Discovery of the fossil otter *Enhydritherium terraenovae* (Carnivora, Mammalia) in México reconciles a paleozoogeographic mystery

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Electronic Supplemental Materials

Biology Letters

Systematic Paleontology

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1945

Superfamily Musteloidea Swainson, 1835

Family Mustelidae Swainson, 1835

Subfamily Lutrinae Baird, 1857

Enhydritherium Berta and Morgan, 1985

Enhydritherium terraenovae Berta and Morgan, 1985

(Figure 2, Table 1)

Referred specimen and locality—MPGJ 3586, partial left dentary with m1, broken p4, and alveoli of canine and p1-3. Collected by A. Pacheco-Castro on 23 March 2017 in El Resbalón locality (ZacJuch 47), in a grayish sandstone layer that is approximately 18 m below the U-Pb dated ash layer capping the section with an age of 5.59±0.11 Ma (ESM Figs. 1-2).

Description and Comparison—The recovered specimen preserves a single almost complete tooth, m1, that is diagnostic of specimens of *Enhydritherium terraenovae*. As in the holotype UF 18928 and paratype UF 32001, the m1 has a rectangular outline [1]. The anterobuccal border of the tooth, at the position of the paraconid, is broken; nevertheless, the paraconid is preserved, and very rounded in occlusal view. A short buccal cingulum is present at the base of the hypoconid. The protoconid is bulbous and rounded as in the paraconid, and both are similar in size. The metaconid is about equal in size to the protoconid, and situated directly lingual to it. The buccal cusps (paraconid, protoconid, hypoconid) are more worn than the lingual cusps (metaconid and metastylid). The talonid basin is shallow, with the posterior edge broken. There is a small accessory cusp directly behind the hypoconid, exhibiting wear, but to a lower degree compared to the hypoconid. All of these characteristics are also observed in the holotype (UF 18928), and unlike UF 32001 and UCMP 32970 [1], MPGJ 3586 does not have an accessory cusp behind the metastylid.

Depositional Environment of the Juchipila Basin

The Juchipila Basin occupies a N10E-trending graben, which was formed in the Late Oligocene [2] and that has had several periods of activity after its formation. Graben-fill sediments exposed within the Juchipila graben include diatomaceous marl, clayey lime mudstone, thinly laminated lime mudstone and minor oolitic grainstones and cryptalgal boundstones. In addition to these lithofacies, which were identified and interpreted by López [3] as open lacustrine or transitional (shallow-water lacustrine and fluvial-deltaic lake-margin deposits), in areas that were located closer to the margins of the graben, occur epiclastic-volcanic channel sandstones and conglomerates that represent alluvial fan deposits. Reddish tuffaceous sandstones with rootcasts and reddish tuffaceous claystones often interlayered with green ostracode calcareous mudstones were deposited in floodplain influenced by sedimentary cycles caused by tectonic and climatic variations [3]. Very fine-grained ash-fall layers are commonly interlayered both with the lacustrine and fluvial sediments and suggests active volcanism in a nearby region, outside of the basin. As pointed out by López [3] as whole, lithofacies nature and distribution, pollen, spores and plant fossils, as well as the fossil mammal fauna [4] are consistent with the presence of an open-basin freshwater perennial lake fed by an axial river and its tributaries within a fault-bounded basin during a period when climate was warm temperate to subtropical. The stratigraphy of the basin-fill sediments [3, 4] and cross-cutting relations between faults and strata in selected outcrops suggest that normal faulting was active during the Late Miocene while the sedimentary sequence accumulated.

The sedimentary sequence at El Resbalón (ESM Fig. 1C), dominated at the base by pale greenish yellow claystone and pale red, sometimes mottled with green, tuffaceous claystones, overlain by fine- to medium-grained volcaniclastic sandstones with few layers of pebble conglomerates represent fluvial floodplain overbank deposits.

Biochronology, Geology, and Functional Anatomy

Enhydritherium terraenovae is known from California (San Mateo Formation, late Hemphillian North American Land Mammal Age [NALMA]; Etchegoin Formation, Hemphillian NALMA) [5, 6] and Florida (Upper Member of Bone Valley Formation, late Hemphillian NALMA; Withlacoochee River Site 4A, medial Hemphillian NALMA; Moss Acres Racetrack, medial Hemphillian NALMA) [1, 7] by a single species, *E. terraenovae* (ESM Table 1). In the original description of the genus and species, Berta and Morgan [1] distinguished what they called the "North American sea otter" from the European species of the genus *Enhydriodon*, to which North American specimens were previously referred, by m1 metaconid being larger than the m1 protoconid, m1 with a square-shaped talonid, and presence of m1 metastylid and absence of m1 protostylid. Although our specimen contains only a single relatively complete tooth, m1, all of these diagnostic characteristics are present (Fig. 2), allowing us to unambiguously refer the new specimen to *E. terraenovae*.

