Title

The first Paleogene mustelid (mammalia, Carnivora) from southern North America and its paleontologic significance

Permalink

https://escholarship.org/uc/item/8835167f

Authors

Ferrusquía-Villafranca, Ismael

Wang, Xiaoming

Publication Date

2021-08-01

DOI

10.1016/j.jsames.2021.103236

Peer reviewed

The first Paleogene mustelid (mammalia, Carnivora) from southern North America and its paleontologic significance

Ismael Ferrusquía-Villafranca [a,*], Xiaoming Wang [b]

[a] *Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación Sin Número, Coyoacán, Ciudad de México, C.P. 04510, México*
[b] *Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA, 90007, USA*

ARTICLE INFO

ABSTRACT

Mustelidae are the largest and most diverse family of carnivores, its record dates back to the Early Oligocene, and its early history occurred in western Europe; therefore, the finding of a basal mustelid in southeastern Mexico (northwestern Oaxaca) is quite important.

The material found is a very small, nearly complete skull collected from the Yolomécatl Formation, a ~650 m thick lacustrine/fluvial succession interbedded by tuff sheets, yielding a ^{40}Ar-^{39}Ar age of 40.3 ± 1.0 Ma, which places this unit and associated fauna in the latest Uintan-earliest Duchesnean NALMAs. However, a purported early Arikareean age has been proposed on the basis of uncritical/unsupported biochronological and isotopic data. The skull is referred to a new genus and species of Mustelidae on the basis of its unique combinaton of plesiomorphic and derived characters. Cladistically, it falls in an unresolved polytomy that inludes only basal European mustelids. This poses a biogeographic problem unsolvable with the evidence at hand: either the new taxon originated in Europe from as yet unknown ancestors, then migrated to southern (tropical) North America, or it evolved there, independently attained the synapomorphies of basal Mustelidae, and migrated to Europe. Finally, the new taxon fits the weasel-ecomorph, approaching the appearance of the extant *Mustela frenata*, thus suggesting tunnel-hunting habits.

1. Introduction

The Sierra Madre del Sur Morphotectonic Province in southeastern Mexico is very significant for both academic and economic reasons. It contains important mineral resources (iron, coal and many others). Its complex geologic makeup includes Precambrian to Quaternary rock units, and records their development and evolution, as well as the assemblage of the tectonic terranes that now form this region. In the study area, the Paleogene sequence unconformably overlies older formations, and includes two volcanic units, two pyro-epiclastic units, and a small ?dacitic intrusion.

Additionally, from one of the pyro-epiclastic units, the Yolomécatl Formation in northwestern Oaxaca (at ~17° N. Lat., in the tropics), we recovered an ?early Oligocene or less likely late Eocene mammal assemblage, the Yolomécatl local fauna, which has a direct bearing on the constitution, evolution and biogeographic relationships between mammal faunas of North and South America, as well as those of Eurasia. The description and discussion of a new carnivore presented here, is a significant addition to the reports coming out on this fauna (e.g.,

Jiménez-Hidalgo et al., 2015; 2018; Ferrusquía-Villafranca et al., 2018a; Ortíz-Caballero et al., 2020). Such reports are also a welcome increase to the meager published record of Paleogene terrestrial vertebrates in Mexico which includes the following occurrences:

(a) Las Tetas de Cabra local fauna, Wasatchian of Baja California (Novacek et al., 1991). (b) Marfil local fauna, early Bridgerian of Guanajuato; a lava flow interbedded in the faunal bearing Guanajuato Red Conglomerate was K–Ar dated as 49.3 ± 1.0 Ma by Aranda-Gómez and McDowell (1998); faunal reports are in Fries et al. (1955), Black and Stephens (1973), Ferrusquía-Villafranca (1989, 2005). (c) Yolomécatl (= Iniyoo) local fauna, ?early Arikareean or possibly latest Uintan-earliest Duchesnean of Oaxaca; a glass shards sample from the tuff sheet interbedded in the namesake, fossil-bearing formation was ^{40}Ar-^{39}Ar dated as 40.3 ± 1.0 Ma (Ferrusquía-Villafranca et al., 2016); faunal reports are in Jiménez-Hidalgo et al. (2015, 2018) and Ferrusquía-Villafranca et al. (2018a). (d) Rancho Gaitán local fauna, Chadronian of Chihuahua (Ferrusquía-Villafranca, 1969; Ferrusquía-Villafranca et al., 1997).

---

2. Geographic and geologic settings

The study area (Fig. 1) includes some 90 sq. km of rugged terrain within the Mixteca Region, northwestern Oaxaca State, Sierra Madre del Sur Morphotectonic Province, southeastern Mexico, between 17°25′–17°30′ N. Lat. N and 97°29′–97°36′ W Long. (Fig. 2). The Cenozoic sequence (Figs. 2 and 3) unconformably overlies carbonate rock units of Late Jurassic to Late Cretaceous ages. The area also includes the Mixteco/Oaxaca Terrane boundary, namely the Tamazulapam fault.

The Paleogene sequence (Figs. 2 and 3) unconformably overlies older formations, and consists of five lithostratigraphic units (Ferrusquía--Villafranca et al., 2016): Nduayaco "Group" (pre-Late Eocene, largely an andesitic lava flow stack), Yolomécatl Formation (seemingly late Middle Eocene or ?early Oligocene, largely fine clastic, and fossiliferous), Nicananduta "Group" (early Late Oligocene, another andesitic lava flow stack ^{40}Ar-^{39}Ar dated as 27 ± 1.0 Ma), it intertongues the Chilapa Formation (a tuffaceous, fluvio-lacustrine succession), and the Ticú Dome (a small, shallow ?dacitic intrusion). Finally, Quaternary deposits and soils unconformably overlie the preceding units (Figs. 2 and 3). The structural record chiefly includes folds in the Mesozoic units, and faults in the Paleogene ones.

Paleontologically, the most interesting unit is the Yolomécatl Formation (wrongly taken as the Chilapa Formation, Jiménez-Hidalgo et al., 2015 and subsequent papers), a ~650 m thick, vertebrate-bearing, red clastic, lacustrine/fluvial succession (Ferrusquía-Villafranca et al., 2018b) that fills the namesake triangular graben, which traces its origin to the Tamazulapam fault dynamics. Felsic tuff sheets interbed this succession, one of them yielded from glass shards a ^{40}Ar-^{39}Ar age of 40.3 ± 1.0 Ma (Ferrusquía-Villafranca et al., 2016), which places this unit and its fauna in the late Middle Eocene, i.e., latest Uintan-earliest Duchesnean North American Land Mammal Ages (NALMA, but see below). We are aware that the dependability of glass dating increases with the number of samples dated, however limited resources prevented us from ordering more than one analysis. It should be noted that the Holotype of *Oaxacagale ruizi* was dug out from brick red, clayey siltstone strata some 55 m above the dated tuff sheet, within a continuous stratal succession of the Yolomécatl Formation, which lies exposed throughout its outcrop area, forming an extensive zone of badlands. This setting precludes the possibility that the specimen could have been secondarily derived from an overlying, younger unit.

2.1. The probable early Arikareean age of the Yolomécatl Formation and local fauna

Jiménez-Hidalgo et al. (2019a) revised the age of the Iniyoo local fauna (= the Yolomécatl l.f.), changing it from Chadronian (Late Eocene, Jiménez-Hidalgo et al., 2015) to early Arikareean (Early Oligocene) on the basis biochronologic data from taxa that have not been formally described (nor illustrated for the most part), and a radioisotopic age of 30.6 Ma derived not from analytic work ordered by him or his team, but from citing or adjusting ages published by others, as shown: (a) Guerrero-Arenas et al. (2018) present an age of 32.9–35.7 Ma taken from Martiny et al. (2000), and Santamaría-Díaz et al. (2008), dating of the Cañada María Andesite, which concordantly overlies the Chilapa Formation (actually the Yolomécatl Formation, as discussed previously). (b) Jiménez-Hidalgo et al. (2019b) mentioned the age of 30.6 Ma that falls in the geochronometric range expressed by Santamaría-Díaz et al. (2008), 29.0 to 35.6 Ma obtained by the U–Pb isotopes from detrital Zircon crystals. (c) Jiménez Hidalgo et al. (2019c) reports an age of 30.6 to 28–29.0 Ma obtained from U–Pb isotopes in detrital Zircon crystals taken from a sandstone bed that overlies the fossiliferous strata, whose geographic location is not given; the geochronometric interval corresponds to the early Arikareean NALMA. (d) Jiménez-Hidalgo et al. (2019a) mention that the Early Oligocene lithostratigraphic units represent a fluvio-lacustrine succession assigned to the Chilapa Formation. The correction of this mistake is presented in the Geologic Setting section of this manuscript. (e) Guerrero-Arenas et al. (2020) cited the age reported by Santamaría-Díaz et al. (2008) of 35.6 to 29.0 Ma for the Chilapa Formation (actually the Yolomécatl Formation as discussed above) and disclose how they arrived at the 30.6 Ma datum. (f) Ortiz--Caballero et al. (2020) mention a new U–Pb Zircon maximum (sic) depositional age of 28–29 Ma for the Chilapa Formation (actually the Yolomécatl Formation as shawn above), but fail to tell the source reference and the location of the dated material; they add that such unit in the study area is capped by volcanic rocks (i. e., Nicananduta Group, Ferrusquía-Villafranca et al., 2016) dated as of 27.7 ± 0.7 Ma. Finally, (g) Butrón-Xancopinca and Jiménez-Hidalgo (2020) insist that the fossiliferous unit is the Chilapa Formation (an error corrected previously), and that its age is 30.6 Ma obtained by the U–Pb isotopes from detrital Zircon crystals collected in the site, but neglect to explicite the source reference, as well as to locate the site either by geographic coordinates, or plotting it in an appropriate map. Under these circumstances, the new age assignment is taken as provisional for want of objective evidence.

