First Mexican records of Anthracotheriidae (Mammalia: Artiodactyla)

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ABSTRACT: Anthracotheres are generalised artiodactyls that have an extensive record in the Cenozoic of Eurasia and Africa. In North America they have been collected in middle Eocene to early Miocene localities from the California Coast, the Great Plains and the Gulf Coast of the United States, with a single record from the early Miocene of Panama. Here we report few specimens from the early Oligocene (Ar1) Iniyoo Local Fauna of north-western Oaxaca, and the earliest Miocene of Simojovel de Allende, in northern Chiapas. This material has diverse features that indicate they belonged to the bothriodontine *Arretotherium*, such as selenodont cristids associated with the protoconid and hypoconid, the absence of a premetacristid, and the crenulated enamel. They share with *Arretotherium acridens* and *Arretotherium meridionale* the absence of a mesiolingual metacristid, but their general morphology and size indicate a close relationship to *Ar. meridionale*. Nevertheless, in absence of better-preserved specimens, we decided not to assign the fossil material to this species. Specimens from Oaxaca and Chiapas are the first records of anthracotheres in Mexico. These new records link the previous ones from temperate North America and tropical Central America and indicate that Anthracotheriidae had a very wide geographical distribution in North America during the Palaeogene and the Neogene. Additionally, they represent the southern-most records of *Arretotherium* in North America during the Oligocene and the early Miocene.

KEY WORDS: Arikareean, Chiapas, Iniyoo, Miocene, Oaxaca, Oligocene, Simojovel de Allende, Santiago Yolomécatl.

1. Introduction

Anthracotheriidae is a family of generalised artiodactyls that have an extensive fossil record in Eurasia and Africa, spanning from the late Eocene to the late Pliocene (Kron & Manning 1998; Lihoreau & Ducrocq 2007; Lihoreau *et al*. 2014). In North America, their fossil record is more restricted and ranges from the middle Eocene to the middle Miocene of the California Coast, the Great Plains and the Gulf Coast of the United States (Macdonald 1956; Kron & Manning 1998; Albright 1999; Prothero *et al*. 2022). Also, there is a single record from the early Miocene of Panama (Rincon *et al*. 2013).

Anthracotheres are characterised by a set of derived characters: amastoid skull, brachydont and bunoselenodont molars, enlarged M3 and m3, P4 and p4 never molariform, M1–M3 with four or five cusps with a well-developed distolingual metaconule, postprotocrista never reaching the metaconule, m3–m1 without paraconid, distinct metacristid, V-shaped hypolophid (when is present), cingulum spur on the distal face of m1–m2, m3 with well-developed hypoconulid, and dimorphic canines, among others (Lihoreau & Ducrocq 2007).

It has been proposed that Anthracotheriidae appear to root in Helohyidae (e.g., Coombs & Coombs, 1977), but there are no known transitional forms between both families (Lihoreau & Ducrocq 2007). The family is divided into two subfamilies, Anthracotheriinae and Bothriodontinae (*sensu* Kron & Manning, 1998). The Anthracothere fossil record in North America includes members of both subfamilies: *Heptacodon* Marsh, 1894a from the Late Uintan–Duchesnean (middle Eocene) of Texas, Utah, Oregon and Saskatchewan, the late Eocene Chadron Formation of Wyoming, and the Orellan and Whitneyan (early Oligocene) of South Dakota, Colorado and Nebraska, is the earliest known anthracothere in North America and the only member of the subfamily Anthracotheriinae in this subcontinent (Kron & Manning 1998; Prothero *et al*. 2022). On the other hand, Bothriodontinae has a more extensive record, with 11 species included in five genera, among which are included *Elomeryx armatus* Marsh, 1894b from the late Eocene–early Oligocene Sespe Formation (late Uintan–late early Arikareean), Simi Valley area, California; the early Oligocene Brule Formation (Whitney Member, early Arikareean) of South Dakota and Cypress Hills Formation (Whitneyan) of Saskatchewan in Canada; *Elomeryx garbanii* Macdonald, 1970 from the top of Sharps Formation (early Arikareean) of South Dakota (Prothero *et al*. 2022); *Bothriodon advena* Rusell, 1978 from the late Eocene Cypress Hills Formation (Cypress Hills Fauna; early Chadronian), of Saskatchewan; *Bothriodon rostratus* (Scott 1894) from the early Oligocene Brule Formation (early Arikareean) of South Dakota; *Aepinacodon americanus* (Leidy 1856) from the late Eocene Chadron Formation (early–late Chadronian) of South Dakota and Nebraska; *Aepinacodon deflectus* (Marsh 1890), from the late Eocene Chadron Formation