Although previous studies have grouped *Enhydritherium* with the living sea otter based on dentition, evidence from postcranial skeletal remains of *Enhydritherium* suggests that locomotor capabilities are likely different between the two otters [8]. In *Enhydra*, the relative enlargement of hind limb bones is associated with hind limb-propelled locomotion in water, and limited locomotion on land [9]. In contrast, no relative increase in hind limb robusticity is observed in *Enhydritherium*; in fact, the highly robust great tubercle and deltopectoral ridge on the humeri of *Enhydritherium* suggest a fore limb emphasis for walking or for swimming [8]. The increased ability for terrestrial locomotion in *Enhydritherium* relative to *Enhydra* is consistent with our interpretation of an over-land dispersal scenario between Florida and California, via central México.

A recent phylogenetic analysis combining fossil and extant otters unambiguously places *Enhydritherium* in a clade that contains non-marine otters *Paludolutra*, *Paralutra garganensis*, and *Tyrrhenolutra helbingi* [10], a largely middle to late Miocene group from Europe and North America. In contradiction to previous ideas [1, 5], the sea otter is not closely related to *Enhydritherium* in this analysis, i.e., its bunodont dentition is convergent to those in the latter. If this is correct, *Enhydritherium* may not be constrained to marine environments, as also suggested by its postcranial skeletons [8].

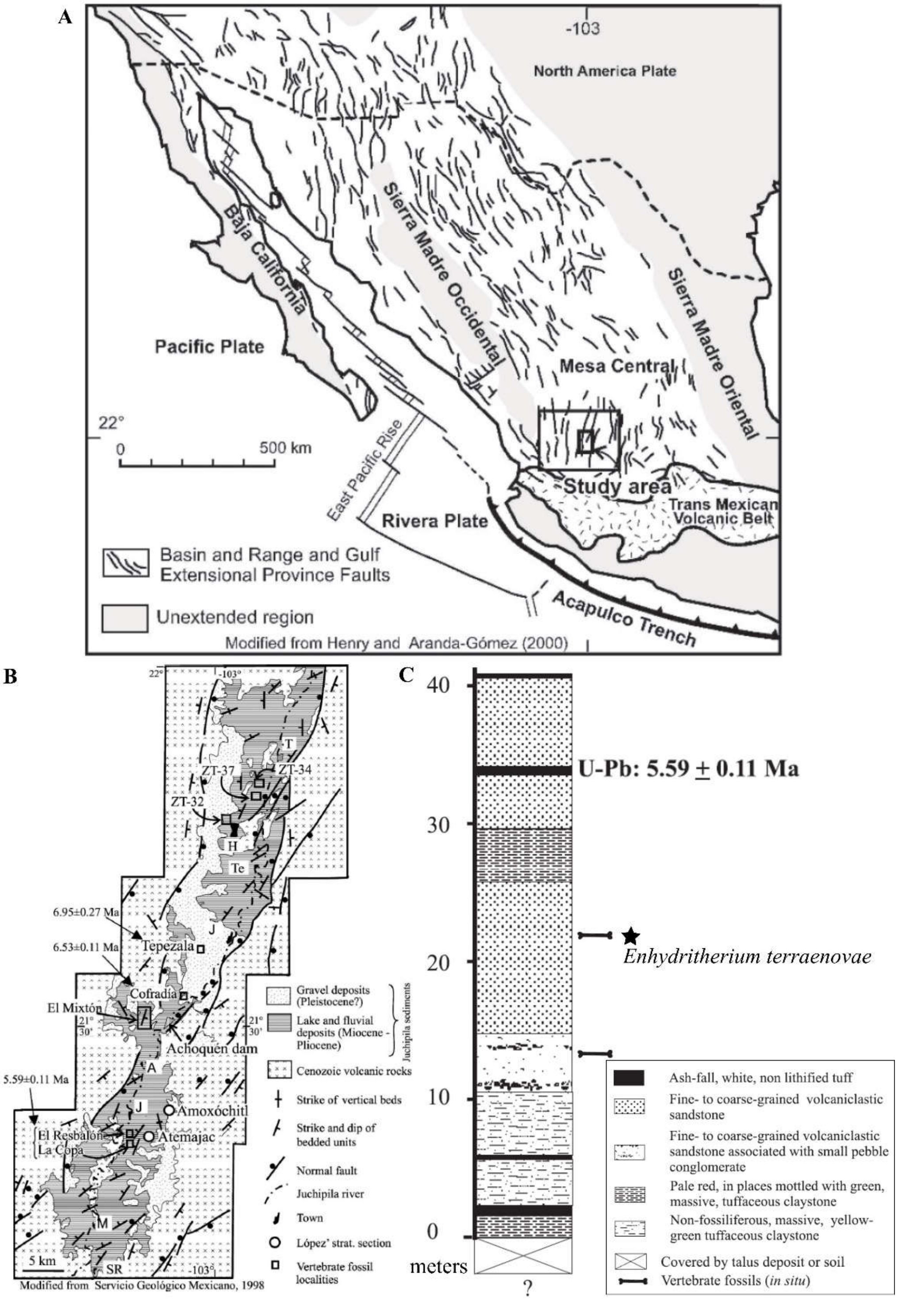
Tectonically Juchipila Basin is a north-south oriented graben and together with a series of similarly oriented grabens and half grabens bounded by high-angle normal faults, it forms the southern (Mexican) extension of the Basin and Range Province of the United States [11-13]. Drainages in these basins are controlled by predominant orientations of graben and horst, which may be initiated as early as early or middle Miocene, but they eventually converge to an east-west oriented drainage system in the form of modern Rio Santiago to the south, offering longitudinal as well as latitudinal dispersals for river-bound organisms.

