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PRESENCE OF *AMPHIMACHAIRODUS COLORADENSIS* (Cook, 1922) (FELIDAE: MACHAIRODONTINAE) IN THE NEOGENE OF HIDALGO, CENTRAL MEXICO

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ABSTRACT–The Neogene *Amphimachairodus coloradensis* appears to be one of the most abundant species of Machairodontine in Mexico. However, its fossil record is composed of scarce, fragmented, and poorly studied material. New remains discovered in La Plegaria locality (late Hemphillian), in the State of Hidalgo, in Central Mexico, offers the opportunity to review some morphological aspects and phylogenetic relationships of this species within the subfamily Machairodontinae. Our observations allow us to recognize that the material from La Plegaria looks like the paratype of *A. coloradensis* (DMNH EPV 207, from the Ogallala Fm. in the western United States); this means, m1 with reduced talonid and paraconid almost as large as protoconid, and p4 with posterior cingulum. Phylogenetic analysis confirms the relationship of La Plegaria felid with *A. coloradensis* and *A. alvarezi*; although the last one presents autapomorphies that differentiate it from others *Amphimachairodus*: highly developed mandibular flange. We concluded that the material from La Plegaria corresponds to the southernmost record of an *A. coloradensis*. This work made it possible to review variation within this species and its morphological relationship with *M. catocopis*.

Keywords: Hemphillian; *Machairodus*; Miocene; Pliocene; Scimitar-toothed.

1. Introduction

In Mexico felines represent 18.2% of the current diversity of land carnivorans (order Carnivora Bowdich, 1821), with six species (Ceballos, 2014). During the Neogene and Quaternary, the feline richness was slightly different and included the extinct Long-toothed felids or Machairodontines (Machairodontinae Gill, 1872) (Ferrusquia-Villafranca et al., 2010; Ruiz-Ramoni et al., 2020, 2019).

Since the second half of the Neogene, Machairodontines were probably one of the largest predators of the region (Carranza-Castañeda et al., 2013; Carranza-Castañeda and Miller, 1996; Miller and Carranza-Castañeda, 1998; Ruiz-Ramoni et al., 2019), because of their adaptations to hypercarnivory (Antón, 2013). As its name indicates, Machairodontines are distinguished by their hypertrophied and flattened upper canines; a homoplasy that is shared with other non-feline mammals, such as Thylacosmilids and Barbourofelids (Antón, 2013; Turner, 1997). But, the main features that define the Machairodontine group are their small upper molars and lower canine, and the large parastyle present in the upper third premolar (Christiansen, 2013).

Two groups of Machairodontines have been recognized in Mexico: Saber-toothed felids, with elongated upper canines in dirk-shaped, and Scimitar-toothed felids, with canine slightly shorter than the previous ones and with a marked crenulation (Kurtén, 1952; Wheeler, 2018, 2011). Saber-toothed belonging to the genus *Smilodon* has been reported from the Pleistocene of the Central Plateau, the Sierra Madre Oriental, the Trans-Mexican Volcanic Belt, and the Yucatan Platform (Morales-Mejía et al., 2009; Ferrusquia-Villafranca et al., 2010; Chatters et al., 2014). While the Scimitar-toothed *Homotherium* has been reported from the Irvingtonian NALMA (1.6 to 0.2 Ma) of Sonora (Lindsay,

1984) and Jalisco (Rodríguez-de La Rosa et al., 2007), although the latter report is based on a footprint.

Other Scimitar-toothed recognized in Mexico is *Amphimachairodus coloradensis*, that has been reported from the Hemphillian (9.0 to 4.8 Ma) and Blancan (4.8 to 1.6 Ma) NALMAs of Baja California Sur, Jalisco, Guanajuato, Zacatecas, and Hidalgo (Carranza-Castañeda et al., 2013; Carranza-Castañeda and Miller, 1996; Guzmán, 2014; Miller and Carranza-Castañeda, 1998; Padilla, 2004). Few studies review in detail the fossil material of *A. coloradensis* from this country. Recently, the material from the late Hemphillian of Guanajuato (Carranza-Castañeda and Miller, 1996) was re-assigned to a new species of *Amphimachairodus* due to the significant differences to *A. coloradensis*: *A. alvarezi* Ruiz-Ramoni et al., 2019.

Other fossil remains have not yet been studied in detail. Such is the case of the fossil remains of a Machairodontine recovered from La Plegaria locality, at the Hidalgo State (Fig. 1). Padilla (2004) was the first to mention material from La Plegaria that he assigned to *Machairodus* (= *Amphimachairodus*) *coloradensis*. Later, Guzmán (2014) described the new material of a Machairodontine from this locality, and he identified it as *Machairodus* cf. *M. coloradensis*. In this paper, we provide a review of the taxonomic affinities of the material reported by Guzmán (2014), plus new elements obtained from La Plegaria in recent fieldwork.

2. Material and methods

The specimens described here are housed at the Colección Nacional de Paleontología, Museo María del Carmen Perrilliat (IGM), Instituto de Geología, UNAM, Mexico City, Mexico.

2.1. Locality and geological context

La Plegaria is located in the surroundings of the Tepeji del Río de Ocampo (19° 50’ N, 99°, 24’ W), in the southwest region of the State of Hidalgo (Fig. 1). The geology in the region is closely related to the genesis and development of the Mexican Volcanic Belt geological province, which began during the Oligocene and evolved during episodic pulses through the Neogene, and Pleistocene, related to the volcanic-tectonic activity (Ferrari et al., 1999). This activity produced a wide variety of volcanic structures and trenches that led to the development of endorheic basins, which includes lacustrine, residual, and flux deposits. The stratigraphic section of the La Plegaria locality is about 25 m thick. At its base, it is formed by volcanic ashes, sands, and well-consolidated clays that constitute a massive stratum about 13 m thick. Overlying this massive stratum lies a volcano-sedimentary block with well-consolidated volcanic ashes that alternate with a well-consolidated whitish and greenish tuff about 50 cm thick. The beds deposited over this last tuff are mainly composed of volcanic ashes, coarse and fine-grained sands and clays. The fossil material described here was collected from the upper part of this sequence. The vertebrate remains consist of mammalian bones and dental elements found disarticulated or fragmented, but in good state of preservation.

The faunal association of the equids *Nannippus aztecus* (Hh1-Hh4; subages of the Hemphillian), *Dinohippus mexicanus* (Hh2-Hh3), *Astrohippus stocki* (Hh3-Hh4), and *Neohipparion eurystyle* (Hh3-Hh4); the rhinoceros *Teleoceras fossiger*; the antilocaprid *Hexobelomeryx fricki*; the camels *Pleiolama vera* and *Alforjas* sp. and the peccary *Catagonus brachydontus*, recovered from La Plegaria suggests a late Hemphillian age (Hh4; Carranza-Castañeda et al., 2013). This locality correlates to other late Hemphillian

Mexican local faunas, including Rancho El Ocote, Rancho Viejo area, Tepalcates, and Rinconada, in Guanajuato, Tecolotlán and Teocaltiche in Jalisco, Gigante and Trapiche in Nayarit; and Yepómera in Chihuahua (Carranza-Castañeda et al., 2013). La Plegaria is also related stratigraphically to other Hemphillian local faunas from the United States (e.g., Palmetto, Florida; Mount Eden, California; Tedford et al., 2004).