3. Materials and methods

A nearlyomplete cranium, discovered in the Yolomécatl Formation, northwestern Oaxaca State, is the basis of this study. The taxonomic

Fig. 1. Index map showing the location of the Yolomécatl Area (pointed by an arrow), Oaxaca, Mexico.
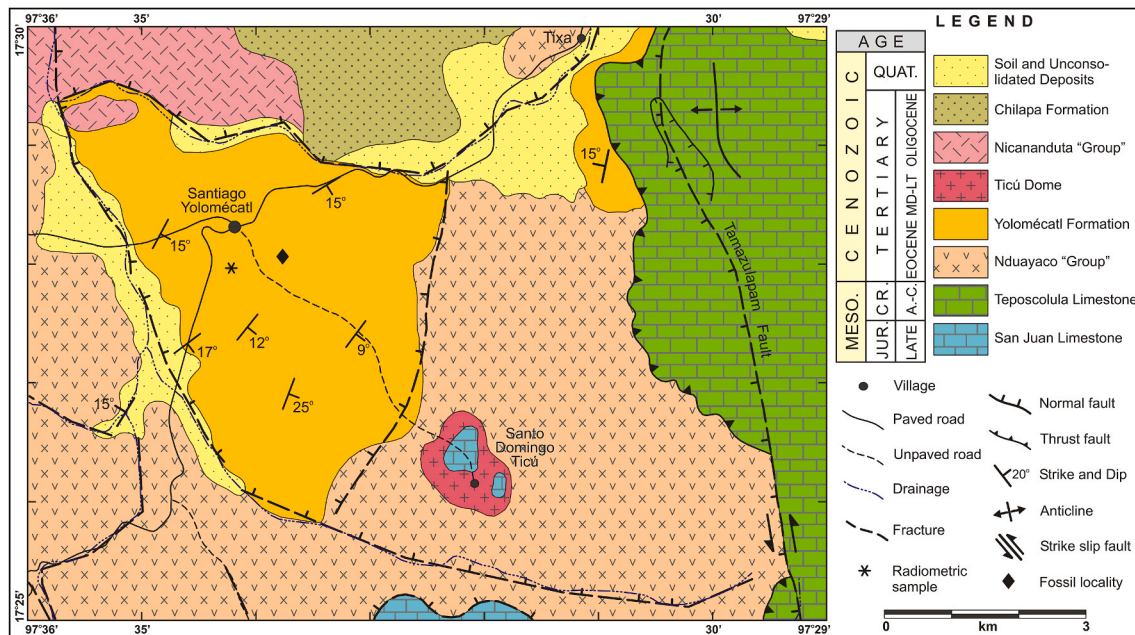
Fig. 2. Geologic map of the Yolomécatl Area, Oaxaca.

identification was obtained following standard procedures, which in this instance include detailed comparisons of key characters and measurements (expressed in milimeters) with those of contemporaneous or potentially related taxa to *Oaxacagale ruizi* new gen. and sp. (see Supplementary Material Appendices A and E) in order to assess their congenerity or lack of with *Oaxacagale ruizi*. The taxonomic position of the new taxon was established through a cladistic analysis ably performed by one of us (X.G., highly experienced in cladistics of basal carnivores), in spite that some anatomical characters like upper dentition (save parts of P3–P4), some cranial foramina, and mandible are poorly preserved or lacking in the holotype, and could only partly be coded in published data matrices, e.g. in that of Valenciano et al. (2016), only 13 characters out of 73 (= 17.8%) could be coded; in the data base of Wang et al. (2005b) only 16 characters out of 39 (= 41%) could be coded; in the data base of Finarelli (2008), 29 characters out of 80 (=36.2%) could be coded; finally, in the data base of Wolsan (1993) only 10 characters out of 66 (= 15.1%) could be coded. We followed the systematics of Wang et al. (2005b).

3.1. Repositories and institutional abbreviations

The type specimen IGM-7998 is housed in the Colección Nacional de Paleontología, Instituto de Geología (IGM), Universidad Nacional Autónoma de México, Ciudad de México, México. A plastic cast is deposited in the Natural History Museum (NHM) of Los Angeles County, Los Angeles, California, USA.

4. Systematic paleontology

Class MAMMALIA Linnaeus, 1758.
Order CARNIVORA Bowdich (1821).
Suborder CANIFORMIA Kretzoi (1943).
Infraorder ARCTOIDEA Flower (1869).
Parvorder MUSTELIDA Tedford (1976).
Family MUSTELIDAE Fischer von Waldheim, 1817
"PALEOMUSTELIDAE" Baskin (1998).
Oaxacagale gen. nov.
Type and only species— *Oaxacagale ruizi*.
Descriptive diagnosis— *Oaxacagale* is distinguished from other carnivores as follows:

Small overall size (skull length < 50 mm); dorso-ventrally low cranium, whose antero-posterior length is ~10% greater than its transverse width; short trapezoid face nearly as antero-posterior long as transversely wide; large, well ossified, antero wider auditory bullae; basicranium with well separated posterior carotid canal and posterior lacerate foramen; shearing, delicate dentition with no trace of cingula.

Differential diagnosis— *Oaxacagale* differs from "Miacids" (*Protictis* and *Miacis*) in having short rostrum with wider muzzle, less elongate cranium, and ossified auditory bullae; from *Lycophocyon* in having a less elongate skull with a narrower rostrum, wider anterior part of postorbital cranium, absence of sagittal crest, small overall size, and ossified auditory bullae; from *Ceruttia* in having slightly smaller overall size, ossified auditory bullae, P4 without cingulum (hypothetically all cheek teeth lack cingula), with occlusally bulging protocone and parastyle; from *Prohesperocyon* in having short rostrum, less laterally expanding maxilla; from *Hesperocyon* in having wider rostrum and a large/unreduced P4 protocone; from "neomustelids" in having a poorly developed suprameatal fossa, as well as a minute alisphenoid canal; from *Mustelavus* in having a lesser developed suprameatal fossa, a more complex, less compressed P3 with minor anterior and posterior cuspules, larger P4 with a protocone anteriorly bulging, and very little developed temporal crests; from *Plesictis* in having a lesser developed suprameatal fossa, very faintly developed temporal crests (low, laterally projected crest on the postero-external corner of the cranium), wider anterior part of the rostrum, maxilla (anterior base of the zygomatic arch) flared laterally starting at P4, and transversely wider auditory bullae; from the basal mustelids *Plesictis* in having very little developed suprameatal fossa and temporal crests; from *Mustelictis* in having a less elongate skull and larger tympanic bullae and very shallow suprameatal fossa; from *Bavarictis* in lacking Y-shaped, strong sagittal crest and having a delicate skull built; from *Pseudobassaris* in being much smaller, having a delicate skull built and occiput not distinctly higher than the brain case; from *Corumictis* in being much smaller and lacking well-developed suprameatal fossa and temporal crests; from Leptarctinae in having a delicate skull, very faintly developed temporal crests, ectotympanic (bulla) not fused with the glenoid process, shearing dentition, and not quadrate cheek teeth; from the leptarctine *Kinometaxia* in having the P4 without cingulum; from *Schultzogale* in being much smaller, and having very faint double temporal crests, and dorso-ventrally deep, laterally flared zygomatic plate; from *Palaeogale* in having no transverse sulcus
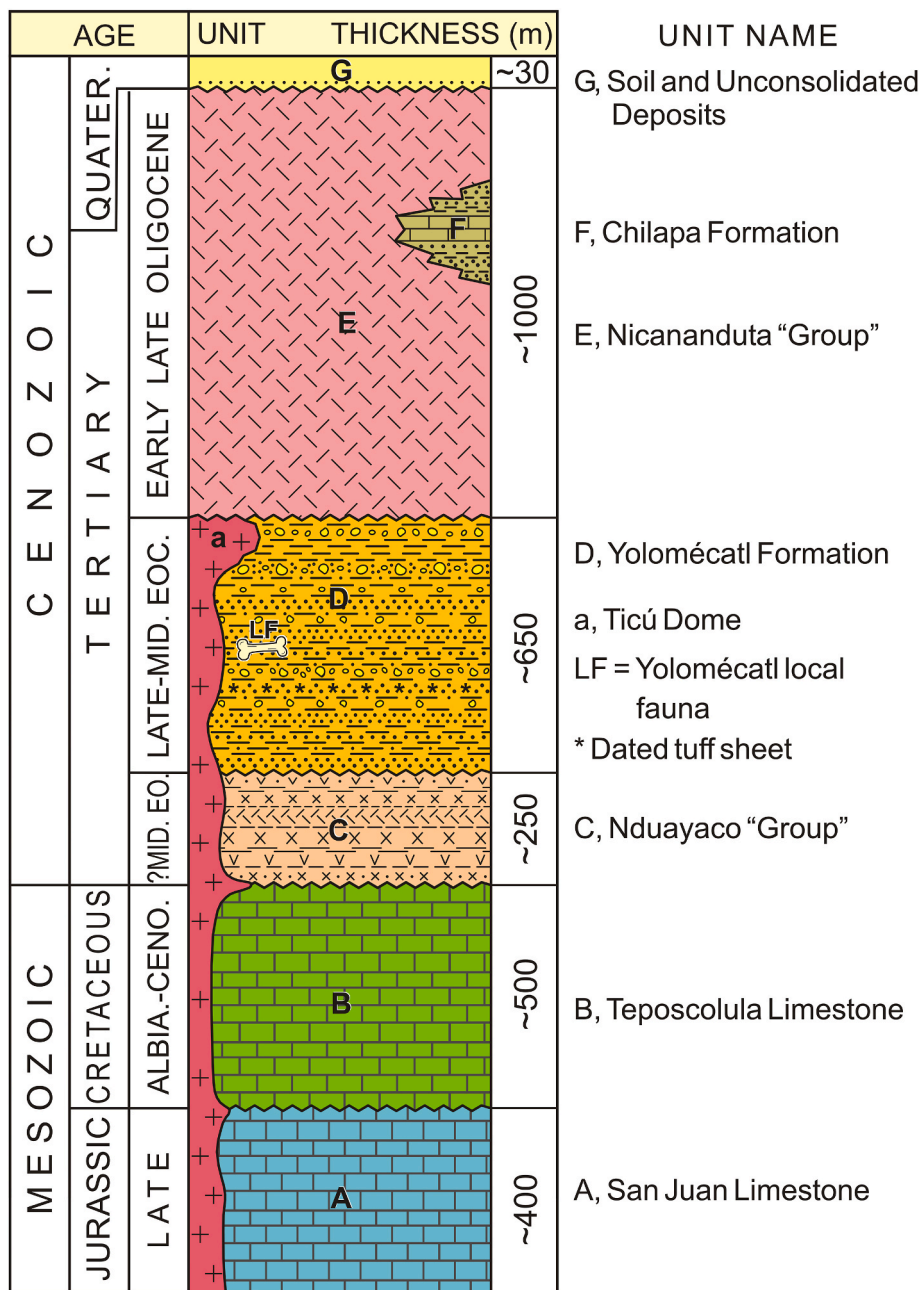
Fig. 3. Lithostratigraphic column of the Yolomécatl, Oaxaca Area. Notice the level of occurrence of *Oaxacagale ruizi* and the dated layer.

separating the cerebral and cerebellar cranial regions, larger tympanic bullae, P4 with stouter parastyle and protocone bases separated by a deeper concavity.