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(early–late Chadronian) of South Dakota (Kron & Manning 1998); *Arretotherium acridens* Douglass, 1901, from the early Oligocene Gering Formation of Nebraska and the Garvin Gully Local Fauna (early Hemingfordian) of Texas (Prothero *et al.* 2022), the early Miocene Blacktail Deer Creek Formation (Blacktail Deer Creek Local Fauna, early late Arikareean) of Montana (Douglass 1901), and the Toledo Bend Local Fauna (LF) of Texas (Albright 1999); *Arretotherium fricki* Macdonald & Schultz, 1956, from early Miocene of the Batesland Formation (early Hemingfordian), South Dakota, Runningwater Formation (early Hemingfordian), Nebraska (Macdonald & Schultz 1956; Macdonald & Martin 1987), and the Cypress Hill Formation of Saskatchewan (early Hemingfordian) (Prothero *et al.* 2022); *Arretotherium leptodus* (Matthew 1909) from the early Miocene of the Lower Rosebud beds (late early Arikareean), White River on the Pine Ridge Reservation, South Dakota (Matthew 1909), Wagner Quarry (middle Arikareean) of Nebraska (Prothero *et al.* 2022); *Arretotherium meridionale* Rincon *et al.* 2013, from the early Miocene Las Cascadas fossil assemblage (late Arikareean), Panama (Rincon *et al.* 2013); and *Kukusepasutanka schultzi* Macdonald, 1956, from early Miocene, Cabbage Patch beds (late early Arikareean), Drummond Granite County, Montana (Macdonald 1956).

In Mexico, Palaeogene and early Neogene mammalian faunas are poorly known compared to those from the United States. Before this article, no fossil records of anthracotheres have been reported. The aim of this article is to describe anthracothere fossils from the early Oligocene (Ar1) Iniyoo LF of Santiago Yolomecátl, Oaxaca, and from the earliest Miocene of Simojovel de Allende, in northern Chiapas, both located in southern Mexico (Fig. 1), and to discuss their palaeobiological implications.

2. Study areas

Santiago Yolomécatl is located in the south-eastern portion of the Tlaxiaco Basin, within the Sierra Madre del Sur physiographic province and the Mixteca alta sub-province, in the State of Oaxaca (Jiménez-Hidalgo *et al.* 2022). Anthracothere specimens are part of the Iniyoo LF, earliest Arikareean (Ar1) in age, based on the first appearance datum of the amphicyonid *Mammacyon* and the last appearance datum of the tayassuid *Perchoerus probus* and the rhinocerotid *Subhyracodon* (Jiménez-Hidalgo *et al.* 2018). Specimens were collected from a fluvio-lacustrine sequence conformed by silty–clayey sediments with occasional lithics, which represents the marginal facies of the early Oligocene Chilapa Formation (Jiménez-Hidalgo *et al.* 2021). Two uranium–lead dating maximum depositional ages of 30.6 ± 0.77 and 30.62 ± 0.67 Ma, for detrital zircon grains from sandstone beds occurring above the bottom and top of the vertebrate fossil-bearing interval, indicate an early Oligocene age for the formation (Guerrero-Arenas *et al.* 2020; Jiménez-Hidalgo *et al.* 2021).