2.2. Phylogenetic affinity

A Maximum Parsimony Analysis was carried out to evaluate the relationships between the IGM 11452 to other Machairodontines. This analysis was based on the proposal of Werdelin and Flink (2018) because it allowed us to score more craniodental characters using the material available from La Plegaria. The proposal of Werdelin and Flink (2018) integrates some characters originally from Salesa et al. (2010), Christiansen (2013), and Wallace and Hulbert (2013). Nevertheless, based on our observations, we made some changes to the original character scored of *Amphimachairodus giganteus* and *Machairodus aphanistus* (see Appendix A). Besides the specimen studied here, we added *A. alvarezi*, *A. coloradensis*, and *M. catocopis* to the final dataset. The final matrix is therefore composed of 48 characters and 28 taxa (Appendix A).

The analysis was carried out with the free software TNT v.1.5 (Goloboff et al., 2016, 2008), employing a traditional search, using implied weights and equal weights. In both cases, the characters were treated as non-additives, and we test the consistency of the tree topology under different values of the concavity constant (k). *Canis lupus* is considered as the external group. To measure node stability, we used the absolute frequency and frequency differences arising from standard Bootstrap (Goloboff et al., 2008; Goloboff and Catalano, 2016) based on 1,000 replicates. Consensus trees are presented.

2.3. Institutional Abbreviations

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, USA; **DMNH EPV**, Denver Museum of Nature & Science, Denver, USA; **ICP**, Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Catalonia; **IGCU**, Instituto de Geología, Ciudad Universitaria, Mexico City, Mexico; **IGM**, Colección Nacional de Paleontología, Museo María Del Carmen Perrilliat, Instituto de Geología, Mexico, Mexico City, Mexico; **MPUAH**, Museo de Paleontología de la Universidad de Hidalgo; **PIK**, Pikermi material at the Muséum National d'Histoire Naturelle, Paris, France; **ROM**, Royal Ontario Museum, Toronto, Canada; **TM**, Toros Menalla Collection, Republic of Chad; **TMM**, Texas Memorial Museum, Texas, USA; **UF**, Florida Museum of Natural History, Florida, USA; **UNAM**, Universidad Nacional Autónoma de Mexico, Mexico City, Mexico.

2.4. Anatomical abbreviations

C/c, upper/lower canine; **i**, lower incisor; **M/m**, upper/lower molar; **P/p**, lower premolar. The numbers that accompany dental abbreviation means the position of the tooth in the dental series.

2.5. Other abbreviations

C.I., Consistency index; **Fm.**, formation; **k**, concavity constant, **Ma**, million years; **NALMA**, North American Land Mammals Age; **R.I.**, Retention index;

3. Systematic paleontology

CARNIVORA Bowdich, 1821

FELIDAE Fischer von Waldheim, 1817

MACHAIRODONTINAE Gill, 1872

Amphimachairodus Kretzoi, 1929

Amphimachairodus coloradensis (Cook, 1922)

(Figs. 2–4)

Machaerodus (*Heterofelis*) *coloradensis*: Savage, 1941: 697

Machairodus coloradensis: Martin and Schultz, 1975: 56-57

Amphimachairodus coloradensis (Cook, 1922) Antón et al., 2013: 1202, 1204, 1205, 1208-2012

3.1. Referred material

IGM 11452, a fragment of right maxilla preserving I1-I3, right C; isolated left P4; a fragment of a right hemimandible preserving p4-m1; a fragment of the most anterior part of a right hemimandible preserving i2, i3, and c; isolated left i1; isolated left p4; isolated left m1; IGM 11453, a fragment of right hemimandible with the alveolus of the p3 and part of diastema; IGM 11454, right p4 incomplete; IGM 11455, right lower canine; IGM 11456 right calcaneus.

3.2. Description

The crown of the upper incisors is acute (more than in the lower incisors), and slightly recurved lingually. On each tooth, a ridge on the medial and lateral sides of the crown extends from the base to the tip and ending in an accessory cusp (Fig. 2A). On the lingual side of I1 and I2, the crown is encircled by a well-developed V-shaped cingulum. In the I2, the mesial cingulum shows tenuous crenulations, but in the I3, the cingulum is present only on the medial side and shows small crenulations (Fig. 2a). The I1 is the shortest incisor and I3 the tallest. These incisors are organized in a parabola or strongly arched.

The upper canine is elongated (Fig. 2B), laterally compressed, and slightly recurved anteroposteriorly. The crenulation is well-developed and observable along the anterior and posterior tooth margins (Fig. 2b).

The isolated left P4 has a developed protocone, positioned distal to the level of the paracone, but not at the same level as the parastyle (Fig. 2C). The paracone is the tallest of the dental cusps. Smooth serrations are observed in the anterior slope of the paracone (Fig. 2c). An ectoparastyle (or ectostyle) is present. The metacone forms the extended portion of the carnassial blade and is low-crowned relative to the paracone. The shearing surface of this tooth is observed on the lingual side of the posterior crest of the paracone, and the metacone-metastyle.

The ramus of the hemimandible is straight and slender (Fig. 2D). Although it is incomplete, a ventral curvature is appreciated indicating the presence of the flange. On the labial side, a masseteric fossa extends to the posterior end of the m1, and in the most anterior part, an incomplete mental foramen is present.

The crowns of the i2 and i3 are acute and slightly recurved, with the inner face to the mouth ‘flattened’. The crowns have a lateral accessory cusp, where the right cusp is more developed than the medial one. Crenulations are observed on the medial-lateral ridge of i3. The i3 is larger than i2. The lower canine is incisiform, although slightly more massive than i3. In this tooth, the lingual side is ‘flattened’. The posterior and anterior ridges of the lower canine bear a well-developed serration (Fig. 2d). As in the upper incisors, the i2, i3, and the lower canine are organized in a strongly arched (Fig. 2E).

The crow of the p4 consists of one well-developed cuspid (protoconid) along with two accessory cuspids, one anterior and one posterior (Fig 2D–G). This premolar has a well-differentiated posterior cingulum. There is a light serration in the crest that runs from the tip of the main cuspid to the anterior side.

The m1 presents a very reduced talonid, which is fused with the trigonid just below the protoconid and is more visible on the lingual face (Fig. 2D–H). Martin and Schultz (1975) differentiate between the talonid and metaconid of m1, but since these structures are very simplified, we only make reference to talonid. The protoconid of m1 is taller than the paraconid; both cuspids are blade-like. Shearing surfaces are present on the labial side of the paraconid and protoconid blades. Serrations are observed on the posterior side of the protoconid (Fig. 2e). The anterior margin of m1 slightly overlaps the posterior border of p4 (Fig. 2D).

3.3. Other material

IGM 11453 shows a double rooted p3 and a marked diastema between the lower canine and the p3 (Fig. 3A). The morphology of the lower canine of IGM 11454 is the same as in IGM 11452, but the serration is restricted to the accessory cusps (Fig. 3C). The p4 IGM 11454 shows the same morphology of the p4 of IGM 11452, but with the roots slightly more closed (Fig. 3B). In the calcaneus IGM 11456 (Fig. 4), the ectal, sustentacular, and cuboidal articular facets are well differentiated; ectal and cuboidal are more developed than sustentacular. Above the ectal facet and on the neck of the calcaneus, there is a prominent cleft for the astragalus. There is a very prominent tuberosity in the left-anterior end of the calcaneus for the calcaneal tendon.