Occurrence— IGM 7998, holotype of *Oaxacagale ruizi*, the type and only species of this genus, was collected from the questionably early Oligocene or possibly late Middle Eocene Yolomécatl Formation, in the vicinity of Santiago Yolomécatl, northwestern Oaxaca, southeastern México. See further information in the geographic and geologic settings section above.

Etymology— From the State of Oaxaca where it was found, and *gale*, Greek for a small carnivore like cat or weasel.

Oaxacagale ruizi sp. nov.

Figs. 4–6; Table 1.

Holotype and only specimen— IGM 7998, a nearly complete cranium lacking both zygomatic arches, and bearing partial right P3–P4.

Diagnosis— As for the genus.

Occurrence— The fossil-bearing locality lies at 17°28' N and 97°33' W, 1.7 km ESE of Santiago Yolomécatl, within a continuous section of the Yolomécatl Formation placed ~55–65 m above the ^{40}Ar-^{39}Ar dated tuff sheet. The specimen was dug out from the fossil-bearing stratum, thus excluding any possibility of contamination from younger material up section.

Etymology— The vernacular name *ruizi* comes from the last name of M. Sc. José E. Ruiz-González, a member of the field party that found and collected the holotype, and helped in all aspects of the project.

Description— Skull generalities. It (Fig. 4; Table 1) is elongate, short-faced and small: antero-posterior length = 48.50 mm; transverse width = 21.68 mm (across parietals), and H = 18.83 mm (~35% of antero-posterior length), thus resembling particularly in the face that of the extant *Mustela frenata*, the ferret (Supplementary Material Appendix B, Fig. B.28), whereas other extant mustelids such as *Eira barbara*, *Galictis vittata*, *Taxidea taxus* and *Spilogale pygmaea* are clearly different
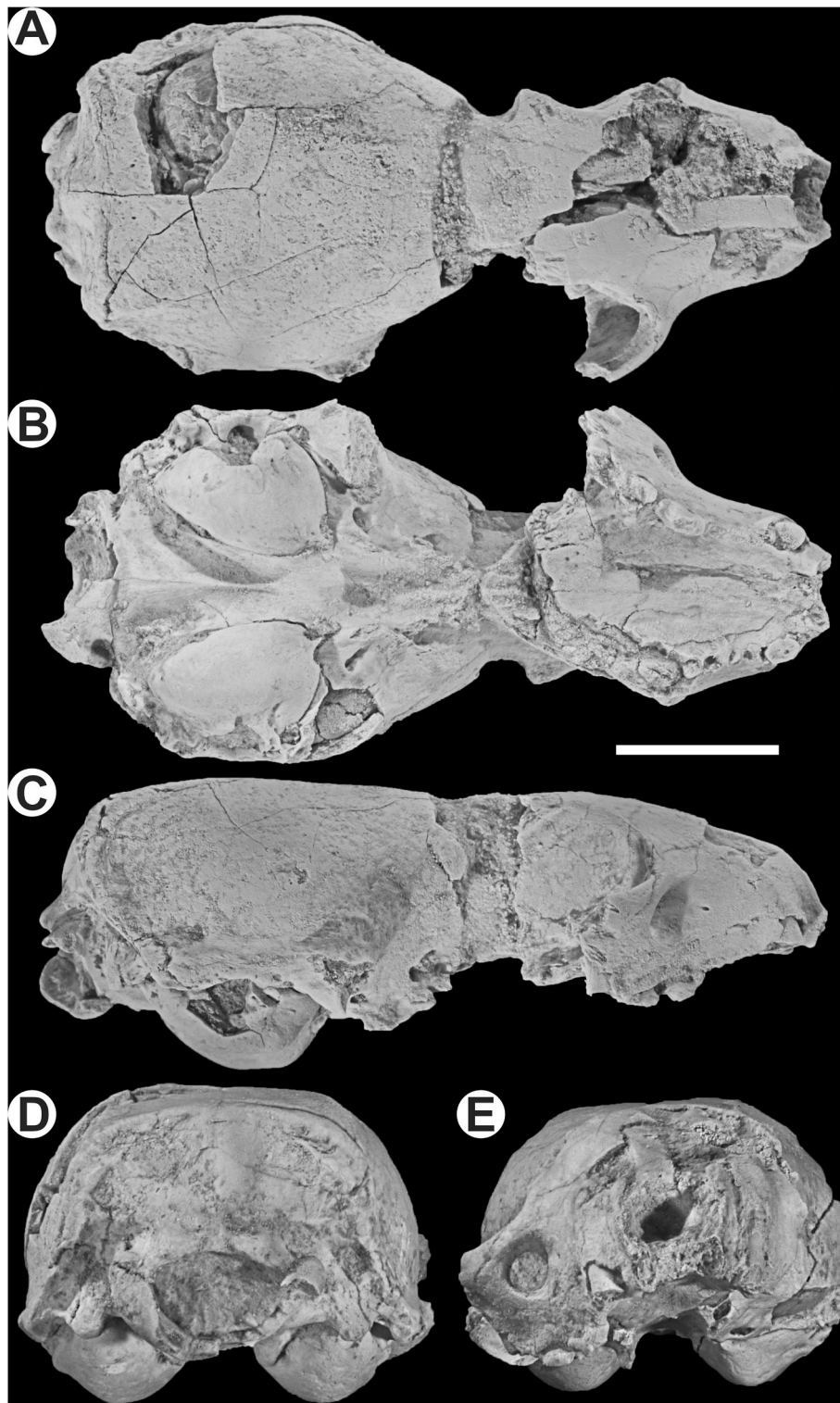
Fig. 4. A nearly complete cranium with partial P3–P4 of *Oaxacagale ruizi*, Holotype IGM 7998. **A,** Dorsal view. **B,** Ventral view, notice the large tympanic bullae. **C,** Lateral (right) view. **D,** Posterior view. **E,** Anterior view, notice the large left infraorbital foramen. Scale bar = 10 mm.

(see Supplementary Material Appendix A; Supplementary Material Appendix B, Figs. B.24–27). It should be noted that this close correspondennce in size and facial morphologic resemblance with *Mustela frenata* lead us to restrict the comparisons of *Oaxacagale* with extant mustelids to this taxon. Other resembling taxa include procyonids and some early to early middle Paleogene small carnivores such as *Hesperocyon*, *Mustelavus*, and *Palaeogale* (Supplementary Material Appendix B, Figs. B7, 8–10, 14–16). The bones that make up the skull are already fused, hence their sutures are not discernible, which precludes a detailed anatomical description of individual bones. This condition is also observed in the extant *Mustela*, felids and other carnivores. In spite of its delicate thickness (approximately that of a turkey egg shell), the cranium bones form a compact, resistant box.

The skull (Fig. 4A–C, 6) is readily divided in two unequal regions:

Fig. 5. Dentition of Holotype IGM 7998, *Oaxacagale ruizi*. **A,** occlusal view. **B,** enlargement of P3–P4. **C,** restored C1–P2 of the right half of the face; it should be noted that M1-2 are hypothetical. Scale bar = 2 mm.
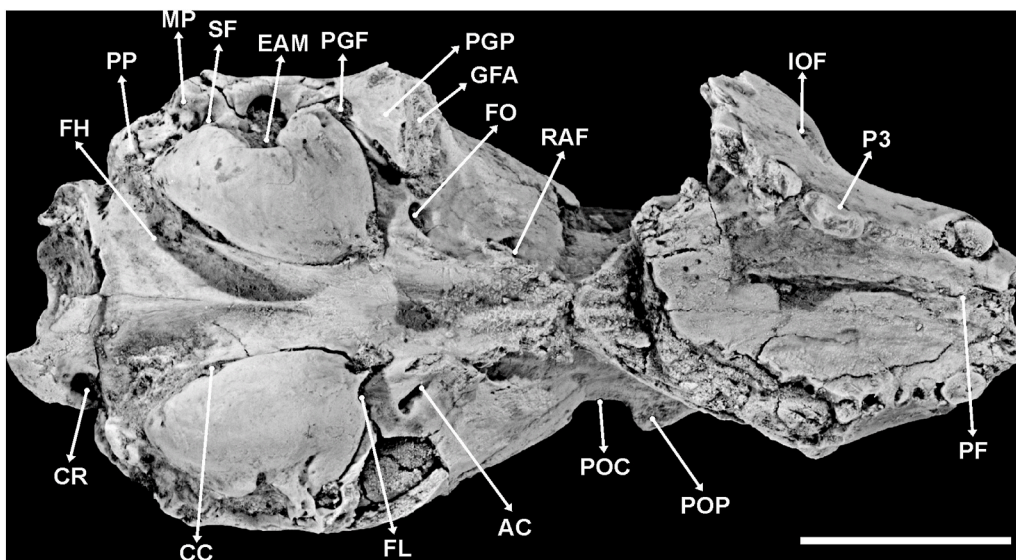
Fig. 6. Ventral view of Holotype IGM 7998, *Oaxacagale ruizi* showing main structures. Abbreviations: **AC,** Alisphenoid canal. **CC,** Carotid canal. **CR,** Condylar recess. **EAM,** External acoustic meatus. **FH,** Foramen for the hypoglossus. **FL,** Lacerum foramen. **FO,** Oval foramen. **GFA,** Glenoid fossa area. **IOF,** Infraorbital foramen. **MP,** Mastoid process. **PF,** Palatine foramina. **PGF,** Postglenoid foramen. **PGP,** Postglenoid process. **POC,** Postorbital constriction. **POP,** Postorbital process. **PP,** Paroccipital process. **RAF,** Rostral alar foramen. **SF,** Stylomastoid foramen. Scale bar = 10 mm.

facial (small, short, and broadly trapezoidal), and **cranial** (antero-posteriorly much longer than the facial region); both meet at the postorbital constriction, which is somewhat narrower than in *Mustela* skulls (Supplementary Material Appendix B, Fig. B.28) of similar size. The skull is rather flat, but laterally round (Fig. 4D–E); its cranial height is about 1/3 that of the antero-posterior length. The total width is unknown because both zygomatic arches are broken off (Supplementary Material Appendix C).