Simojovel de Allende, in the southern Mexican State of Chiapas, is famous for its amber mines. Here, a marine and terrigenous sedimentary sequence that contains amber in association with pollen, benthic foraminifera, corals, echinoids, bivalves, marine gastropods, crabs, shark teeth and some terrestrial vertebrates crop out (Langenheim *et al.* 1966; Frost & Langenheim 1974; Tomasini-Ortíz & Martínez-Hernández 1984; Webb *et al.* 2003; Ferrusquía-Villafranca 2006; Vega *et al.* 2009; Perrilliat *et al.* 2010; Carbot-Chanona *et al.* 2020). The base of this sequence is La Quinta Formation, which is divided in three members: Camino Carretero (in the base); Florida Limestone (in the middle); and Finca Carmito (at the top) – they are mainly conformed by sandstone, shale and limestone. La Quinta Formation is covered by a sequence of 310 m of dark-grey shales named Mazantic Shale (Allison 1967). Overlaying the Mazantic Shale is the Balumtum Sandstone, conformed by 760 m of grey sandstone (Frost & Langenheim 1974; Perrilliat *et al.* 2010). The anthracothere specimen was recovered from Los Pocitos amber mines, near Simojovel de Allende town, 125 km northwest of Tuxtla Gutiérrez, Chiapas. Los Pocitos mines are located within the Mazantic Shale. This sedimentary deposit has been dated with an absolute age of 23 Ma based on strontium ($^{87}Sr/^{86}Sr$) isotopes of a sample taken from a well-preserved shell of the gastropod *Turbinella maya*, placing it in the Aquitanian (early Miocene; Vega *et al.* 2009). A similar age (22.8 Ma) was obtained by the same radiometric method from the amber deposits in Campo La Granja mines, which is within La Quinta Fm (Serrano-Sánchez *et al.* 2015).

3. Material and methods

Specimens from Oaxaca are housed in the Colección Científica of Laboratorio de Paleobiología, campus Puerto Escondido, Universidad del Mar (UMPE), Oaxaca, Mexico. Universidad del Mar is registered as the legal custodian of the specimens in Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos of the Instituto Nacional de Antropología e Historia, the national database of palaeontological monuments of the Mexican instance in charge of the preservation and custody of Mexican fossils. The registry number of Universidad del Mar as a legal custodian is 3024 P.M.

The specimen from Chiapas was reported to researchers of the Museo de Palentología 'Eliseo Palacios Aguilera', Tuxtla Gutiérrez, Chiapas, Mexico – some photographs of the specimen were sent to them, but unfortunately, this was not deposited in the palaeontological collection.

Teeth nomenclature follows Scherler *et al.* (2019). Measurements were taken with a digital caliper with a resolution of 0.01 mm and with Fiji software (Schindelin *et al.* 2012). Anatomical comparisons were performed with published literature (Douglass, 1901; MacDonald 1956; Albright 1999; Lihoreau *et al.* 2009; Rincon *et al.* 2013) and fossil specimens housed in the Florida Museum of Natural History.

Used abbreviations include: c = lower canine; dc = lower deciduous canine; km = kilometres; LF = local fauna; m = lower molar; M = upper molar; mm, millimetres; and p, lower premolar.

4. Systematic palaeontology

Class Mammalia Linnaeus 1758
Order Artiodactyla Owen 1848
Family Anthracotheriidae Leidy 1869
Subfamily Bothriodontinae Scott 1940
Arretotherium Douglass 1901
Arretotherium sp.
(Fig. 2)

4.1. Referred material

From Santiago Yolomécatl, early Oligocene of Oaxaca: UMPE 193, an almost complete upper molar; and UMPE 1271, a partial lower molar. From Simojovel de Allende, early Miocene of Chiapas: unnumbered dentary fragment with p4–m2.