Before this study, Padilla (2004) reported some material of a Machairodontinae from La Plegaria. The morphology of the material he described complements the fossil material reported in this work. He described a P4 (IGCU 12011), a left m1 (MPUAH 489) with the same morphology of IGM 11452 (i.e., without talonid), a p3 (IGCU 12014), and a p4 (IGCU 12013) which in our opinion is a P3 because the roots are less open compared to the p4 of IGM 11452 and 11454 (see 'Figure 8' in Padilla, 2004), a left I3 (IGCU 12015), a distal part of a right humerus (IGCU 12001), a metacarpus V (IGCU 12002), and a proximal part of a phalanx (IGCU 12009). About this material, IGCU 12014 confirms the presence of a double rooted p3.

3.4. Remarks

The material recovered from La Plegaria belongs to at least two different individuals. This is based on the presence of two left m1 (IGM 11452 and MPUAH 489), and two right p4 (IGM 11452 and 11454). For its part, IGM 11453 (fragment of the hemimandible with the third premolar and diastema) does not match with the hemimandible of IGM 11452.

4. Discussion

4.1. Morphological comparisons

IGM 11452 presents a hypertrophied and laterally flattened upper canine, also a lower canine less developed than upper canine. These features fit with the characters of the subfamily Machairodontinae and within the clade Eumachairodontia (Christiansen, 2013; Werdelin et al., 2010).

Most dental pieces present a strong crenulation (Fig. 2), which is a feature typically described in Scimitar-toothed felids, while in Saber-toothed felids this crenulation is less evident (Christiansen, 2013; Kurtén, 1952; Martin et al., 2011; Rincón et al., 2011; Werdelin et al., 2010). Also, the fragments of the anterior region of the skull show a teeth arrangement into a strongly arched. It is frequently observed this condition in Scimitar-toothed felids as *Amphimachairodus, Machairodus*, *Xenosmilus*, and some *Homotherium* (Anton et al., 2004; Ballesio, 1963; Martin et al., 2011), whereas in Saber-toothed, as in *Smilodon fatalis* and *S. populator*, the arcade is straight, and *Megantereon* is slightly parabolic.

The Machairodontine from La Plegaria exhibits several features resembling the genera *Amphimachairodus* and *Machairodus*, as the P4 with a developed ectoparastyle, a well-developed protocone, and double rooted p3 (Christiansen, 2013; Ruiz-Ramoni et al., 2019), while *Homotherium* and *Xenosmilus* do not have the P4 protocone and ectoparastyle, and the p3 is reduced or absent (Antón et al., 2014; Martin et al., 2011b).

IGM 11452 is not a *Machairodus* because of the presence of a developed mandibular flange (Fig. 2), and instead, this genus does not present it (Hodnett, 2010; Martin and Schultz, 1975; Ruiz-Ramoni et al., 2019). Since IGM 11452 presents a mandibular flange, we can relate it to *Amphimachairodus*. Despite this, it is unknown the degree development of the flange because of the fragmentary condition of the material. This feature would be useful to differentiate it from *A. alvarezi*, which is the *Amphimachairodus* with the most developed flange (Ruiz-Ramoni et al., 2019). Nevertheless, other features allow to relate the morphology of IGM 11452 with *A.*

coloradensis and the Eurasian *A. kurteni*: the m1 with reduced talonid and paraconid almost as large as protoconid, and p4 with posterior cingulum.

IGM 11452 and MPUAH 489 have a sharply reduced m1 talonid, a condition that also is present in *A. alvarezi*, *A. kurteni* (PIN 2433/287) (Sotnikova, 1991), and some specimens of *A. coloradensis* (see below for a detailed comparison against this species). In counterpart, in *A. kabir* (TM-266-02-102), and *A. giganteus* (AMNH 20606, PIK 3387, ROM 55066/cast), the m1 talonid is more developed (Antón et al., 2013; Beaumont, 1978; Peigné et al., 2005; pers. observation). On the other hand, the p4 posterior cingulum is present in almost all *Amphimachairodus*, except in *A. alvarezi* (IGM, 6414; see Ruiz-Ramoni et al., 2019).

A detailed comparison with *A. kurteni* is not made because of the lack of access to the material, but it is considered that this comparison should be made on the scale of *A. coloradensis* vs. the Eurasian material (i.e., *A. kurteni* and *A. giganteus*).

From a size perspective, the elements recovered at La Plegaria correspond to a relatively large size feline, but smaller compared to other Machairodontines (Fig. 5). It is one of the smallest *Amphimachairodus* specimen described, but only for a few millimeters; about 1.04 mm respect to the second smallest specimen, IGM 6414 (*A. alvarezi*).

4.2. Phylogenetic affinity

According to the consensus trees obtained (Fig. 6), IGM 11452 (La Plegaria felid) is a Machairodontinae felid grouped within the clade of Eumachairodontia. The topology resulting from this group indicates that the differentiation between Saber-toothed and Scimitar-toothed is not a natural organization (i.e., not monophyletic), which has also been observed by Christiansen (2013) and Werdelin and Flink (2018). Under an implied weights analysis with a k value of 3 (Fig. 6 A–C), *Rhizosmilodon* and *Machairodus* are basal taxa of Eumachairodontia, but at k ≥ 52 *Machairodus* is grouped near *Amphimachairodus*, *Xenosmilus*, and *Homotherium*, in a unique clade which also includes the *Smilodon* and *Megantheron* (Fig. 6D). This situation is reversed when *M. catocopis* and *M. aphanistus* are removed in a restricted consensus (Fig. 6D'), which means that these taxa present an instability within the analysis, but that it does not affect the position of the La Plegaria felid with respect to *A. coloradensis* and *A. alvarezi*.

In all the analyses carried out, IGM 11452 is grouped among Scimitar-toothed felids, that are defined by a long and bladelike p3 (Fig. 6A). In contrast, the more derived Saber-toothed felines are defined by several synapomorphies that allow recognizing that the material La Plegaria does not belong to this group: arcade of the upper incisors slightly parabolic, upper canines dirk-shape, size of the m1 short relative to hemimandible length, and extreme p4 distal lean.

Under equal weights (Fig. 6B), all members of *Amphimachairodus*, including IGM 11452, form a monophyletic clade together with *Xenosmilus* and *Homotherium*. *Amphimachairodus* differs from *Xenosmilus* and *Homotherium* by the degree of development of the P4 protocone. Using implied weights, *A. giganteus* is located as an external group of *Amphimachairodus*, *Xenosmilus*, *Homotherium*, *Smilodon*, and *Megantereon* (Fig. 6A). This relationship is maintained when *M. catocopis* was added (Fig. 6C). However, in this case, the topology of the non-Eumachairodontia, specifically the clade *Panthera* and *Lynx*, is located unexpectedly below *Metailurus* spp. In all topologies obtained with k = 3 (Fig. 6A–C), *M. aphanistus* forms a paraphyletic clade with the rest of the Eumachairodontia. A similar case resulted from the analysis of Christiansen (2013), where this taxon should be considered as part of the clade *Amphimachairodus*, *Homotherium*, and *Xenosmilus*.