Face. (Fig. 4A–C, 4E, 5–6; Table 1). The skull is antero-posteriorly short, slightly less so than in *Mustela* skulls of similar size, its facial anterior part (muzzle transverse width ~7.0 mm) is less acute than that of Recent *M. frenata* (~5.3 mm in UAM-2247, common size for the species, Hall, 1981), and bears a nearly circular narial opening (Fig. 4E, diameter = 5.4 mm) that is much smaller than that of extant *Mustela* skulls of similar size, which is ovoid (dorso-ventral height = 6.5 mm, transverse width = 4.6 mm). Laterally, the maxilla is concave, because

Table 1

Skull measurements of IGM 7998, slightly damaged skull with P3–P4 (only the base), Type specimen of *Oaxacagale ruizi* (A) and UAM-138 (B), skull of the extant *Mustela frenata*.

	A	B
Antero-posterior skull length (Eliminating the ~1.81 mm thick fracture filling)	48.5	47.14
Antero-posterior facial length (measured down to the postorbital process)	22.5 (18.0)	15.26
Antero-posterior cranial length (measured from the postorbital process)	26.1 (27.7)	32.81
Dorso-ventral cranial height (including the auditory bulla)	18.8	17.78
Maximal transverse cranial width (measured across parietals)	23.0	20.78
Minimal transverse cranial width (measured at the postorbital constriction)	08.0	10.26
Right Auditory Bulla transverse width	07.9	8.74
Right Auditory Bulla antero-posterior length	11.6	14.41
Occipital condyles transverse width (external)	11.5	13.18
Dorsoventral height of the right zygomatic arch maxillary base	7.2	4.55
Foramen magnum width	07.8	8.05
Foramen. magnum dorso-ventral height	05.2	5.40
Intercanines internal width (measured from the canines lingual side)	05.87	5.45
Intercanines external width (measured from the canines labial side)	09.2	9.09
Infraorbital foramen diameter [circular in IGM 7998, oval in UAM-138]	02.0	1.8–3.5

Measurements (in mm).

at P3 it makes a sharp, postero-externally directed bend (not as pronounced as in *Puijila darwini*, an early pinniped, Rybczinski et al., 2009), thus stressing the short-facedness of the skull (Fig. 4B, 5A), and expanding the mouth roof postero-laterally; in *M. frenata*, the maxilla is laterally slightly less concave. The left side of the facial roof is largely missing (Fig. 4A), save from the posterior part, which bears a short, blunt postorbital process (Fig. 6) that separates the orbit from the much larger masseteric fossa. Pointed apophyses are common in both primitive and advanced carnivores. The orbit seems to have been slightly larger (~18% judging from the transverse width = 8.3 mm) than in the extant *M. frenata* (transverse widtth = 6.8 mm in the UAM-2247 specimen). On the right side, the dorsal region includes the nasal, premaxilla, frontal, maxilla, lacrimal and jugal. Ventrally (Fig. 4B, 5A, 6), the face includes the premaxillae, and maxillae (palatal portion). The palate is short and broad (Figs. 5 and 6) resembling that of the Bridgerian creodont *Patriofelis* (Gazin, 1957), and it is also both antero-posteriorly and transversely concave (thus providing more space than a flat roof). The incisive foramina (barely discernible) are far anteriorly set, just behind the incisors and anterior to the canines, as in the extant *Mustela*; no palatine fenestrae or fissures are present (also as in *Mustela*); the palatine sulcus is not well developed. Most of the left maxilla and palatine parts are missing.

Both zygomatic arches are lacking too (Fig. 4A–B, 6), but the zygomatic plate of the right arch is preserved (Fig. 4A–B, 5), its dorso-ventral height is 7.7 mm, i.e., slightly taller than in *Mustela*, and in the leptarcines; it bears a large, anteriorly faced, round infraorbital foramen (Fig. 4C, diameter = 2 mm) set above the posterior half of P3 and the anterior half of P4; in the in the much larger and stronger, early Miocene Chinese *Kinometaxia*, this foramen, as expected, is quite larger (diameter = 8.5 mm, Wang et al., 2004); in *Mustela*, this plate is less high (h = 5.2 mm), bears also an equally set, transversely elongate, oval infraorbital foramen, which is slightly larger than in *Oaxacagale ruizi*. The small nutrient foramina set above (at the junction of the zygomatic arch) and behind the infraorbital foramen present in *Mustela*, are absent in *O. ruizi*. The antero-posteriorly short and transversely wide bony structure that supports the right glenoid fossa is present (Fig. 6; Supplementary Material Appendix D), and so is the fossa; the left fossa is not preserved. The alisphenoid canal is minute and placed very close to the ovale foramen.

The palatine foramina (set just behind the incisors in *Mustela*) are not observed because the anterior part of the palate is partly damaged (Fig. 4B, 6). Notice also that the posterior part of the palate is broken off, so it is not possible to determine how far posteriorly the palate and internal nares extended. In the Chadronian-Orellan *Mustelavus* and the long ranged Chadronian-Arikareean) *Palaeogale* (Supplementary Material Appendix B, Figs. B.8–10, 14–16), the choanae are placed anteriorly (i.e., not far from P4-M1). This feature is a plesiomorphic character in musteloids; whereas in extant mustelids, the choanae reach farther to a point corresponding to the posterior third of the temporal fossa antero-posterior length.

Cranium (Fig. 4; Table 1). It is longer (and wider) than the face, but its antero-posterior length is ~24% shorter and transversely about 10% narrower than in the extant *Mustela frenata*, which is also slightly taller (Supplementary Material Appendix B, Figs. B1 and B-28). None the less, the cranium (and cranial capacity) of *O. ruizi* is relatively large for an early/basal mustelid. Dorsally the cranium is flat (Fig. 4C) not dome-like as in *M. frenata* (Supplementary Material Appendix B, Fig. B.28), and the following bones (actually "bone regions," because sutures are not discernible) are observed: Frontal, temporal, parietal and upper part of the occipital, which forms a well-developed nuchal crest. The cerebellar and cerebral regions are not distinguished externally by broad and shallow transverse depressions, as in *Palaeogale* (Scott and Jepsen, 1936, pl. XIV). Lack of a sagittal crest (Fig. 4A) or of well temporal crests suggests that the temporal muscles were weaker than in *Mustela*, whose skull shows a modest, Y-shaped sagittal crest that reaches the postorbital processes, thus providing firm anchorage for such muscles. However, the cranium of *Oaxacagale ruizi* shows a faint ridge on the right side that emerges from the postero-external corner of it (barely shown in Fig. 4A), where it laterally stands out from the temporal surface, meets the nuchal crest and runs anteriorly towards the cranial constriction (without meeting it); the cranial surface along this ridge is on both sides a little rough, suggesting that it is an incipient right temporal crest of a cranium with two temporal crests, seemingly anticipating the fully developed condition observed in the early Miocene Chinese leptarctine *Kinometaxia guangpui* (Supplementary Material Appendix B, Fig. B.13) and other leptarctines (Wang et al., 2004), or in the Early Oligocene-Early Miocene French mustelid *Plesictis* (Piveteau, 1961, p. 736, Fig. 117). Dorsally, the anterior cranial part behind the post-orbital constriction is narrower (~20%) than in *Mustela* (whose cranium is also taller), thus indicating a (moderately) smaller cranial capacity. On the postero-lateral part of the cranium, the mastoid and parocciptal processes are present, but little developed.

The posterior cranial region exhibits a quadratic outline (slightly dorsally narrower, Fig. 4D); it entirely consists of the occipital bone which bears the foramen magnum (ovoid, dorso-ventral diameter = 5.2 mm; transverse diameter = 9.2 mm), laterally flanked by the occipital condyles (the right one is nearly missing) that articulate the skull with the vertebral column. Above the foramen magnum, this bone shows in the right side a shallow and narrow, three-sulcated depression that provided anchorage to the neck muscles; on the left side, this depression is not well developed. It should be noted that the occipital of *Mustela* shows five depressions (one central and two lateral ones) separated by short, wide and low ridges, which afford stronger anchorage to such muscles than in *Oaxacagale ruizi*. The occipital margin is fused with that of the parietals, forming a well-developed nuchal crest (Fig. 4A, 4D, for additional anchorage to the neck muscles). The mastoid process is laterally short and set postero-externally to the bulla tympanica; the parocciptal process is short too, posteriorly very close to the other process and placed behind it, adjacent to the bulla.

Ventrally (from back to front) the following features are observed (Fig. 4B, 6): Basilar portion of the occipital, basisphenoid, vomer, pterygoid (including parallel wings), all roof the naso-pharyngeal canal, which shows a delicate (thin and low) sagittal ridge that laterally separates two, very shallow and relatively wide, antero-posteriorly set depressions. Such ridge is less developed in *Mustela*.

Tympanic bullae. Large, inflated and fully ossified, being the dominant features of the cranium in ventral view (Fig. 4A–C, 6; Table 1); however, the bullae of *Mustela* are much (~33%) larger (Table 2). The bulla surface is smooth in both *Oaxacagale ruizi* and in the extant taxon. In the cranium of *O. ruizi* the bulla outline is ovoid, antero-posteriorly elongate, and diminishing transversely in size posteriorly, so that their end is a blunt apex. The bulla cross section is round, not flat as in *Mustela*. The bullae are set significantly closer anteriorly than posteriorly (Fig. 4B, 6), a character present in many basal arctoids, and a narrow nasopharyngeal canal separates them. In *Mustela* however, the bullae are set nearly parallel to each other, and the canal is wider. The left bulla is partly broken, exposing the external acoustic meatus (whose cross section is roughly circular, and its estimated diameter ~2.5 mm), partly filled with hard silty matrix. Even further preparation of both left and right meati did not disclose a well developed suprameatal fossa, but only a shallow depression (Supplementary Material Appendix D), so we parsimoniously assume that if it was at all present in *Oaxacagale ruizi*, is very little developed for a basal mustelid, given its purported Arikareean age; alternatively, such little development could be interpreted as a sign of this structure becoming lost, which eventually would make *Oaxacagale* an early neomustelid.