4.2. Description

The upper molar UMPE 193 is selenodont and heavily worn. Its protocone and metaconule are crescentic, and it does not have a paraconule (Fig. 2a); it has a deep transverse valley extending from the lingual margin towards the mesostyle, its enamel is very crenulated on the fossae and on the transverse valley; and the anterior and posterior cingula are slightly developed and

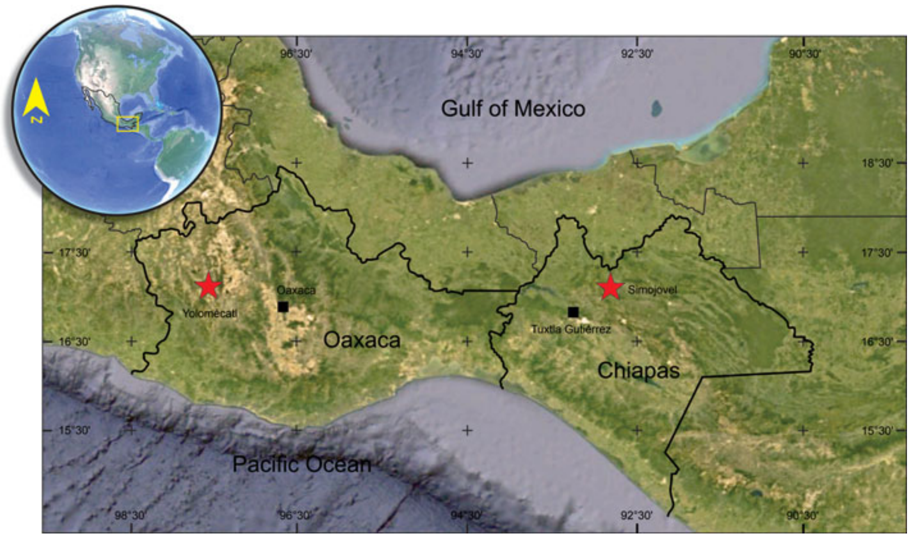

Figure 1 Map of southern Mexico indicating the location of the *Arretotherium* localities in the states of Oaxaca and Chiapas.

there is a shelf-like lingual cingulum. The labial part of the tooth is missing. Its length is 17.13 mm and its width is 14.3 mm.

The anterior part of the lower molar UMPE 1271 is preserved. A rostro-labially directed endometacristid, the metaconid, a linguo-labially directed postmetacristid and a rostro-caudally postectometacristid can be observed (Fig. 2b). There is a moderately developed anterior cingulid. The rostral part of the distolingual metacristid is also observed. The preprotocristid, the protoconid and the postprotocristid form a labial crescentic cusp. The postprotocristid reaches the postmetacristid. The enamel is slightly crenulated especially in the basal part of the tooth (Fig. 2b). The length between the preprotocristid and the postprotocristid is of 11.4 mm and the preserved part of the molar has a width of 16.4 mm.