In any case, La Plegaria felid forms a polytomy, including *A. coloradensis* and *A. alvarezi*. IGM 11452 is defined by the non-existent p4 distal lean. *A. alvarezi* differs by the large mandibular flange and the mandibular fossa termination posterior to the carnassial (m1). Interestingly, the only difference between IGM 11452 and *A. coloradensis* is the p4 distal lean. In *A. coloradensis* can be nonexistent (ch.48 in 0) and slight (ch.48 in 1), while in IGM 11452 is only nonexistent. This allows to considered IGM 11452 within the variability of *A. coloradensis*.

4.3. Variation in Amphimachairodus coloradensis*?*

In a review of the material assigned to *Amphimachairodus coloradensis* (Cook, 1922), it is clear that the presence of talonid in m1 is quite variable (Fig. 7). Some specimens present a very small or absent m1 talonid (morphotype a'), while other specimens have a well-developed m1 talonid (morphotype b'). IGM 11452 could be included in the morphotype a', resembling the paratype of *A. coloradensis* (DMNH EPV 207) and the specimen from Ash Hollow Fm. (Nebraska) UNSM 25510 (Martin and Schultz, 1975). This morphology was also observed in MPUAH 489 (see Padilla, 2004). Nevertheless, unlike most *A. coloradensis* revised, the orientation of the cuspids of the molar and premolar of IGM 11452 is perpendicular to the corpus of the hemimandible (Fig. 2D). In the specimen TMM 41261-9 from Coffee Ranch (Ogallala Fm., Texas), the posterior lean of the cusps is very evident, but in DMNH EPV 207 (from Colorado) there is practically no inclination.

Historically, Martin and Schultz (1975), Hodnett (2010), and Antón et al. (2013), point out that *A. coloradensis* is often confused with *Machairodus catocopis* (Cope, 1887), especially in specimens lacking the anterior-most portion of the hemimandible (avoiding to discern the degree of development of mandibular flange). Burt (1931), Dalquest (1969), Matthew (1924), and Mawby (1965) described material from Nebraska and Texas, which assigns to *M. catocopis*. Martin and Schultz (1975), expose that the material described by these authors as an *M. catocopis* must be considered *A. coloradensis*. *A. coloradensis*, unlike *M. catocopis*, has an m1 paraconid almost as large as protoconid and a developed mandibular flange. Even when is not the main goal of the present contribution, we consider that under the description of Martin and Schultz (1975), the taxonomy of the specimens DMNH EPV 208, 209, and 210 (Fig. 7) from the Ogallala Fm., western United States, must be revised as they might belong to *M. catocopis*.

5. Conclusions

Padilla (2004) and Guzmán (2014) originally indicated that La Plegaria feline was more related to *Amphimachairodus coloradensis*. Guzmán (2014) presented some doubts about this assignment, but here, under a more detailed review and comparison with other specimens, we confirm that this felid material is the southernmost record of this species in North America and the smallest specimen. We found that this fossil material falls within the morphological variability of the specimens assigned to this species, which was already noticed or mentioned by previous authors. Phylogenetic analysis confirms the observations made on this material and indicates that this species was closely related to the contemporary *A. alvarezi*.

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Appendix A. Phylogenetic matrix modified from Werdelin and Flink (2018)

Canis_lupus 00000000000000000000101000000000000000000000000
Cryptoprocta_ferox 10001201111??20001111?1?100??1200000101000101000
Amphimachairodus_giganteus 02221211111?1112121110111[0,1]11111110111111[1,0]11011
Dinofelis_barlowi 100112111111101212112 01?1111110111011110011?000
Dinofelis_cristatus 10011211111100121211201011111110111 0?11100111000
Dinofelis_petteri 1?01121111111012121120111110111011 10?11100111000
Homotherium_crenatidens 022212211111311022112111111111112101121111111021
Homotherum_latidens 022212211111311022112111111111112101121111111021
Homotherium_serum 022212211111321022112111111111112101121111111021
Machairodus_aphanistus   022112111110011122111 0001[0,1]111110111112111 0111011
Megantereon_cultridens 13021221111?10311211200011111111200110112111 1122

Megantereon_falconeri 13021221111?1031121120001111111120011011211111 22
Megantereon_whitei 13021221111?223112112000111111112001101121111132
Metailurus_major 21011211111?0011221110011111111010101011001110?0
Metailurus_parvulus 21011211111110122211100111111110101010110011 10?0
Nimravides_pedionomus 2101120111110010121110001 01?????????0?10010?000
Promegantereon_ogygia 210112111111001112111001101111201011101100111000
Smilodon_fatalis 13121211211021122211201011111111300111211111 1132
Smilodon_populator 131212?121102112222112010111111113001112111111132
Xenosmilus_hodsonae 02221321?1103230221120111111111121011211111111031
Panthera_leo 20001211111000111211101011111111010 02?01100112000
Lynx_rufus 2000121111110210221110101111112000?2?01100110000
Rhizosmilodon_fitae ???1??????????????11201?111?????????????1?11??01
Smilodon_gracilis 13121211?110201?2211201011111111130?0?1?11111?122
Amphimachairodus_coloradensis ??????1111101?10?211201111111???2???12??11111?1[1,0]
Amphimachairodus_alvarezi 0222??11111???????11200 1111??????????2???2?01??11
Amphimachairodus_LaPlegaria 02221211111???????11200?111??????????2??1?01??10
Machairodus_catocopis 0221121111101???221110?01111111131?11??11001?010

Changes in the score with respect to the original proposal of Werdelin and Flink (2018). *Amphimachairodus giganteus*, ch. 7: from 2 to 1; ch. 15: from 2 to 1; ch. 26: from 0 to 0,1; ch. 33: ? to 1; ch. 43: from 1 to 0,1; ch. 47: from 0 to 1. *Machairodus aphanistus*, ch. 1: from 2 to 0; ch. 3: from 1 to 2; ch. 12: from ? to 0; ch. 17: from 1 to 2; ch. 24: from ? to 0,1; ch. 34: from 0 to 1; ch. 38: from ? to 2.

Figure captions

Figure 1. La Plegaria locality, near Tepeji del Río de Ocampo, Hidalgo State, Mexico.

Figure 2. *Amphimachairodus coloradensis* from La Plegaria. IGM 11452. **A,** right maxilla in buccal (left), occlusal (middle), and lingual (right) view. **B**, right upper canine in lateral view. **C**, left upper fourth premolar in lingual (left), buccal (middle), and occlusal (right) view. **D**, fragment of a right lower hemimandible in lateral (up), medial (middle), and occlusal view (down); in lateral and medial view is appreciated the ventral projection of the horizontal branch that indicates the presence of the flange. **E**, anterior part of a right hemimandible in occlusal (left), buccal (middle), and lingual view (right). **F**, left first

incisor in lateral(left) and lingual (right) view. **G**, left lower fourth premolar in buccal (up) and lingual (down) view. **H**, left first lower molar in buccal (up) and lingual (down). The serration details of some teeth are shown in a, b (bar: 0.5), c (bar: 5 mm), d, and e (bar: 1 mm).