Basicranial foramina. The moderate state of preservation of the specimen (fractured and missing some parts), allowed us to confidently identify only these foramina (Fig. 6): rostral alar (large), oval (also large), alisphenoid canal (adjacent to the oval), lacerum (slightly smaller than the oval), carotid canal (placed far from the lacerum, on the medial margin of the tympanic bulla, about two thirds posteriorly to its anterior margin, see Fig. 4A, 6). Other ventral features include these: postglenoid foramen, short, small mastoid and paroccipital processes (larger than in *Mustela frenata* though), the very small foramen for the hypoglossus nerve, and a relatively large condyle recessus (see Fig. 6 and Supplementary Material Appendix D). No further foraminal description is needed, given the state of preservation of the *O. ruizi* holotype.

Teeth. The teeth are unfortunately largely missing.

Incisors. The muzzle tip is transversely narrow, leaving room only for minute incisors (Fig. 4B, 5A, 6), which are largely gone. The lateralmost incisors (right and left I3) are broken off at the base, they are antero-posteriorly elongate (antero-posterior length = 2.3 mm, transverse width = 1.3 mm), with a middle constriction, thus roughly producing an 8-like occlusal outline. The left side shows a broken portion of enamel, interpreted as an I2. The muzzle shows room for I1, but damage prior to collecting prevented its preservation.

Canines. There is a small space between I3 and Canine, which accommodates the lower canine tip. The canines are broken at the base (Fig. 4B, 5A; Table 2), their outline is ovoid, they are antero-posteriorly

longer than transversely wide (antero-posterior length = 3.5 mm; transverse width = 2.5 mm). Given the relatively close size (and up to certain extent morphology) of *Oaxacagale ruizi* face and that of *Mustela frenata*, it could be assumed that the canines were probably vertically set too (not inclined, which would be less effective in piercing), delicate and perhaps moderately tall (5–6 mm as in that taxon).

Premolars 1–3. They are poorly and unevenly preserved (Fig. 4B, 5A, 6; Table 2). On the right side there are three postcanine alveoli anterior to P3, we interpret them as follows: The first one held the root of a single-rooted P1; the other two housed a bi-rooted, longer than wide P2. P3 crown is partly broken off, but what remains shows that it is roughly trenchant, transversely thicker than the delicate P3 of extant *Mustela*, bi-rooted, antero-posteriorly longer than transversely wide (antero-posterior length = 3.3 mm; transverse width = 1.8 mm), with a high, central, blunt principal cusp, from which the abraded anterior margin (gently) descends toward the base of a small anterior cuspule; the posterior cuspule is met by the abruptly descending abraded posterior margin. The resultant overall configuration is trenchant.

On the left side, the maxilla is broken off, so that only four, nearly circular, postcanine alveoli remain; the three anterior ones are interpreted as above, and the fourth contains the anterior root of a bi-rooted P3. The right P3 antero-posterior length and transverse width are slightly smaller than those of the late Chadronian-early Orellan *Mustelavus priscus* (Tab. 2; Supplementary Material Appendix E, Tab. E.21). This fact could be expected from a somewhat older musteloid.

Right P4. It is large (antero-posterior length = 5.6 mm; transverse width = 3.2 mm), antero-posteriorly elongate, exhibits a roughly cuneiform occlusal outline, with a bilobed anterior margin, a round posterior margin much narrower than the former, and the crown largely gone (Fig. 4B, 5.A–B, 6; Table 2), but what remains indicates that this is the carnassial tooth. The antero-lingual cusp (protocone) is blunt, moderately bulging, antero-posteriorly elongate (ovoid), nearly as long and large as the antero-labial cusp (parastyle, also bulging), but anteriorly reaching a little further; the parastyle is also antero-posteriorly elongate, unreduced (in Viverravinae this cusp is large too), and with the protocone forms the anterior bilobed margin. There is a very faint transverse constriction at the posterior end of these cusps.

The posterior half of P4 is transversely much narrower than the anterior (about half), its posterior end is u-shaped. Given that most of the crown is missing, the structure of the (large) shearing blade (including the significant datum of the presence/absence of the carnassial notch) is unknown. No trace(s) of cingulum(a) is(are) discernible, if truly lacking, *O. ruizi* stands in strong contrast with the *Chaprongictis* (Late Oligocene of Thailand, Peigné et al., 2006, p. 790), whose cheek teeth show very well-developed basal cingula.

Right ?M1. It should be noted that the specimen is broken off right at the posterior end of P4 (Fig. 4B, 5A, 5C, 6), hence no molar(s) is(are) preserved. However, a close examination shows a smoothly outlined neckline (not a breakage) in the right postero-lateral part of the palate, which might correspond to an incomplete alveolus for the internal root of a transversely elongate M1 (Figs. 5 and 6). No trace of M2 (and/or M3) is discerned. The posterior part of the naso-pharyngeal wall posterior to the neckline, is lost.

Dental formula. Parsimoniously, the probable upper teeth formula of *Oaxacagale ruizi* is: I1-3, C1, P1-4, (?M1), the parenthesis indicates that this tooth is inferred. Whether or not M2-3 were present is unknown, however, given the old geologic age of *Oaxacagale* (at least early Arikareean or even, but less likely Duchesnean), M2-M3 might have existed, since broadly contemporaneous carnivores like basal canids (a small percentage of Chadronian *Hesperocyon*, Wang, 1994; Munthe, 1998) are known to have small M3's.

A primitive dental formula like this is observed in several late Eocene-early Oligocene carnivores such as the late Chadronian-early Orellan *Mustelavus*, Canidae (e.g. the Duchesnean-early Arikareean *Hesperocyon*), and in the middle Chadronian-late Hemingfordian Carnivora inc. sed. *Palaeogale*.

Table 2
Alveolar and teeth measurements of IGM 7998, Holotype of *Oaxacagale ruizi* (A) and of UAM-138 (B), a skull of the extant *Mustela frenata*.

Feature/ Character	A antero-posterior length	A transverse width	B antero-posterior length	B transverse width
Right Incisor 3	1.8[a]	1.4[a]	1.58	0.92
Right Canine	2.3[a]	1.5[a]	2.26	1.69
Left P1	1.2[a]	~1.2[a]	–	–
Left P2 (ant. alv.)	1.3[a]	1.3[a]	–	–
Left P2 (post. alv.)	1.9[a]	1.5[a]	–	–
P2 length	2.5 e	–	1.84	.084
Right P3	3.4	2.0	3.17	1.31
Right P4 (ant. part)	5.7	3.0	5.13	2.81
Right P4 (post. part)	–	1.8	–	1.68

[a] Measured at alveolus. e, estimated. Measurements in mm.

Remarks. The short-faced skull of *Oaxacagale ruizi* fits the mustelid-like ecomorph (Martin, 2007), which in the late Eocene-early Oligocene was independently developed in several carnivoran clades such as miacoids, canids, musteloids, Carnivora inc. sed. *Palaeogale*, and others (Supplementary Material Appendix B, Figs. B.1–28; Supplementary Material Appendix E, Tabs. E.1–34). However, *O. ruizi* (purportedly early Arikareean, or less likely latest Uintan-early Duchesnean) surprisingly shows some advanced characters for such an early mustelid including: (1) Modern aspect of the skull (i.e., particularly a short, transversely broad face and wide muzzle), a character also shared with a few other basal mustelids like *Pseudobassaris*, *Bavarictis* and the more advanced *Kinometaxia*, as well as the extant *Mustela*, in which the muzzle is not so wide (Supplementary Material Appendix B), to which *O. ruizi* is moderately close in size and facial gross morphology). (2) Ossified, inflated bullae. (3) Faint double temporal (parietal) crests (fully developed in *Plesictis* (Early Oligocene of France), and *Kinometaxia* (Early Miocene of China). As mentioned earlier, the lack of some key characters in the holotype of *O. ruizi* (see Material and Methods) prevented us from performing an extensive, all-inclusive cladistic analysis; however, we do present a somewhat restricted analysis, which together with a detailed comparison of other broadly contemporaneous taxa (Supplementary Material Appendix A), allowed us to determine the taxonomic identity and most plausible phylogenetic relationships of this taxon from southern North America.

5. Discussion

5.1. Taxonomic aspect

5.1.1. Initial remarks

The overall size (Tables 1 and 2; Supplementary Material Appendix A; Supplementary Material Appendix E, Tabs. E.1–34), cranial morphology (Figs. 4–6), and dentition shows that *Oaxacagale*, in spite of sharing a few characters with most of the discussed taxa, particularly with basal carnivores, including among others musteloids, mustelids, *Mustelavus*, *Plesictis*, canids (like *Hesperocyon*), and Carnivora inc. sed. *Palaeogale*, is significantly different from all of them, as shown below.

5.1.2. Phylogenetic analysis

A 23 taxa by 39 characters morphological matrix of basal caniforms are assembled based on the published matrix by Wang et al. (2005a). Because of the poor preservation of *Oaxacagale*, only 16 of the 39 characters (41%) can be coded (Table 3). This matrix is analyzed by TNT (Goloboff et al., 2008; Goloboff and Catalano, 2016) using Implicit Enumeration option. Eight equally parsimonious trees were found with a length of 91 steps. A strict consensus tree is presented in Fig. 7. *Oaxacagale* is shown at the base of the unresolved multichotomy of "paleomustelid", a term often used to include stem musteloids that lack a carnassial notch (true mustelid) (Baskin, 1998, 2005; Flynn et al., 2010; Valenciano et al., 2016). Because this group is often defined by a lack of derived characters (such as the carnassial notch), it is likely a paraphyletic group, as is depicted in our cladogram. The upper carnassial of *Oaxacagale* is badly broken, and the presence or absence of a carnassial notch awaits future discoveries.