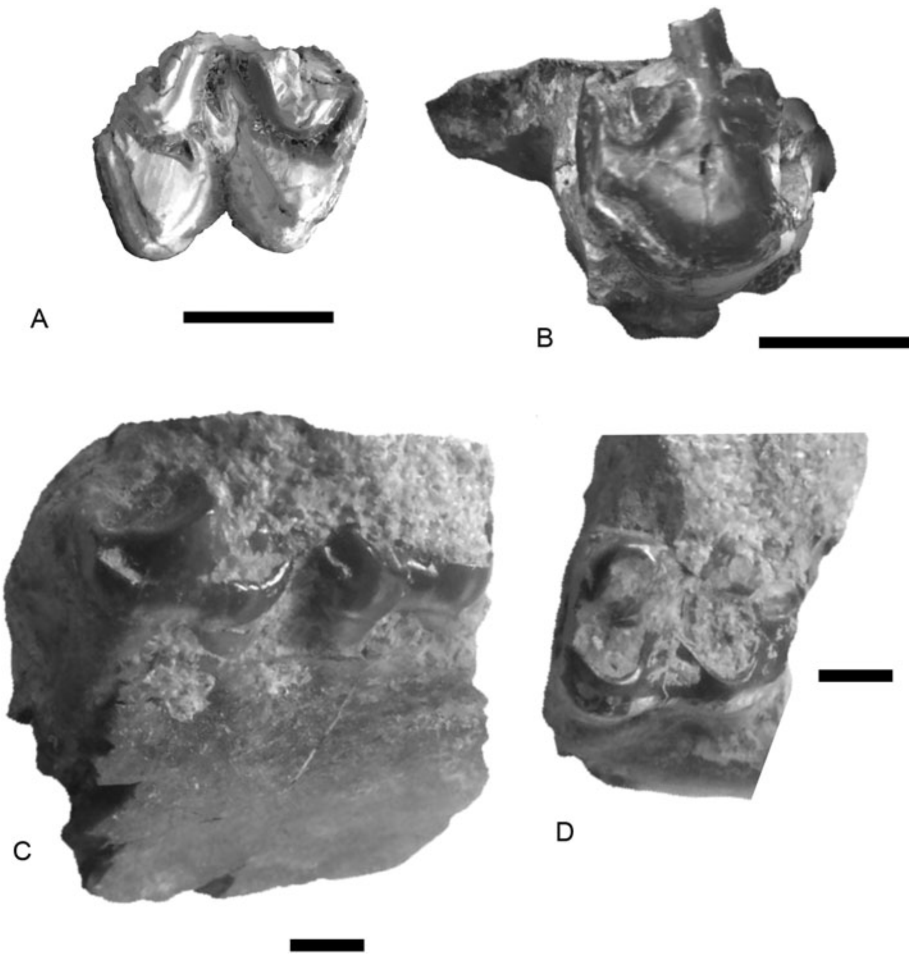

Figure 2 (a) UMPE 193, upper molar from Santiago Yolomécatl in occlusal view; (b) UMPE 1271, anterior part of a lower molar and dentary fragment in occlusal view; (c) lower p4 and m1 of a partial left mandible from Simojovel de Allende; and (d) lower m2 of the same partial left mandible in occlusal view. Scale bars = 10 mm.

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The p4 of the partial mandible from Simojovel de Allende is ovoid in outline, the protoconid is the higher cuspid of the tooth, the mesiostylid and the metastylid have a similar height, and the mesiostylid is connected to the protoconid by a strong preprotocristid (Fig. 2c). A preprotofossid is evident and the postprotofossid is deep; there is a strong cingulum in the anterior and the labial portion of the p4, running from the mesiostylid to the distostylid. The length of the premolar is 28.7 mm. The lower molars are bunoselenodont and crenulated; both protoconid and hypoconid are crescentic whereas the metaconid and the entoconid are somewhat bulbous (Fig. 2d); they have a well-developed to moderately-developed anterior cingulid, a well-developed labial and posterior cingulids and a well-developed hypoconulid (Fig. 2d). The m1 has a length of 27.1 mm and the m2 has a length of 32.5 mm (including the hypoconulid) and a width of 21.4 mm. In the m2 the length between the preprotocristid and the postprotocristid is of 13.0 mm, which is similar to that of the Iniyoo LF specimen.

4.3. Discussion

The upper molar from the Iniyoo LF of Oaxaca shares with the molars of *Arretotherium* the absence of a paraconule (that also makes it different from the rest of the North American anthracotheres, excepting *Kukusepasutanka*), the deep and continuous transverse valley and the shelf-like lingual cingulum (Albright 1999; Rincon *et al*. 2013). The Oaxacan specimen has a narrower transverse valley than the one observed in the upper molars of *Kukusepasutanka* (Macdonald 1956) and it is smaller in size. Its size is closer to the M1 of *Arretotherium acridens*, *Arretotherium fricki* and *Arretotherium leptodus* (18.0–19.25 mm of length range; see Macdonald 1956 and Albright 1999).