Given the close association of *E. terraenovae* with near-coast marine habitats, but also with fluvio-lacustrine environments, the question remains whether *E. terraenovae* had similar sensory adaptations to detect prey underwater as in living sea otters. Evidence from cranial endocast and histological studies of sea otters suggests that an enlargement of the coronal gyrus is correlated with greatly increased innervation of the vibrissae [14, 15]. Further research on the only known fragmentary skull of *E. terraenovae*, UF 100000, and future discoveries of complete cranial specimens of this fossil otter will clarify whether *Enhydritherium* had similar expansion of the endocranial regions for increased vibrissae sensitivity. If so, *Enhydritherium* may represent “transitional” otters intermediate between freshwater forms and the entirely marine *Enhydra* in sensory and locomotor adaptations.

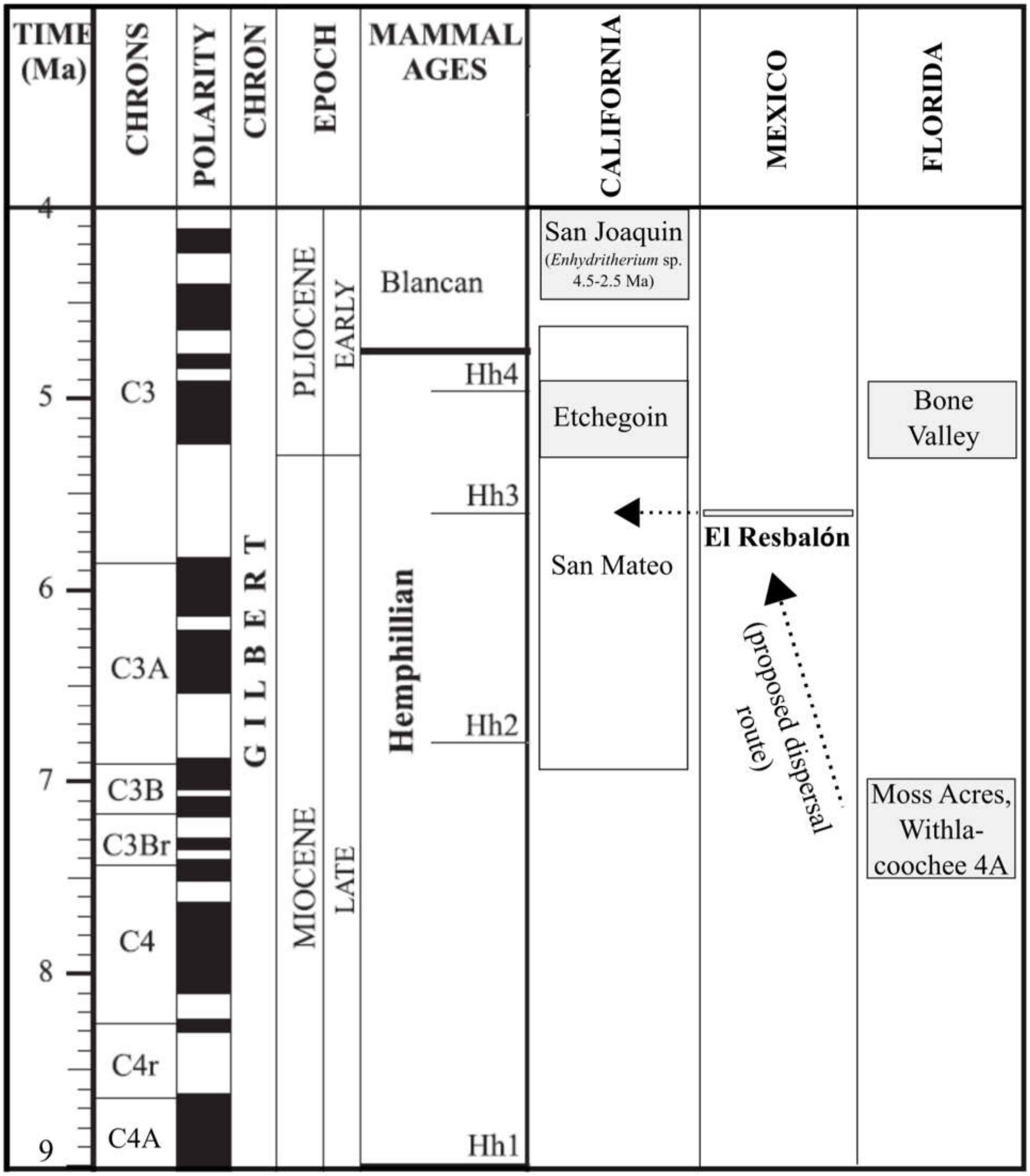
ESM Table 1. Fossil localities containing *Enhydritherium* and their geologic ages.

Locality	Formation	Age	Reference
Kettleman Hills, CA (*Enhydritherium* sp.)	San Joaquin	4.5-2.5 Ma	Repenning (1976)[5]; Boessenecker (2013)[16]
Palmetto Mine, FL	Bone Valley	4.9-5.3 Ma/L. Hemphillian	Berta and Morgan (1985)[1]; Morgan (2005)[17]
Fort Green Mine, FL	Bone Valley	4.9-5.3 Ma/L. Hemphillian	Berta and Morgan (1985); Morgan (2005)