The "paleomustelids" that fall in the unresolved polytomy are illustrated and described/compared with *Oaxacagale* in the Supplementary Material Appendices A and E, which shows that morphologically none of them is particularly close to the latter, but all show adaptations to hypercarnivory (particularly strong in *Pseudobassaris* and *Bavarictis*). In addition, the geologic age of these "paleomustelids" is early Oligocene. Interestingly enough, the geographic distribution of these basal mustelids is strictly European (southern Germany, Pohle, 1917; Mödden, 1991; and southwestern France, Bonis, 1997; Bonis et al., 2019), which suggests that the early phase of mustelid evolution occurred there. If so, the co-occurrence of the southern North American Oaxacagale within this group is incongruent.

Table 3

Character matrix for phylogenetic analysis. See Wang et al. (2005a) for descriptions of individual characters.

Taxa	Characters
Miacis	000000?0000000000000000000000?00000000
Hesperocyon	000000?00001000000000000000001100011110
Mustelavus	01000??00001000?000001000??101?100???11
Amphictis	010010?0000200000031010200001?10011?11
Simocyon	010011?001020003103121021110010110111011
Ailurus	010010010022000302312122111001000011011
Broiliana	0011200000120003023121200000001??0011?1?
Stromeriella	0011101001120000031010000??001?100???1?
Mustelictis	00002000000201000100011?0??001?10011?11
Bavarictis	00001000000200000100011???0001??0011?1?
Pseudobassaris	0001100000020000100001?0?000010?001101?
Plesictis	11112000000200010110011?000001??0011?11
Promartes	01110000000100010110110000101?10011011
Potamotherium	011100000110011011011110000101010111011
Kinometaxia	11113??1100110?2????1?10???101?100???11
Paragale	011130?0100110?21120111100001017?01??11
Plesiogale	0111301010011022120111????101??00???11
Amphicticeps	000010?00001001100101001000101?10111?11
Amphicynodon	000000?00002000000000001000011?10111?11
Cephalogale	00000??001020003003020010??011011111?11
Pachycynodon	01000??00112000300002001??00110111011011
Allocyon	010000?0011200030000200?0?00?1011111?11
Oaxacagale	1?012?0?0?00?????????0??10????1?1001???1

5.1.3. Size

Oaxacagale is smaller than the "paleomustelids" retrieved in the above phylogenetic analysis (particularly so with respect to *Pseudobassaris* and *Bavarictis*), and in fact smaller than all named taxa there, as well as other primitive carnivores (Supplementary Material Appendix A; Supplementary Material Appendix E, Tabs. E.1–34). This fact strongly suggests that the small size of *Oaxacagale* is a derived (apomorphic) not a plesiomorphic character. It should be noted that the size of the latter (as well as its overall skull morphology, especially that of the face) is close to that of the extant, tunnel-hunter *Mustela frenata*, which adds credence to this tenet.

5.1.4. Morphology

In spite of its early occurrence (about 30–28 Ma, or less likely 40.3 ± 1.0 Ma), the skull of *Oaxacagale* shows a relatively modern outlook, particularly so in the face, as noted above, as well as in the very small size (discussed at length elsewhere, see Supplementary Material Appendices A and B), whereas the cranium is dorsally comparable to those of middle Paleogene taxa such as *Hesperocyon gregarius*, *Mustelavus priscus* and *Palaeogale lagophagus* (without separation of the cerebral and cerebellar cranial regions, which is typical of the latter taxon), and certainly with the early Oligocene basal mustelids such as *Plesictis*, *Mustelictis*, *Pseudobassaris* and *Bavarictis*. However, ventrally the cranium of *Oaxacagale* shows moderate resemblance to that of the extant *M. frenata* in having a large, completely ossified, inflate auditory bullae, which are relatively much larger than that of contemporary -Early Oligocene- basal mustelids such as *Pseudobassaris* and *Bavarictis*, which are quite bigger than *Oaxacagale* in absolute terms.

Surprisingly, *Oaxacagale* bears slender (incipient?), double temporal crests, a feature fully developed in the European, Early Oligocene basal mustelid *Plesictis genettoides* (Piveteau, 1961), and in the Asiatic, Early Miocene leptarctine *Kinometaxia guangpui* (Wang et al., 2005b). The last two characters add to the modern outlook of *O. ruizi*. This combination of derived and plesiomorphic characters seems to be unique to *O. ruizi*, and sharply place it apart as a separate clade among the Musteloidea, such clade inludes the basal mustelids (see phylogenetic analysis above).

5.1.5. Results of the comparative analysis

In addition, the detailed comparative analysis of *Oaxacagale* with Early and Late Paleogene carnivore taxa discussed above (Supplementary Material Appendix A) demonstrates that excluding basal mustelids,
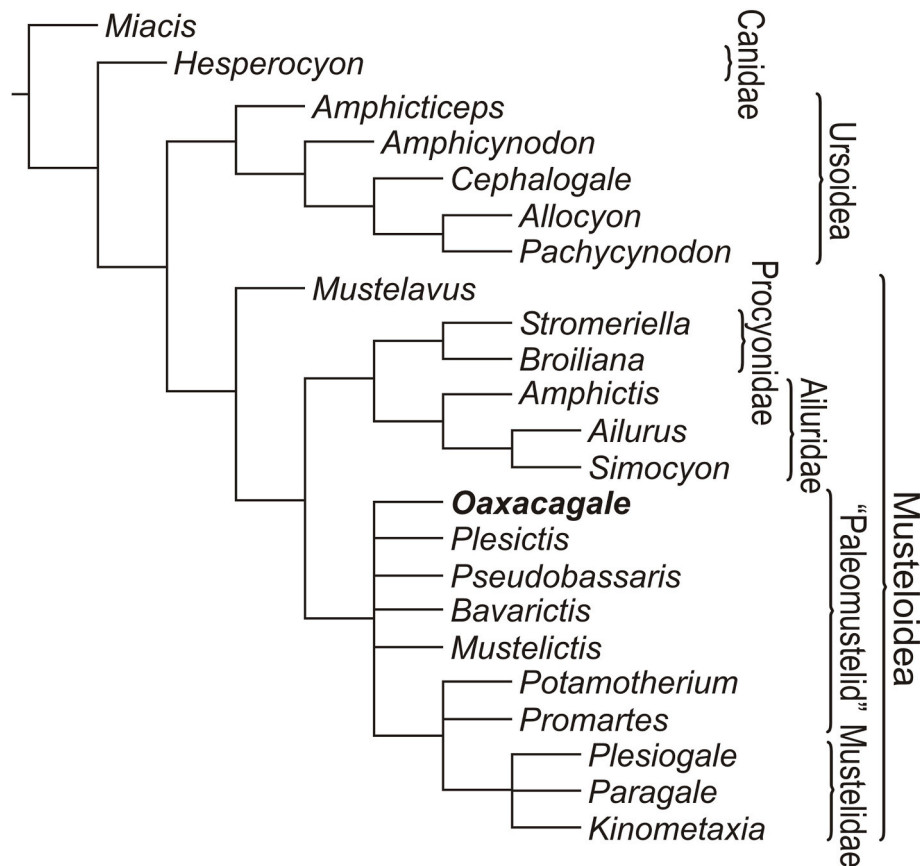
Fig. 7. Strict consensus of eight most-parsimonious trees found by TNT (Goloboff and Catalano, 2016). Tree length = 91 steps.

the latter shares a greater number of character states with *Mustelavus* (late Chadronian-Orellan, thus biochronologically earlier than the latter), as befitted with a sister stem taxon than with other, less closely related ancestral clades (see phylogenetic analysis above). Such comparative analysis also shows the unique set of character states (features) that set *Oaxacagale* apart from other related taxa, underlining its status as an undescribed (thus new) taxon at least of generic rank, named *Oaxacagale*, that includes by monotypy *O. ruizi* as the type species.

5.2. Paleoecological aspect

Several ecological attributes of Oaxacagale are discussed as follows.

5.2.1. Size and food habits (data from Baskin, 1998, and Van Valkenburgh, 2007a-b)

Oaxacagale ruizi was about the size of the Late Eocene-Early Oligocene *Palaeogale* (Supplementary Material Appendix B, Figs. B.1–28), but slightly to considerably smaller than most of its contemporary carnivoran taxa, as discussed above (see Supplementary Material Appendix E, Tabs. E.1–34), or of the extant *Mustela frenata*. In addition, *O. ruizi* skull morphology, particularly the facial, closely resembles that of such taxon, whose short face is a characteristic feature of the hypercarnivore morphotype (Holliday, 2010), in this instance superbly adapted for tunnel-hunting on (small) rodents, surpassing *Corumictis* in miniaturization (Patterson et al., 2020). If the analogy holds, it could be safely said that *Oaxacagale* was well adapted to prey on small mammals, probably rodents such as those already reported from the Yolomécatl Formation (e.g., Jiménez-Hidalgo et al., 2015; 2018; Ferrusquía-Villafranca et al., 2018a; Ortiz-Caballero et al., 2020). If the analogy is further stretched to tunnel-hunting, it excelled in praying efficiency in the tropics as *Corumictis wolsani* did it in temperate northwestern North

America (Paterson et al., 2020). The delicate built of the *O. ruizi* skull discussed above, probably would make it little fit to cope on open ground with potential prey as large or larger than itself.

These facts and analogies suggest that *Oaxacagale ruizi* probably was a tunnel hunter preying upon small adult rodents and/or the young offspring of larger ones. However, lack of the postcranial skeleton in *O. ruizi* or of indirect material evidence to that effect, leaves this idea as a plausible hypothesis not as a proven fact. The description of burrow systems in the same area (Guerrero-Arenas et al., 2020) lends it further credence. The mammal fauna associated with *Oaxacagale* (e.g. Jiménez-Hidalgo et al., 2015; 2018; Ferrusquía-Villafranca et al., 2018a; Ortiz-Caballero et al., 2020) includes abundant remains of small to very small rodents that could well have supported a population of this small carnivore.