The p4 from Simojovel de Allende is shorter and more ovoid than the p4 of *Elomeryx* (Tsubamoto & Kohno 2011), but it is similar to the p4 of *Arretotherium* in the presence of strong cingulids and a strong preprotocristid that join the protoconid to the mesiostylid (Albright 1999). It is larger than the p4 of *Ar. acridens* and *Ar. fricki* (length range of 15.6–18.0 mm; see Albright, 1999).

The lower molars from Chiapas and Oaxaca have the typical bunoselenodont antracothere cheek teeth (Lihoreau & Ducrocq 2007) and share with *Arretotherium* the selenodont cristids associated with the protoconid and hypoconid, the absence of a premetacristid, and the crenulated enamel (Rincon *et al*. 2013) – they share with *Ar. acridens* and *Ar. meridionale* the absence of a mesiolingual metacristid (Rincon *et al*. 2013). Direct comparison of the partial lower molar UMPE 1271 with UF 244187, a partial left mandible with dc, c, dp2–dp4 and m1–m2, which is the holotype of *Ar. meridionale* (from the upper Las Cascadas Formation of Panama), and with LSUMG-V 2270, a cast of a partial right mandible fragment with m1–m3 of *Ar. acridens* (from Toledo Bend LF of Texas), revealed that the size of the Santiago Yolomécatl specimen is similar to the anterior part of the m2 of UF 244187 and that it is larger than the anterior part of the m2 or the m3 of LSUMG-V 2270. The length between the preprotocristid and the postprotocristid of the m2 of *Ar. meridionale* is 11.95 and in *Ar. acridens* is of 10.23 mm. Likewise, the length of the m1 and m2 from Simojovel de Allende, is very similar to such teeth of *Ar. meridionale* (m1 length = 26.9 mm, m2 length = 31.7 mm; Rincon *et al*. 2013; table 1).

The above-described features of the specimens from southern Mexico indicate that they can be confidently identified as *Arretotherium.* Their general morphology and size indicate a close relationship to *Ar. meridionale*, but we preferred not to assign the fossil material to the Panamian species and to wait for the discovery of additional specimens that would allow to evaluate potential intraspecific variation.

5. Palaeobiological implications

The record of *Arretotherium* in the early Oligocene Iniyoo LF of Oaxaca and in the earliest Miocene of Simojovel de Allende in Chiapas, southern Mexico, extend the geographical record of this genus in around 1600 km to the south, from the Toledo Bend LF in Texas, and in around 1692 km to the north, from the Cascadas faunal assemblage in Panama.

The genus *Arretotherium* had a very wide geographical distribution in North America during the early–middle Oligocene, from the Great Plains of South Dakota and Nebraska (Macdonald 1956; Prothero *et al*. 2022), to north-western Oaxaca, in southern Mexico – such wide geographical distribution persisted during the earliest Miocene, with records in Saskatchewan, Texas (Albright 1999; Prothero *et al*. 2022) Chiapas and Panama (Rincon *et al*. 2013). Additionally, the genus persisted in southern Mexico since the early Oligocene to the earliest Miocene.

6. Conclusions

Some anthracothere teeth and a mandible fragment from the early Oligocene Iniyoo LF of Santiago Yolomécatl in north-western Oaxaca and the earliest Miocene of Simojovel de Allende in Chiapas were described. The observed morphology and size of these specimens indicate that they represent the first records of *Arretotherium* in México.

These new records link the previous ones from the early Miocene of Texas and Panama. *Arretotherium* had a comparable age range in Mexico and the United States, spanning from the early Oligocene to the early Miocene.

7. Acknowledgements

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9. Conflicts of interest

None.

10. References

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