Figure 3. *Amphimachairodus coloradensis* from La Plegaria. **A**, IGM 11453, fragment of the hemimandible with the third premolar and diastema. **B**, IGM 11454, right lower fourth premolar in lingual (left) and buccal (right) view. **C**, IGM 11455, right lower canine in lingual (left) and buccal (right) view; serration on the accessory cusp in lingual view.

Figure 4. IGM 11456, right calcaneus.

Figure 5. Scatter plot comparing the size of the first lower molar (m1) of *Amphimachairodus coloradensis* from La Plegaria to other Machairodontines.

Figure 6. Phylogenetic relationships of the La Plegaria felid to other Machairodontines. **A**, Strict consensus from 15 trees (993810 steps) analyzed using traditional search trees with implied weights; black squares mark the nodes where synapomorphies are listed (character and status); C.I: 0.560, R.I: 0.783. **B**, Strict consensus from 8 trees (130 steps) analyzed using a shear tree based on equal weights; C.I: 0.577, R.I: 0.798. In ‘A’ and ‘B’ *Machairodus catocopis* was excluded from the analysis. **C**, Strict consensus from 15 trees (1055595 steps) analyzed using traditional search trees with implied weights and including in the analysis *M. catocopis*; C.I: 0.556, R.I: 0.783. The concavity constant used for these analyses was k = 3. **D**, Strict consensus from 6 trees (107732 steps) analyzed using

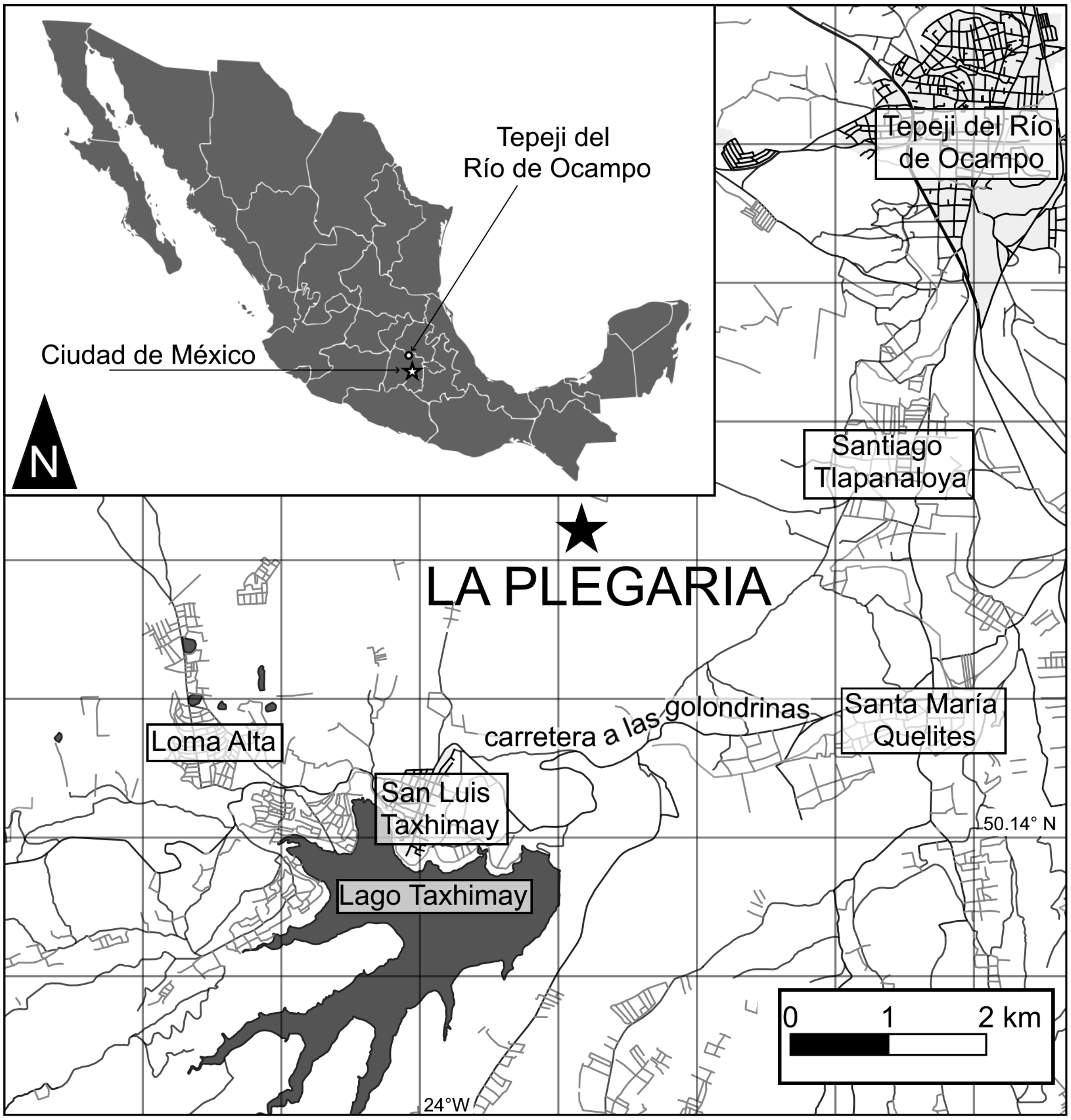
traditional search trees with implied weights and with k = 52; C.I: 0.560, R.I: 0.783. **D'**, restricted consensus from 'D' when is removing *M. catocopis* and *M. aphanistus*; only the clade Eumachairodontia is shown. Supports of the branches are symmetric resampling. Gray taxa are the non-Eumachairodontia felids. A list of characters taken from Werdelin and Flink (2018) is shown in Appendix A.