As expected from a predator, its population density would have been much smaller than that of its rodent purported prey, a condition that could be reflected in the fossil record; accordingly, the remains of rodents in the Yolomécatl fauna vastly outnumber those of *Oaxacagale* (and of other carnivorous mammals as well).

5.2.2. Other aspects

Additional, somewhat speculative and/or controversial ecological aspects are presented in the Supplementary Material Appendix F, none of them is essential to characterize *Oaxacagale ruizi*, but allow to improve understanding on the paleobiology of this interesting carnivore.

5.3. Biogeographic

The phylogenetic analysis reported above yielded an unresolved polytomy placing *Oaxacagale* with these early Oligocene basal mustelids (Paleomustelidae Baskin, 1998): *Plesictis* and *Mustelictis* (Phosphorites

du Quercy, France), as well as *Pseudobassaris* and *Bavarictis* (central Germany). The geographic distribution of such mustelids suggests that the early evolution of Mustelidae took place in Europe, and then they dispersed eastward to Asia and eventually to North America. This clear biogeographic pattern is blurred by the fact that the late Chadronian-early Orellan sister stem taxon of this family, *Mustelavus*, is North American, and by the incongruent presence of the early Arikareean southern North American *Oaxacagale* within this basal mustelid clade. Seemingly an even earlier migration event might explain this presence (and that of the coeveal northwestern North American *Corumictis*), but it does not help to remove the above-mentioned blurring.

The biogeographic origin of Mustelidae is considered by many as Eurasian, thus their record in North America is interpreted as the result of repeated or episodic invasions from Asiatic or European taxa via Beringea or Artic Canadian islands respectively (Tedford et al., 1987, 2004; Baskin, 1998). Further, such immigration episodes/data have been used to establish the beginning of some Neogene North American Land Mammal Ages (NALMAs, Tedford et al., 1987; 2004.). However, an equally likely North American or European (Euroasiatic) biogeographic scenery for such origin has been convincingly argued by Wang et al., 2005b).

5.4. Climatic

The Yolomécatl Formation and its fauna lie between 17°25′–17°30′ N. Lat. in southeastern Mexico, well within the current tropical biogeographic region (and climatic zone) of North America/Mexico. Given that paleogeographic/paleomagnetic data indicate little or no northward displacement of this region with respect to its present-day position during the Oligocene (Golonka et al., 1994; Scotese, 1997, 2017), it follows that the Yolomécatl local fauna is tropical also. Finally, much remains unknown about low latitude North America as well as the early evolution/history of the Carnivora. This report adds a new record of a Paleogene carnivore from tropical North America that sheds some much needed light about this very interesting subject.

6. Summary and conclusions

1. The Paleogene sequence in the Yolomécatl area (17°25′–17°30′ N Lat., and 97°29′–97°36′ W Long.), northwestern Oaxaca State, Sierra Madre del Sur Morphotectonic Province of Mexico includes two volcanic andesitic lava-flow units, one dacitic dome, and two pyro-epiclastic units; one of them is the Yolomécatl Formation, a red, vertebrate-fossiliferous, ~650 m thick, lacustrine-fluvial succession forming badlands, interbedded by felsic tuff sheets; one of them yielded a ^{40}Ar-^{39}Ar age of 40.3 ± 1.0 Ma, which places this unit and the namesake fauna in the late Middle Eocene (i.e., latest Uintan-earliest Duchesnean NALMAs). However, a purported early Arikareean age (about 28–30 Ma), based on uncritical and/or unproven biochronologic and radioisotopic data has been proposed. Anyhow this fossil-bearing locality lies about 3°31′ south of the Marfil locality (Bridgerian of Guanajuato, central Mexico which bears *Viverravus* sp.), formerly the southernmost Paleogene carnivoran locality of North America, a record that now passes on to Yolomécatl, Oaxaca.
2. The Yolomécatl local fauna is fairly diverse (with at least five mammalian orders), includes the basal mustelid *Oaxacagale ruizi* new gen. and sp., who displays a unique combination of plesiomorphic (e.g., shearing dentition, relatively low cranium) and derived characters (e.g., very small size, well ossified, inflated tympanic bullae muh larger than those of other basal mustelids), that set it appart from other members of such clade.
3. The skull morphic appearance of *Oaxacagale ruizi* fits very well the weasel ecomorph, which includes semifossorial to fossorial, elongate, short-legged body and short-faced predators with shearing dentitions, closely approaching the appearance of *Mustela frenata* in its very small size and short face, well suited for tunnel hunting.

4. The cladistic analysis presented above places *Oaxacagale* in an unresolved polytomy that includes these basal, early Oligocene European mustelids (paleomustelids): *Plesictis*, *Mustelictis*, *Psudobassaris* and *Bavarictis*. The presence of Early Oligocene mustelids in central western North America (*Corumictis*) and southern Noth America (*Oaxacagale*) calls for a migration event occurring at latest very shortly before this time.

Credit author statement

Declaration of competing interest

The authors have no conflict of interest.

Acknowledgments

Supplementary Material Appendices data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2021.103236.

References

Aranda-Gómez, J.J., McDowell, F.W., 1998. Paleogene extension in the southern basin and range Province of Mexico: syndepositional tilting of Eocene red beds and Oligocene volcanic rocks in the Guanajuato mining district. Int. Geol. Rev. 40, 116–134.

Baskin, J.A., 1998. Mustelidae. In: Janis, C.M., Scott, K.M., Jacobs, L.J. (Eds.), Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, pp. 152–173.

Baskin, J.A., 2005. Carnivora from the late Miocene love bone bed of Florida. Bull. Fla. Mus. Nat. Hist. 45 (4), 413–434.

Black, C.C., Stephens III., J.J., 1973. Rodents from the Paleogene of Guanajuato, Mexico, vol. 14. Occasional Papers of the Museum of Texas Technical University, pp. 1–10.

Bonis, L., 1997. Précisions sur l'âge géologique et les relations phylétiques de *Mustelictis olivieri* nov. sp. (Carnivora, Mustelidae), carnassier de l'Oligocène inférieur (MP 22) des phosphorites de Quercy (France). Geobios 20, 55–60.

Bonis, L., Gardin, A., Blondel, C., 2019. Carnivora from the early Oligocene of the 'phosphorites du Quercy' in southern France. Geodiversitas 41, 601–621.

Bowdich, T.E., 1821. An Analysis of the Natural Classification of Mammalia for the Use of Students and Travelers. Printed by J. Smith, Paris.

Butrón-Xancopinca, P.G., Jiménez-Hidalgo, E., 2020. Tafonomía del esqueleto postcraneal del rumiante basal nanotragulus (Artiodactyla: hypertragulidae) de la Fauna Local Iniyoo, Oligoceno Temprano (Arikareeano) del Sur de México. Reunión Ann. Unión Geof. Mexic. 2019, Geos 39 (2), 194.

Ferrusquía-Villafranca, I., 1969. Rancho Gaitán local fauna, northeastern Chihuahua, México. Bol. Soc. Geol. Mex. 30, 99–138.

Ferrusquía-Villafranca, I., 1989. A new rodent genus from central México and its bearing on the origin of the Caviomorpha. In: Black, C.C., Dawson, M.R. (Eds.), Papers on Fossil Rodents in Honor of Albert Elmer Wood. Natural History Museum, Los Angeles, Science Series, vol. 33, pp. 91–117.

Ferrusquía-Villafranca, I., Barrios-Rivera, H., Galindo-Hernández, C., 1997. Los mamíferos oligocénicos de México: revisión y adición a la fauna local Rancho Gaitán, Formación Prietos, Chadroniano de Chihuahua nororiental. In: Arroyo-Cabrales, J., Polaco, O.J., Coords (Eds.), Homenaje Al Profesor Ticúl Álvarez. Colección Científica INAH 357. Instituto Nacional de Antropología e Historia, Secretaría de Educación Pública, México, D.F., pp. 97–134

Ferrusquía-Villafranca, I., 2005. The Marfil local fauna, Bridgerian of Guanajuato, Central Mexico: review and significance. A progress report on the southernmost tetrapod assemblage of North America. J. Vertebr. Paleontol. Abstracts Pap. 24, 56A.

Ferrusquía-Villafranca, I., Ruiz-González, J.E., Torres-Hernández, J.R., Anderson, T.H., Urrutia-Fucugauchi, J., Martínez-Hernández, E., García-Villegas, F., 2016. Cenozoic geology of the Yolomécatl-Tlaxiaco area, northwestern Oaxaca, southeastern Mexico: stratigraphy, structure and regional significance. J. S. Am. Earth Sci. 72, 191–226.

Ferrusquía-Villafranca, I., Flynn, L., Ruiz-González, J.E., Torres-Hernández, J.R., Martínez-Hernández, E., 2018a. New Eocene rodents from northwestern Oaxaca, southeastern México and their paleobiological significance. J. Vertebr. Paleontol. https://doi.org/10.1080/02724634.2018.1514615.

Ferrusquía-Villafranca, I., Torres-Hernández, J.R., Ruiz-González, J.E., Martínez-Hernández, E., 2018b. Depositional systems of the late Eocene Yolomécatl Formation, nortwestern Oaxaca, southeastern Mexico: a first approach. Rev. Mex. Ciencias Geol. 35, 142–157.

Finarelli, J.A., 2008. A total evidence phylogeny of the Arctoidea (Carnivora: mammalia): relationships among basal taxa. J. Mamm. Evol. 15, 231–259.

Fischer von Waldheim, G., 1817. Adversaria Zoologica, fasciculus primus. Mémoir. Soc. Impériale Natl. Moscou 5, 357–446.

Flower, W.H., 1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. Proc. Zool. Soc. Lond. 4–37, 1869.

Flynn, J.J., Finarelli, J.A., Spaulding, M., 2010. Phylogeny of the Carnivora and Carnivoramorpha, and the use of the fossil record to enhance understanding of evolutionary transformations. In: Goswami, A., Friscia, A. (Eds.), Carnivoran Evolution: New Views on Phylogeny, Form and Function. Cambridge University Press, Cambridge, pp. 25–63.

Fries Jr., C., Hibbard, C.W., Dunkle, D.H., 1955. Early cenozoic vertebrates in the red conglomerate at Guanajuato, Mexico. Smithsonian Misc. Collect. 123, 1–25.