Rockland Mine, FL	Bone Valley	4.9-5.3 Ma/L. Hemphillian	Berta and Morgan (1985); Morgan (2005)
Gardinier Mine, FL	Bone Valley	4.9-5.3 Ma/L. Hemphillian	Berta and Morgan (1985); Morgan (2005)
Payne Creek Mine, FL	Bone Valley	4.9-5.3 Ma/L. Hemphillian	Berta and Morgan (1985); Morgan (2005)
Kettleman Hills, CA	Etchegoin	4.9-5.3 Ma/L. Hemphillian	Berta and Morgan (1985); Repenning (1976)[5]; Scheirer and Magoon (2009)[18]; Boessenecker (2013)[16]
Lawrence Canyon, CA	San Mateo	7-4.6 Ma	Barnes et al. (1981)[6]; Berta and Morgan (1985); Repenning (1976); Domning and Deméré (1984)[19]; Boessenecker (2013)[16]
El Resbalón, MX	**-**	**5.59 Ma**	**Carranza-Castañeda et al (2013)[4]**
Moss Acres Racetrack, FL	-	7.0-7.5 Ma	Lambert (1997)[8]; Morgan (2005)
Withlacoochee 4A, FL	-	7.0-7.5 Ma/M. Hemphillian	Berta and Morgan (1985); Morgan (2005)

ESM Figure 1. Map and geology of locality area. **A**. Regional map showing study area. **B**. Juchipila Basin geology and vertebrate fossil localities. **C**. Stratigraphic section at El Resbalón. All modified from Carranza-Castañeda et al (2013).



ESM Figure 2. Stratigraphic occurrences of *Enhydritherium terraenovae* and proposed dispersal route. Faunal ages as in ESM Table 1. Modified from Carranza-Castañeda et al (2013).



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