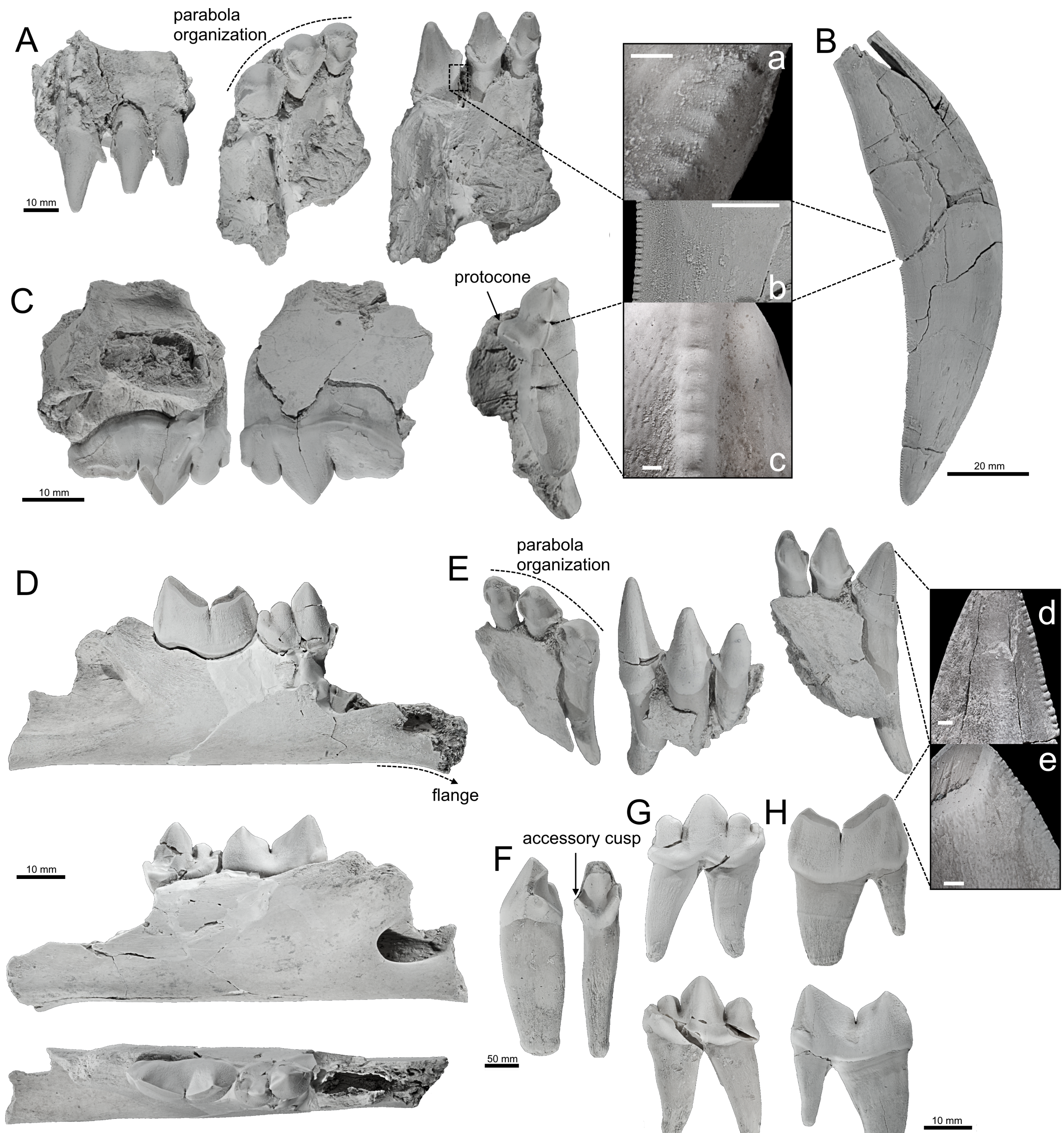
Figure 7. Mandibular teeth of specimens assigned to *Amphimachairodus coloradensis*. Morphotypes: a', absence or poorly developed m1 talonid; b', presence of m1 talonid. Note: DMNH EPV 208, 209 and 210 differ from the diagnosis of the species given by Martin and Schultz (1975), on the contrary, are more related to *Machairodus catocopis*: m1 protoconid higher than paraconid, and present talonid (considered metaconid by Martin and Schultz [1975]). Photographs obtained in the collections web sites of Denver Museum of Nature & Science (DMNH EPV), Florida Museum of Natural History (UF), and A. Rincón (TMM).

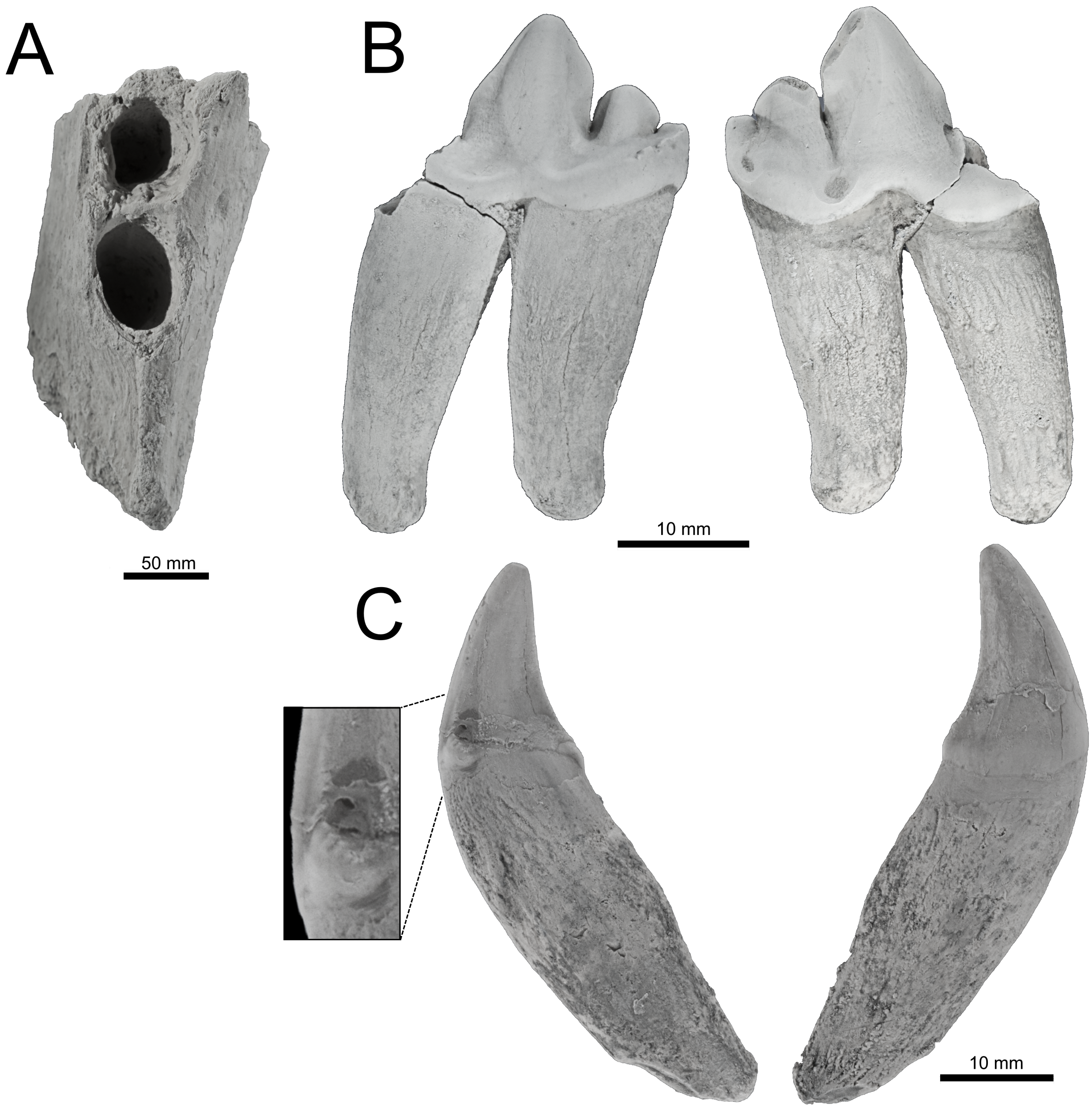
Tables

Table 1. Dental measurements (in mm) of *Amphimachairodus coloradensis* from La Plegaria. *Alveolus.