Gazin, C.L., 1957. A skull of the bridger middle Eocene creodont Patriofelis ulta leydi. Smithsonian Misc. Collect. 174, 1–20.

Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32 (3), 221–238.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24 (5), 774–786.

Golonka, J., Ross, M.I., Scotese, C.R., 1994. Phanerozoic paleogeographic and paleoclimatic modeling maps. In: Embry, A.F., Beauchamp, B., Glass, D.J. (Eds.), Pangea: Global Environments and Resources. Memoir 17. Canadian Society of Petroleum Geologists, Canada, 1–48.

Guerrero-Arenas, R., Jiménez-Hidalgo, E., Genise, J.F., 2018. The oldest beetle and bee ichnofossils from Mexico and their paleoenvironmental implications. Ichnos 25 (4), 269–273. https://doi.org/10.1080/10420940.2017.1386184.

Guerrero-Arenas, R., Jiménez-Hidalgo, E., Genise, J.F., 2020. Burrow systems evince non- solitary geomyid rodents from the Paleogene of southern Mexico. PloS One 15 (3), e0230040. https://doi.org/10.1371/journal.pone.0230040, 1–22.

Hall, E.R., 1981. The Mammals of North America, vol. II. John Wiley & Sons, New York.

Holliday, J.A., 2010. Evolution in Carnivora: identifying a morphological bias. In: Goswani, A., Friscia, A. (Eds.), Carnivoran Evolution New Trends in Phylogeny, Form and Function. Cambridge University Press, Cambridge, pp. 189–224.

Jiménez-Hidalgo, E., Smith, K.T., Guerrero-Arenas, R., Alvarado-Ortega, J., 2015. The first Late Eocene continental assemblage from tropical North America. J. S. Am. Earth Sci. 57, 39–48.

Jiménez-Hidalgo, E., Guerrero-Arenas, R., Smith, K.T., 2018. *Gregorymys veloxikua*, the oldest pocket gopher (Rodentia: geomyidae), and the early diversification of Geomyoidea. J. Mamm. Evol. 25, 427–439.

Jiménez-Hidalgo, E., Guerrero-Arenas, R., Lander, E.B., Israde-Alcántara, I., Rodríguez-Caballero, N., Smith, K., Droser, M., Hughes, N., Bonuso, N., Bottjer, D., Eernisse, D., Gaines, R., Hendy, A., Jacobs, D., Miller-Camp, J., Norris, R., Roy, K., Sadler, P., Springer, M., Wang, X., 2019a. The early Oligocene iniyoo local fauna of northwestern Oaxaca, southern Mexico. In: Vendrasco, M. (Ed.), 11th North American Paleontological Conference Program with Abstracts. PaleoBios 36 (Supplement 1), Ucmp_paleobios_44177, pp. 188–189.

Jiménez-Hidalgo, E., Israde-Alcántara, I., Rodríguez-Caballero, N.W., Guerrero-Arenas, R., 2019b. Cronología y relaciones estratigráficas regionales de los depósitos lacustres y paleosuelos de la Formación Yolomécatl, noroeste de Oaxaca, sur de México. Convención Geológica Nacional 2019. Mexico City, Libro de resúmenes, pp. 186–187, 186-.

Jiménez-Hidalgo, E., Lander, E.B., Guerrero-Arenas, R., 2019c. A Revised (Early Arikareean) Age for the Late Paleogene Iniyoo Local Fauna of Oaxaca State, Southern Mexico. 1st Paleoecological Virtual Congress, p. 92.

Kretzoi, M., 1943. Kochictis centennii n. g. n. sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. Foldtani Kozlony 73, 190–195.

Linnaeus, C., 1758. Systema Naturae Per Regna Tria Naturae Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis, vol. 1. Regnum animale: Editio decima, reformata. Laurentii Salvii, Stockholm [Facsimile reprinted in 1956 by the British Museum (Natural History)].

Martin, L.D., 2007. Fossil history of the terrestrial Carnivora. In: Gittleman, J.L. (Ed.), Carnivore Behavior, Ecolgy, and Evolution. Springer-Verlag, Boston, pp. 536–568.

Martiny, B., Martínez-Serrano, R.G., Morán-Zenteno, D.J., Macías-Romo, C., Ayuso, R.A., 2000. Stratigraphy, geochemistry and tectonic significance of the Oligocene magmatic rocks of western Oaxaca, southern Mexico. Tectonophysics 318 (1–4), 71–98.

Mödden, C., 1991. *Bavarictis gaimersheimensis* n. gen. n. sp., ein früher Mustelide aus der oberoligozänen Spaltenfüllung Gaimersheim bei Ingolstadt. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Histor. Geologie 31, 125–147.

Novacek, M.J., Ferrusquía-Villafranca, I., Flynn, J.J., Wyss, A.R., Norell, M., 1991. Wasatchian (early Eocene) mammals and other vertebrates from Baja California, Mexico: the lomas Las Tetas de Cabra fauna. Bull. Am. Mus. Nat. Hist. 208, 1–88.

Ortiz-Caballero, E., Jiménez-Hidalgo, E., Bravo-Cuevas, V.M., 2020. A new species of the gopher Gregorymys (Rodentia, Geomyidae) from the early Oligocene (Arikareean 1) of southern Mexico. J. Paleontol. 94 (6), 1191–1201.

Paterson, R., Samuels, J.X., Rybczynski, N., Ryan, M.J., Maddin, H.C., 2020. The earliest mustelid in North America. Zool. J. Linn. Soc. 188, 1318–1339.

Peigné, S., Chaimanee, Y., Yamee, C., Srisuk, P., Marandat, B., Jaeger, J.J., 2006. A new member of the mustelida (mammalia: Carnivora) from the Paleogene of southern Asia. J. Vertebr. Paleontol. 26, 788–793.

Piveteau, J., 1961. Carnivora. In: Piveteau, J., Dir (Eds.), Traité de Paléontologie, Mason et Cie, Editeurs, Paris, vol. 1. Tome VI, pp. 641–820.

Pohle, H., 1917. *Pseodobassaris riggsi*, gen. nov., spec. nov. Fur *Amphictis* spec. Riggs. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, pp. 403–411, 1917.

Rybczinski, N., Dawson, M.R., Tedford, R.H., 2009. A semiaquatic Arctic mammalian carnivore from the Miocene Epoch and the origin of the Pinnipedia. Nat. Lett. 458, 1021–1024.

Santamaría-Díaz, A., Alaniz-Alvarez, S.A., Nieto-Samaniego, A.F., 2008. Cenozoic deformations in the Caltepec fault cover, Tamazulapam region, southern Mexico [Deformaciones cenozoicas en la cobertura de la falla Caltepec en la región de Tamazulapam, Sur de México]. Rev. Mex. Ciencias Geol. 25 (3), 494–516.

Scotese, C.R., 1997. Continental Drift, seventh ed. PALEOMAP Project. Department of Geology, University of Texas at Arlington, Texas.

Scotese, C.R., 2017. Atlas of Ancient Oceans & Continents: Plate Tectonics 1.5. Today, PALEOMAP Project, Evanston, IL.

Scott, W.B., Jepsen, G.L., 1936. The mammalian fauna of the white river Oligocene: Part I. Insectivora and Carnivora. Trans. Am. Phil. Soc. 28, 1–153.

Tedford, R.H., 1976. Relationship of pinnipeds to other carnivores (Mammalia). Syst. Zool. 25, 363–374.

Tedford, R.H., Galusha, T., Skinner, M.F., Taylor, B.E., Fields, R.W., Macdonald, J.R., Rensberger, J.M., Webb, S.D., Whistler, D.P., 1987. Faunal succession and biochronology of the arikareean through hemphillian interval (late Oligocene through earliest Miocene epochs) in north America. In: Woodburne, M.O. (Ed.), Cenozoic Mammals of North America, Geochronology and Biostratigraphy. University of California Press, Berkeley, California, pp. 153–210.

Tedford, R.H., Albright III, L.B., Barnosky, A.D., Ferrusquía-Villafranca, I., Hunt Jr., R. M., Storer, J.E., Swisher III, C.C., Voorhies, M.R., Webb, S.D., Whistler, D.P., 2004. Mammalian biochronology of the arikareean through hemphillian interval (late Oligocene through early pliocene epochs). In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York, pp. 169–232.

Valenciano, A., Baskin, J.A., Abella, J., Pérez-Ramos, A., Álvarez-Sierra, M.Á., Morales, J., Hartstone-Rose, A., 2016. Megalictis, the bone-crushing giant mustelid (Carnivora, Mustelidae, oligobuninae) from the early Miocene of North America. PloS One 11, 1–26.

Van Valkenburgh, B., 2007a. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In: Gittleman, J.I. (Ed.), Carnivore Behavior, Ecology, and Evolution, Chap. 15. Comstock Publishing Associates, Cornell Univ. Press, Ithaca, New York, pp. 410–436.

Van Valkenburgh, B., 2007b. Deja vu: the evolution of feeding morphologies in the Carnivora. Integr. Comp. Biol. 47, 147–163.

Wang, X., 1994. Phylogenetic systematics of the hesperocyioninae (Carnivora, Canidae). Bull. Am. Mus. Nat. Hist. 221, 1–207.

Wang, X., Qiu, Z.X., Wang, B.Y., 2004. A new leptarctine (Carnivora: Mustelidae) from the Early Miocene of the northern Tibetan Plateau and implications of the phylogeny and zoogeography of basal mustelids. Zool. J. Linn. Soc. 142, 405–421.

Wang, X., McKenna, M.C., Dashzeveg, D., 2005a. Amphicticeps and amphicynodon (arctoidea, Carnivora) from hsanda gol formation, central Mongolia and phylogeny of basal arctoids with comments on zoogeography. Am. Mus. Novit. 3483, 1–57.

Wang, X., Qiu, Z., Wang, B., 2005b. Hyaenodonts and carnivorans from the early Oligocene to early Miocene of xianshuihe formation, lanzhou basin, gansu Province, China. Palaeontol. Electron. 8, 1–14.

Wolsan, M., 1993. Phylogeny and classification of early European mustelida (mammalia: Carnivora). Acta Theriol. 38, 345–384.