body. The sulcus tali in CFM-2645 is wider than in *P. protistus* or *Megalonyx* spp., and the ectal facet is subtriangular in shape rather than rectangular as in *Pliometanastes protistus* or *Megalonyx* spp. The sustentacular facet in CFM-2645 is partially connected with the cuboid facet, while in *P. protistus* or *Megalonyx* it is fully confluent.

In the astragalus CFM-2645 the fibular facet in dorsal view is straight and differs from *Pliometanastes protistus* where the fibular facet in dorsal view is slightly convexly curved laterally.

All of these differences suggest that the astragalus (CFM-2645) cannot be referred to either *P. protistus* or *Megalonyx*. However, we can not necessarily assign the astragalus CFM-2645 to *Zacatzontli cotobrusensis*, although the astragalus was found in the same area as the mandible but they were not associated.

Biochronology of *Zacatzontli*

Chronologically *Zacatzontli tecolotlanensis* from Jalisco, Mexico was recovered from late Hemphillian (Late Miocene) sediments below the tuff from the San José beds, in the Santa Maria area. This tuff produced some grains of sanidine dated by ^{40}Ar/^{39}Ar and gave an age of 4.95 ± 0.02 Ma. Based on the presence of *Nannippus aztecus*, *Neohipparion eurystyle*, *Dinohippus mexicanus*, *Astrohippus stockii*, *Teleoceras fossiger*, *Borophagus secundus*, *Canis ferox*, and *Agriotherium schneideri*, the stratigraphic sequence of Santa Maria area is considered to be late Hemphillian (Hh3) (McDonald & Carranza-Castañeda, 2017).

The specimen of *Zacatzontli cotobrusensis* was recovered from the same area as two other xenarthrans, the megathere, *Sibotherium ka* and the pampathere *Scirrotherium antelucanus*. These deposits have been dated using on ^{87}Sr/^{86}Sr as 5.80 ±- 0.60/-0.80 Ma, which is also considered to be early late Hemphillian (Late Miocene). This age assignment is also supported by the presence of *Calippus hondurensis*, *Dinohippus mexicanus*, and *Protohippus gidleyi*. Based on the strontium dates and associated fauna from San Gerardo de Limoncito, the Costa Rica stratigraphic sequence is also considered to be early late Hemphillian (Hh3) (Valerio, 2010). Including the first-appearance datum (FAD) and the biochrons of the camel, *Hemiauchenia vera*, and the peccaries, *Protherohyus brachydontus* and *Prosthennops serus*, all of the faunal elements from San Gerardo de Limoncito indicate a Hh3 age and a strong faunal affinity with the localities of La Hacienda and Santa María, Mexico, where *Zacatzontli tecolotlanensis* was found, especially with those taxa whose stratigraphic range extends later and with taxa that have a younger range such as *Dinohippus mexicanus*, *Hemiauchenia vera* and *Protherohyus brachydontus*, but