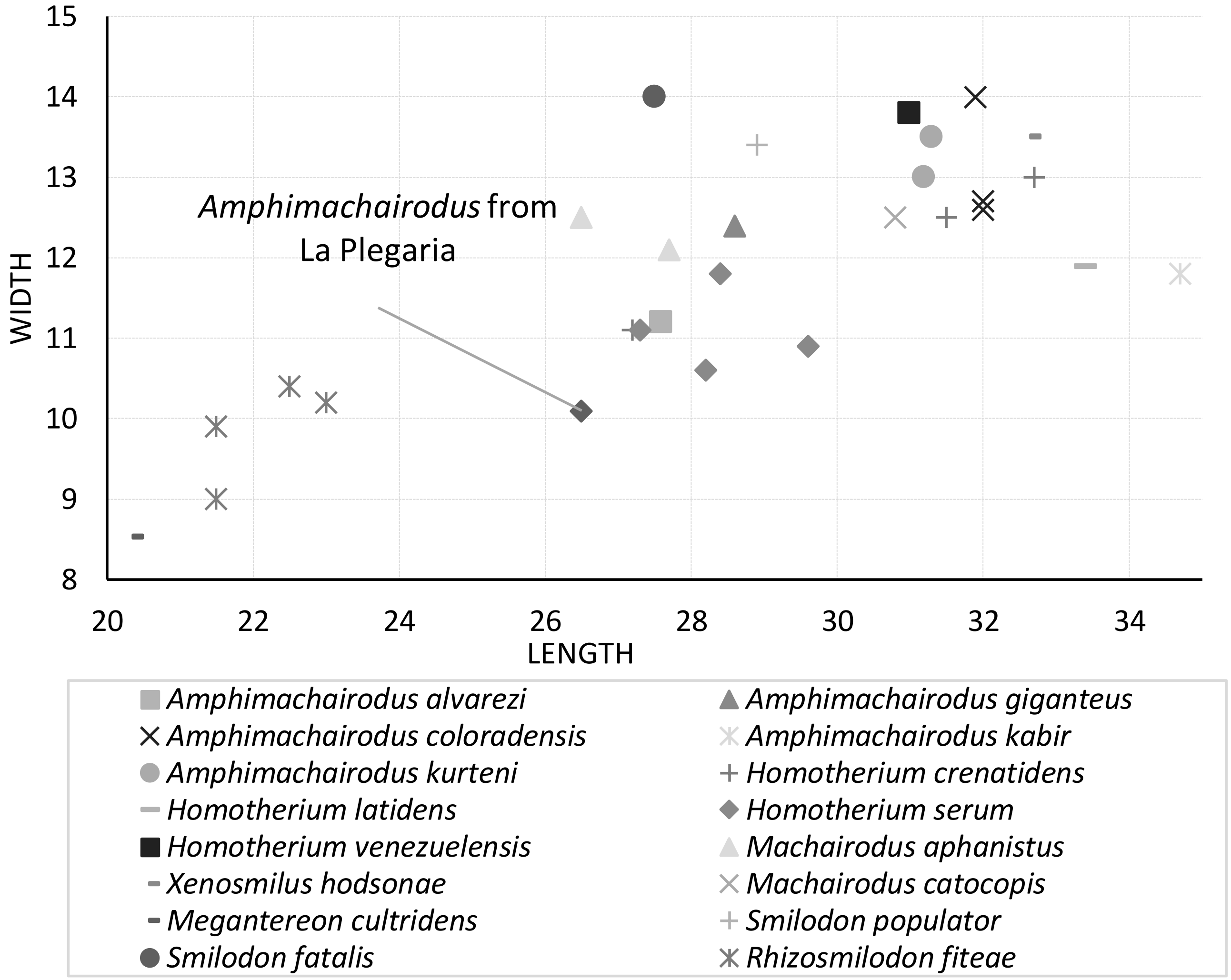
	I1		**I2**		**I3**		**C1**		**P4**			
	L	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**		
IGM 11452-Right	9.7	7.0	10.0	9.6	10.4	12.8	26.1	11.5	38.3	15.1		
	i2		**i3**		**c1**		**p3**		**p4**		**m1**	
	L	**W**	**L**	**W**	**L**	**W**	**L**		**L**	**W**	**L**	**W**
IGM 11452-Right	7.2	5.9	7.4	8.9	12.0	8.7			25.3	10.4	26.5	10.1
IGM 11452-Left									25.3	10.4	26.1	10.4
IGM 11453							10.1*	6.4*				
IGM 11455					12.3	8.5						


Tepeji del
Río de Ocampo
Ciudad de México
N
Tepeji del Río
de Ocampo
Santiago
Tlapanaloya
LA PLEGARIA
carretera a las golondrinas
Santa María
Quelites
Loma Alta
San Luis
Taxhimay
Lago Taxhimay
50.14° N
24°W
0 1 2 km


A
parabola
organization
10 mm
a
b
c
B
20 mm
C
protocone
10 mm
D
flange
10 mm
E
parabola
organization
d
e
F
accessory cusp
50 mm
G
H
10 mm