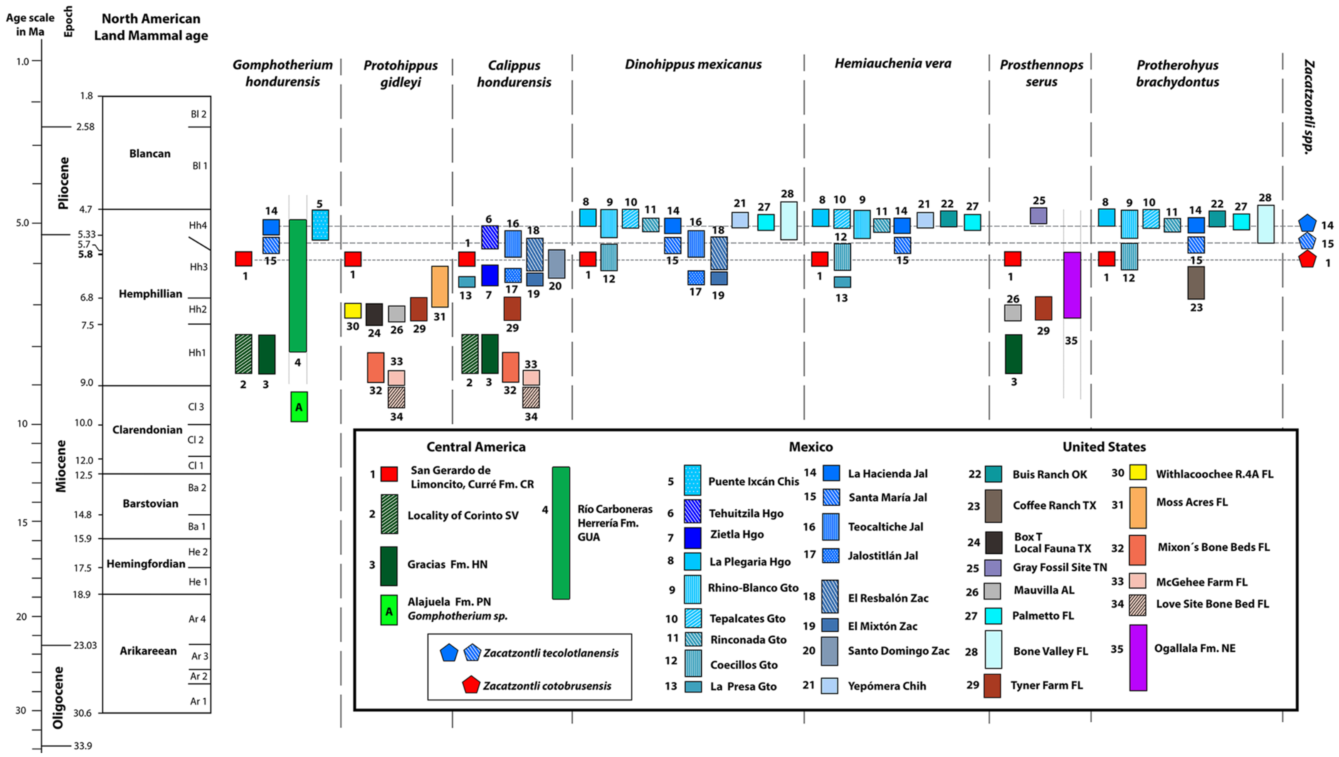


Fig. 6: Comparative biostratigraphic table of the fauna of the San Gerardo de Limoncito locality from southern Costa Rica where *Zacatzontli cotobrusensis* sp. nov. was found, as defined by the concurrent biochrons of different species of mammals of North American ancestry. In addition, the biostratigraphic range for the *Zacatzontli* species as indicated, along with the Central and North American localities with which the San Gerardo de Limoncito locality shares faunal elements. The Biochrons indicate a Late Hemphillin age range, which is consistent with the radiometric age of 5.80±- 0.60/-0.80 Ma, Upper Miocene. Based on: MacFadden et al. (2015) on the oldest record of *Gomphotherium* in Central America; 1. Valerio (2010), Laurito & Valerio (2010), Valerio & Laurito (2020); 2. and 3. Webb & Perrigo (1985), Hulbert (1988); 4. Lucas & Alvarado (2010); 5. Gómez-Pérez & Carbot-Chanona (2018) on the remains of immature individuals of *Gomphotherium* sp. from the late Miocene of Chiapas, as contemporaneous dental remains with *G. hondurensis*. Sites from 6. to 20. Carranza-Castañeda et al. (2013), Carranza-Castañeda (2019), also 10. and 11. Dalquest & Mooser (1980); 14. and 15. McDonald & Carranza-Castañeda (2017), Carranza-Castañeda (2018), 16. Montellano-Ballesteros (1997); 21. Lindsay et al. (2006), MacFadden (1984, 1998a and 1998b); 22. Joyce et al. (2012), Prothero & Sheets (2013); 23. Passey et al., 2002, Webb et al. (2008), Doughty et al. (2018), Prothero & Sheets (2013); 24. Hulbert (1988), 25. Doughty (2016) and Doughty et al., 2018; 26. Hulbert & Withmore (2006) and MacFadden & Dobie (1998); 27. Hulbert & Withmore (2006); Prothero & Sheets (2013), Webb et al., 2008, Wright (1989, 1991 and 1998); 28. MacFadden (2008) and Prothero & Sheets (2013); 29. Hulbert (1988), Hulbert & Withmore (2006), Hulbert et al. (2009); 30. and 31. Hulbert & Withmore (2006); 32. and 33. Hulbert (1988) and Hulbert & Whitmore (2006); 34. Hulbert & Whitmore (2006) and Prothero & Sheets (2013) and 35. Wright (1998).

not with taxa with earlier ranges of appearance such as *Calippus hondurensis* (see Fig. 6).

While the genus *Zacatzontli* appears to be currently be restricted to the late Hemphillian (Late Miocene) of Mexico and Costa Rica, its two species are not contemporaneous, as *Zacatzontli tecolotlanensis* is slightly younger at 4.95 Ma in age [Hh4] while the age of *Zacatzontli cotobrusensis* is 5.80 Ma and is late early Hemphillian in age [Hh3], and the older of the two species. Given the limited record of the genus the age difference between the two species may simply be reflective of the geographic distance between the two localities. An earlier record in the more southern locality in Costa Rica would be expected to document the earlier dispersal into Central America with an expected time lag for its subsequent dispersal northward into Mexico. Such a time lag may be another example of the "holding pen" model (*sensu* Woodburne, 2010), when a taxon occurs earlier in a given location, only to be found later in an adjacent area. But, as noted by Woodburne (2010), the degree to which Central America acted as a holding pen for any trans-isthmian dispersal remains an open question. Woodburne et al. (2006) observed that if the timing of the lapse between the first appearance of a taxon in Central America or Mexico and its subse-

Fig. 7: Hypothetical paleogeographical reconstruction of the Caribbean Region, Gulf of Mexico and North West of South America at the Upper Miocene. SGL: San Gerardo de Limoncito Locality and site of the found of *Zacatzontli cotobrusensis* nov. sp. at the Curré Formation. TCOL and SMA correspond to the localities of Tecolotlán and San Miguel de Allende Basins where *Zacatzontli tecolotlanensis* has been found.

quent presence farther north is accurate and pertinent, there must be some factor or factors retarding the dispersal northward from this southern region. In this case the factor may have been the separation of Costa Rica from northern Central America by a water barrier (Fig. 7) as indicated by the sedimentary unit from which the sloth was recovered, conglomeratic lenses within a subaquatic fan delta facies, indicative of inner neritic platforms to sub-littoral and estuarine coastal environments.

Summary

A partial mandible and associated teeth of a megalonychid sloth from the Early Late Hemphillian (Late Miocene) Curré Formation, San Gerardo de Limoncito, Costa Rica originally referred to *Pliometanastes* cf. *P. protistus*, are now considered to be the genus *Zacatzontli* but a distinct species, *Zacatzontli cotobrusensis* as proposed here. This new record extends the geographic range of *Zacatzontli* from central Mexico to Costa Rica, but the genus is chronologically constrained to the Late Miocene (late Hemphillian Hh3 and Hh4), and the Costa Rican species is slightly older than the Mexican species. The addition of this taxon adds to our knowledge of the xenarthran diversity in the neotropics of Central America and indicates that the diversity of fossil xenarthrans in this region is greater than previously assumed. The increasing number of taxa of South American origin in the tropical portions of North and Central America adds to the complexity of understanding of the different stages of the GABI and the timing of the different dispersal events of different taxa of South American origin into Central and North America during different stages of the Great American Biotic Interchange. In some cases the distribution of these taxa was limited to the tropical environments while others were able to disperse into temperate North America.

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