A
B
C
50 mm
10 mm
10 mm


20 mm


15
14
13
12
11
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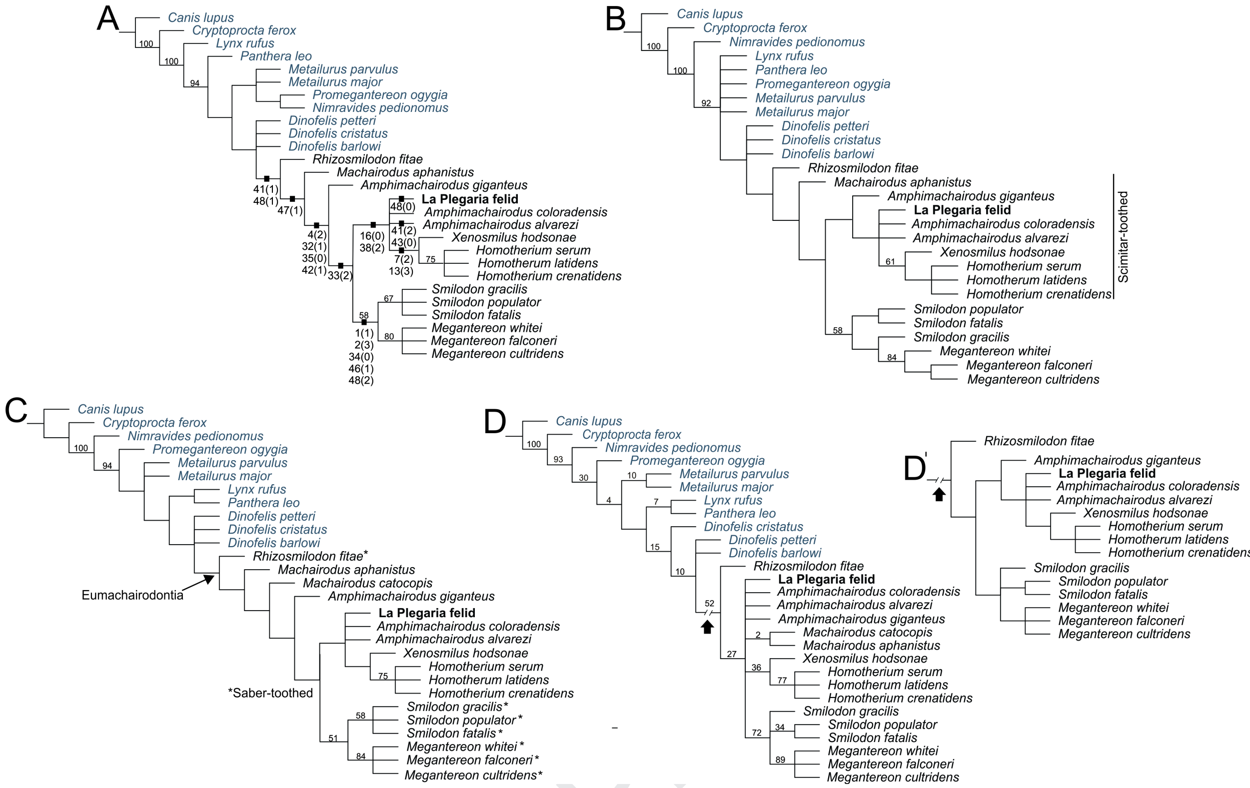
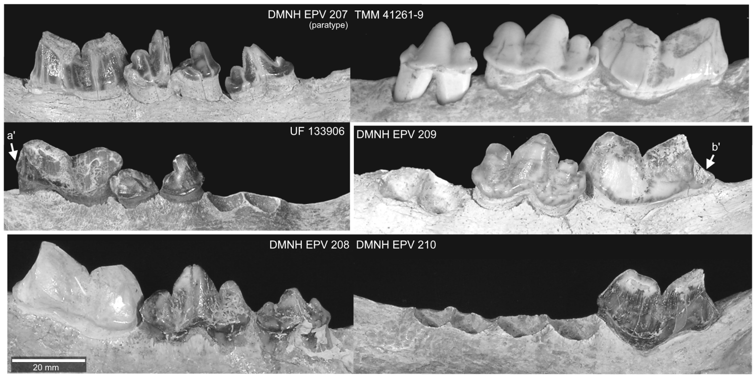
9
8
WIDTH
20
22
24
26
28
30
32
34
LENGTH
Amphimachairodus from La Plegaria
Amphimachairodus alvarezi
Amphimachairodus giganteus
Amphimachairodus coloradensis
Amphimachairodus kabir
Amphimachairodus kurteni
Homotherium crenatidens
Homotherium latidens
Homotherium serum
Homotherium venezuelensis
Machairodus aphanistus
Xenosmilus hodsonae
Machairodus catocopis
Megantereon cultridens
Smilodon populator
Smilodon fatalis
Rhizosmilodon fiteae


A
Canis lupus
Cryptoprocta ferox
Lynx rufus
Panthera leo
Metailurus parvulus
Metailurus major
Promegantereon ogygia
Nimravides pedionomus
Dinofelis petteri
Dinofelis cristatus
Dinofelis barlowi
Rhizosmilodon fitae
Machairodus aphanistus
Amphimachairodus giganteus
La Plegaria felid
Amphimachairodus coloradensis
Amphimachairodus alvarezi
Xenosmilus hodsonae
Homotherium serum
Homotherium latidens
Homotherium crenatidens
Smilodon gracilis
Smilodon populator
Smilodon fatalis
Megantereon whitei
Megantereon falconeri
Megantereon cultridens
100
100
94
41(1)
48(1)
47(1)
4(2)
32(1)
35(0)
42(1)
33(2)
16(0)
38(2)
48(0)
41(2)
43(0)
7(2)
13(3)
75
67
58
1(1)
2(3)
34(0)
46(1)
48(2)
80
B
Canis lupus
Cryptoprocta ferox
Nimravides pedionomus
Lynx rufus
Panthera leo
Promegantereon ogygia
Metailurus parvulus
Metailurus major
Dinofelis petteri
Dinofelis cristatus
Dinofelis barlowi
Rhizosmilodon fitae
Machairodus aphanistus
Amphimachairodus giganteus
La Plegaria felid
Amphimachairodus coloradensis
Amphimachairodus alvarezi
Xenosmilus hodsonae
Homotherium serum
Homotherium latidens
Homotherium crenatidens
Smilodon populator
Smilodon fatalis
Smilodon gracilis
Megantereon whitei
Megantereon falconeri
Megantereon cultridens
100
100
92
61
58
84
Scimitar-toothed
C
Canis lupus
Cryptoprocta ferox
Nimravides pedionomus
Promegantereon ogygia
Metailurus parvulus
Metailurus major
Lynx rufus
Panthera leo
Dinofelis petteri
Dinofelis cristatus
Dinofelis barlowi
Rhizosmilodon fitae*
Machairodus aphanistus
Machairodus catocopis
Amphimachairodus giganteus
La Plegaria felid
Amphimachairodus coloradensis
Amphimachairodus alvarezi
Xenosmilus hodsonae
Homotherium serum
Homotherium latidens
Homotherium crenatidens
Smilodon gracilis*
Smilodon populator*
Smilodon fatalis*
Megantereon whitei*
Megantereon falconeri*
Megantereon cultridens*
100
94
Eumachairodontia
75
*Saber-toothed
58
51
84
D
Canis lupus
Cryptoprocta ferox
Nimravides pedionomus
Promegantereon ogygia
Metailurus parvulus
Metailurus major
Lynx rufus
Panthera leo
Dinofelis cristatus
Dinofelis petteri
Dinofelis barlowi
Rhizosmilodon fitae
La Plegaria felid
Amphimachairodus coloradensis
Amphimachairodus alvarezi
Amphimachairodus giganteus
Machairodus catocopis
Machairodus aphanistus
Xenosmilus hodsonae
Homotherium serum
Homotherium latidens
Homotherium crenatidens
Smilodon gracilis
Smilodon populator
Smilodon fatalis
Megantereon whitei
Megantereon falconeri
Megantereon cultridens
100
93
30
4
10
7
15
10
52
2
27
36
77
72
34
89
D'
Rhizosmilodon fitae
Amphimachairodus giganteus
La Plegaria felid
Amphimachairodus coloradensis
Amphimachairodus alvarezi
Xenosmilus hodsonae
Homotherium serum
Homotherium latidens
Homotherium crenatidens
Smilodon gracilis
Smilodon populator
Smilodon fatalis
Megantereon whitei
Megantereon falconeri
Megantereon cultridens


DMNH EPV 207
(paratype)
TMM 41261-9
UF 133906
a'
DMNH EPV 209
b'
DMNH EPV 208
DMNH EPV 210
20 mm

Highlights

* *Amphimachairodus coloradensis* was present during the Neogene at Central Mexico.

* *Amphimachairodus coloradensis* was a Scimitar-toothed felid phylogenetically related to *A. alvarezi*.

* La Plegaria locality (Hidalgo State) hosted the southernmost record of an *Amphimachairodus coloradensis*.

* Although *Amphimachairodus coloradensis* is morphologically confused with *Machairodus catocopis*, some differences separate them: e.g., m1 talonid and mandibular flange.

Author statement

Damián Ruiz-Ramoni: Conceptualization, Methodology, Investigation, Writing – original draft. **Marisol Montellano-Ballesteros:** Supervision, Resources, Writing – review and editing, Project administration. **Ascanio D. Rincón:** Conceptualization, Supervision, Investigation, Writing – review and editing. **Andrés Solórzano:** Validation, Supervision. **Germán Guzmán:** Supervision.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: