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Authors

Tseng, Z Jack
Pacheco-Castro, Adolfo
Carranza-Castañeda, Oscar
et al.

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Author for correspondence:

Z. Jack Tseng
e-mail: jacktsen@buffalo.edu

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Palaeontology

Discovery of the fossil otter
Enhydritherium terraenovae (Carnivora,
Mammalia) in Mexico reconciles a
palaeozoogeographic mystery

Z. Jack Tseng^{1,2,3}, Adolfo Pacheco-Castro⁴, Oscar Carranza-Castañeda⁴, José Jorge Aranda-Gómez⁴, Xiaoming Wang^{2,3} and Hilda Troncoso⁴

¹Department of Pathology and Anatomical Sciences, Jacobs School of Medicine and Biomedical Sciences, University at Buffalo, Buffalo, NY 14214, USA

²Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA

³Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

⁴Centro de Geociencias, Universidad Nacional Autónoma de México, Boulevard Juriquilla 3001, Juriquilla, Querétaro 76230, Mexico

ZJT, 0000-0001-5335-4230; XW, 0000-0003-1610-3840

The North American fossil otter *Enhydritherium terraenovae* is thought to be partially convergent in ecological niche with the living sea otter *Enhydra lutris*, both having low-crowned crushing teeth and a close association with marine environments. Fossil records of *Enhydritherium* are found in mostly marginal marine deposits in California and Florida; despite presence of very rich records of fossil terrestrial mammals in contemporaneous localities inland, no *Enhydritherium* fossils are hitherto known in interior North America. Here we report the first occurrence of *Enhydritherium* outside of Florida and California, in a land-locked terrestrial mammal fauna of the upper Miocene deposits of Juchipila Basin, Zacatecas State, Mexico. This new occurrence of *Enhydritherium* is at least 200 km from the modern Pacific coastline, and nearly 600 km from the Gulf of Mexico. Besides providing further evidence that *Enhydritherium* was not dependent on coastal marine environments as originally interpreted, this discovery leads us to propose a new east-to-west dispersal route between the Florida and California *Enhydritherium* populations through central Mexico. The proximity of the fossil locality to nearby populations of modern neotropical otters *Lontra longicaudis* suggests that trans-Mexican freshwater corridors for vertebrate species in riparian habitats may have persisted for a prolonged period of time, pre-dating the Great American Biotic Interchange.

1. Background

In present day North America there are two species of freshwater otters and one species of sea otter. The North American river otter, *Lontra canadensis*, has a historical range covering the entirety of the USA and Canada [1] (figure 1). The neotropical otter, *Lontra longicaudis*, is found in riparian environments in western and southern México, and southward into northern South America. The sea otter, *Enhydra lutris*, is currently restricted in range from the north Pacific rim around the Kuril and Commander Islands, the Kamchatka Peninsula, to coastal Alaska, British Columbia, parts of the Pacific northwest, California, and Baja California; the historical range of the sea otter extends westward to Japan, and southward to Mexico's Baja Peninsula. The International



Figure 1. Map of *Enhydritherium* localities with extant *Lontra* and *Enhydra* ranges. Previously proposed dispersal hypotheses are mapped along with the trans-Mexico dispersal hypothesis supported by the new discovery. Modern species ranges taken from the International Union for Conservation of Nature (IUCN) [1]. Red arrow indicates possible southern dispersal route with riparian habitats.

Union for Conservation of Nature (IUCN) classifies *L. longicaudis* as near-threatened, and *E. lutris* as endangered [1].

Although ocean-going otters had to have evolved from freshwater ancestors [2], the fossil record of the North American sea otters is poor, and the evolutionary origin of extant sea otters remains uncertain [3]. Recent phylogenetic analyses of morphological and genetic sequence data suggest that *Enhydra* is most closely related to Asian fossil otters, whereas earlier palaeontological analyses indicate a close relationship between *Enhydra* and the fossil otter *Enhydritherium terraenovae* [4]. The hypothesis of a North American fossil otter population related to *Enhydritherium* giving rise to the present day sea otter *Enhydra* is appealing because the majority (eight out of nine) of the fossil localities containing *Enhydritherium* specimens also have marine vertebrates associated with them [5] (electronic supplementary material, table S1). The only occurrence of *Enhydritherium* in freshwater habitats, in the Moss Acres Racetrack locality, is 70 km from the present day Gulf of Mexico [5]. Therefore, *Enhydritherium* is thought to be a species

closely linked to near-coast marine habitats, with some ability to persist in freshwater habitats. However, the disjointed occurrence of *Enhydritherium* in coastal California and Florida fossil deposits, but not in interior North America, represents a palaeozoogeographic phenomenon that has not been satisfactorily resolved or explained.

Here, we describe a new discovery of an *Enhydritherium* fossil in the land-locked Juchipila Basin in central Mexico (figures 1 and 2; electronic supplementary material, figure S1), a location 200 km from the present day Pacific coast, and more than 500 km from the present day Gulf of Mexico. The new fossil is more than 2000 km from the nearest known localities of *Enhydritherium* in Florida and California. Our new findings remove any doubt that *Enhydritherium* was living in completely freshwater environments in addition to mixed near-coast fresh and marine environments. The new fossil also supports a new, plausible over-land dispersal route connecting the California and Florida occurrences of *Enhydritherium*.

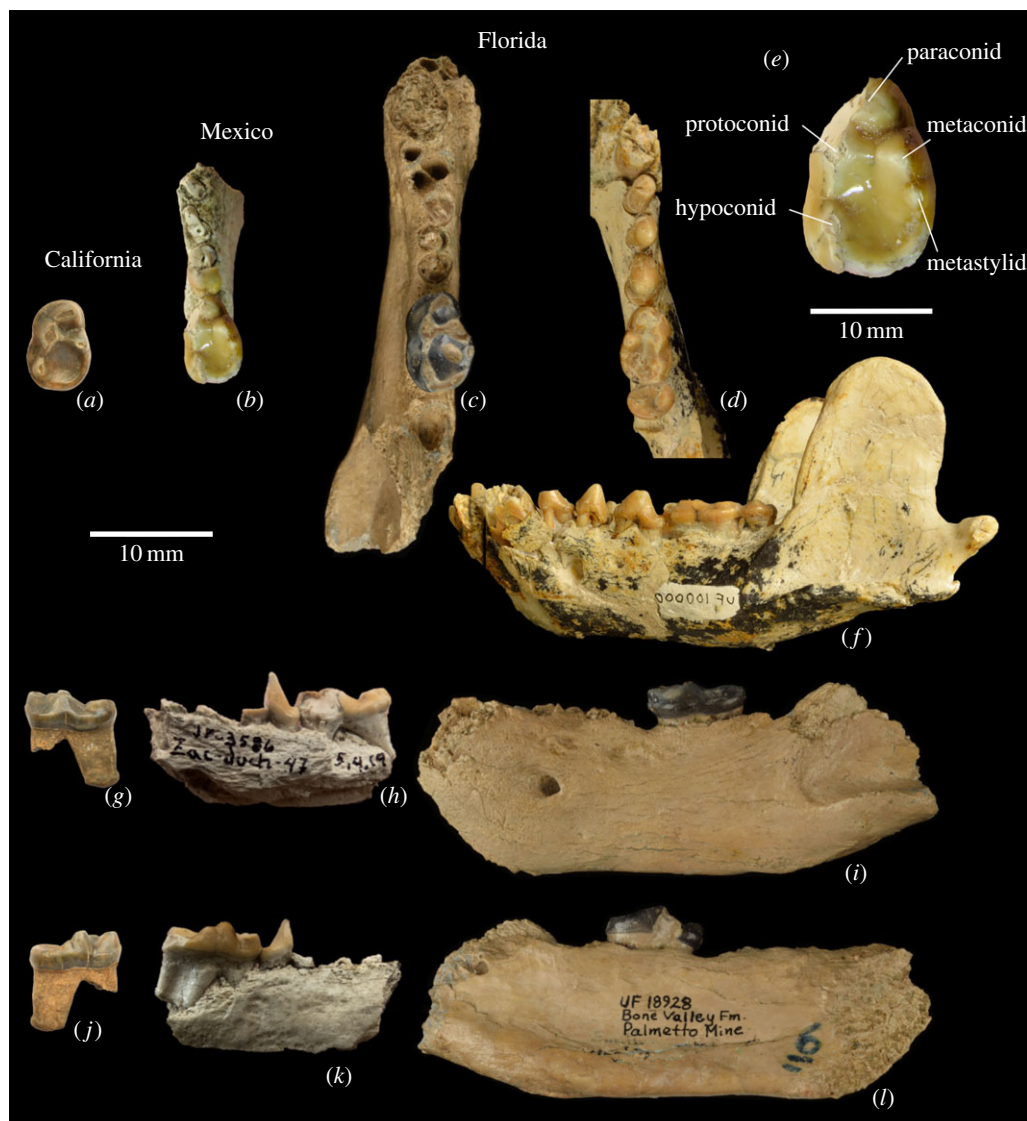


Figure 2. Comparison of new specimen of *Enhydritherium terraenovae* from Juchipila Basin, Mexico, with other *Enhydritherium* specimens. (a) LACM 121591. (b) MPGJ 3586. (c) UF 18928 (holotype). (d) UF 100000, right dentition. (e) Close-up occlusal view of MPGJ 3586, with cusps labelled. (f) UF 100000 (reflected). (g) LACM 121591. (h) MPGJ 3586. (i) UF 18928. (j) LACM 121591. (k) MPGJ. (l) UF 18928. (a–e) Occlusal views. (f–i) Lateral views. (j–l) Medial views. Scale bar on right is for (e); scale bar on left is for all other specimens. UF specimen photos courtesy of R. Hulbert/Florida Museum of Natural History. MPGJ photos by J. Jesús Silva; LACM photos by X.W. (Online version in colour.)

2. Material and methods

(a) Institutional abbreviations

LACM, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, California, USA; MPGJ, Museo de Paleontología del Centro de Geociencias, campus Juriquilla, Universidad Nacional Autónoma de México; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UF, University of Florida Museum of Natural History, USA; ZacJuch, fossil locality in Zacatecas state, Juchipila Basin, Mexico.

The new fossil material described, MPGJ 3586, was collected by A.P.-C. during the 2017 expedition by the authors in the fossil locality of ZacJuch 47 El Resbalón, adjacent to the city of Juchipila. All measurements were taken using callipers or from photographs to the nearest 0.1 mm (table 1).

3. Results and discussion

The new specimen, MPGJ 3586, possesses bunodont cusps and a large talonid basin as in other low-crowned otters,

but differs from *Enhydra* by less bulbous cusps and no posterior expansion of metaconid (figure 2e). Diagnostic *Enhydritherium* characters on MPGJ 3586 include: metaconid equal to protoconid in size; square-shaped talonid; presence of metastylid, and absence of protostylid. A detailed description of the new specimen is included in the electronic supplementary material. Known *Enhydritherium* localities in California and Florida range from early to late Hemphillian North American Land Mammal Ages; the new occurrence in Mexico is bracketed within this age range by the capped ash fall in El Resbalón dated at approximately 5.59 Ma and the U/Pb date of 6.95 Ma at Tepezala, also in the Juchipila Basin [6]. Records of similarly aged *Enhydritherium* are also found at the Withlacoochee 4A and Moss Acres Racetrack sites in Florida, which have a biochronologic age of late early Hemphillian, or 6–7 Ma [5,7] (electronic supplementary material, figure S2).

Our new discovery provides the first intermediate geographical link between the Florida and California occurrences, and reconciles a decades-old palaeozoogeographic mystery of the bi-coastal distribution of *Enhydritherium*,

Table 1. Lower dentition measurements of *Enhydritherium terraenovae* specimens in millimetres. AP, anteroposterior; T, transverse; p, premolar; m, molar.

	AP p2	T p2	AP p3	T p3	AP p4	T p4	AP m1	T m1
MPGJ 3586	—	—	7.5 ^a	4.3 ^a	9.6 ^b	6.0 ^b	16.7	10.8
UF 13860	—	—	—	—	—	—	18.1 ^b	10.3 ^b
UF 18928 ^c	9.7 ^a	3.2 ^a	10.3 ^a	4.2 ^a	11.6 ^a	5.9 ^a	17.1	11.2
UF 32001	—	—	—	—	—	—	15.8	10.3
UF 68000	8.7 ^a	—	—	—	13.2	8.2	17.0 ^a	6.9 ^a
UF 68001	8.5 ^a	—	9.9	5.8	12.0	6.4	16.1	7.5
UF 100000 right	8.4	4.5	9.4	4.5	10.1	6.2	15.3	10.6
UF 100000 left	9.4	5.1	8.1	5.0	10.9	7.4	15.6	10.1
UCMP 32970	—	—	—	—	—	—	—	10.4
LACM 121591	—	—	—	—	—	—	15.6	10.7

^aAlveolar measurement.^bEstimated from incomplete tooth.^cHolotype.

previously with no fossil evidence in interior North America [8]. One prior hypothesis suggested the North Atlantic and Arctic Oceans as a dispersal route, whereas another suggested dispersal via the Central American Seaway from the Pacific to the Caribbean [5,8] (figure 1). Both scenarios require dispersals over a significantly longer distance than by land, by hugging the coastline of the Arctic or the Central American Seaway. This dispersal route requires at least 8000 km of coastal and oceanic route, and is without a single fossil record of *Enhydritherium*. In contrast, our discovery of *Enhydritherium* in central Mexico suggests that a land-based route was much more likely, in terms of shorter distance (less than 4000 km), and is supported by fossils from an entirely land-locked basin containing upper Miocene fluviolacustrine deposits [6]. A recent study of fossil *Enhydra* records indicates that sea otters may have dispersed into the eastern Pacific from the North Atlantic not much earlier than middle Pleistocene [3]; this biogeographic scenario, plus recent cladistics analyses indicating a distant relationship between *Enhydritherium* and extant sea otters [4], and the new fossil evidence presented in this report, together suggest that the previously proposed close relationship between *Enhydra* and *Enhydritherium* is not supported [8].

Fossil mammal fauna in the Juchipila Basin suggests the presence of open habitats mixed with woodlands, and the sedimentary sequence suggests both fluvial and lacustrine environments were present (see electronic supplementary material). Wooded habitat mammals such as the sloth *Pliometanastes* and open/savannah woodland species such as the borophagine canid *Borophagus secundus*, the horses *Calippus*, *Neohipparion* and *Astrohippus*, the antilocaprids *Cosoryx* and *Plioceros*, the camel *Alforjas*, gomphothere proboscideans, and now the otter *Enhydritherium* indicate a diversity of habitats with a significant component of the fauna being associated with riparian or lakeside environments [6]. As the palaeozoogeographic patterns of *Enhydritherium* indicate, the significance of the central Mexico Neogene fossil record, in Juchipila Basin and elsewhere, is not only in clarifying the north–south dispersal of mammalian faunas during the Great American Biotic Interchange (GABI), when North and South American species

immigrated from their respective continents, but also in more regionalized dispersal patterns that may proceed in the east–west direction through riparian corridors.

Modern day distribution of the neotropical otter, *L. longicaudis*, is mainly along the western and southern regions of Mexico, with extension into the arid central interior region [1,9]. The proximity of modern day riparian habitat capable of sustaining wild otter populations to the late Miocene–Pliocene mammal faunas containing a significant component of stream- and lake-associated species suggests that such an east–west corridor for the cross-continental dispersal of *Enhydritherium*, and potentially other vertebrates, may have been persistent for a prolonged period of time. The new occurrence of *Enhydritherium* is the only early Hemphillian record of otters in Mexico, making it also the oldest known. Furthermore, this occurrence is the southern-most early fossil record of otters in North America, demonstrating an early zoogeographic connection between the modern distributions of the North American river otter (*L. canadensis*) in the north and the neotropical otter (*L. longicaudis*) to the south. This new fossil evidence demonstrates that lutrines such as *Enhydritherium* were already adapted to living in palaeoenvironments in the neotropical region, and also is consistent with the notion that a plausible dispersal corridor to central Mexico (see below) for some northern North American mammals was already present prior to the onset of the GABI [10,11].

The distribution of *L. longicaudis* in Mexico roughly traces the Pacific lowlands to the west and the Trans-Mexican Volcanic Belt (TMVB) to the south, suggesting that a possible east–west route of dispersal for stream-dependent otters and other vertebrates may have been along the northern face of the TMVB, and south of the central Mexican Plateau and the Sierra Madre Occidental and Sierra Madre Oriental ranges that flank the plateau to the west and east, respectively (see electronic supplementary material). Current climatic zonation using the Köppen–Geiger mapping method indicates an east–west band of temperate climate zones at the location of our hypothesized corridor, between tropical zones to the south and arid zones to the north [12]. As suggested by the general palaeoenvironmental indications

of the Juchipila fossil mammal fauna, temperate climatic zones may have been extended further north during the late Miocene relative to today.

4. Conclusion

Our discovery of new specimens of the fossil otter *E. terraenovae* suggests a plausible over-land dispersal route for a species closely associated with marginal marine environments. The previously disjointed distribution of *Enhydritherium* in California and Florida is now linked via an occurrence in the upper Miocene (approx. 5.59 Ma) fluvio-lacustrine deposits of central Mexico. This occurrence, along with postcranial osteology from Florida specimens that suggest increased capability for terrestrial locomotion relative to modern sea otters, provides consistent evidence for a significantly terrestrial, rather than entirely near-coast marine, route of dispersal for the extinct 'sea otter' *Enhydritherium* between the Atlantic and Pacific coasts of North America. Lastly, this new southern-most fossil record of a northern species signifies the presence of an early dispersal corridor

that may have persisted through the subsequent Great American Biotic Interchange.

Data accessibility. The new specimen described in the study is accessioned in the research collection of the Centro de Geociencias, Campus Juriquilla, Universidad Nacional Autónoma de México, Boulevard Juriquilla 3001, Juriquilla, Querétaro 76230, Mexico, under the curatorial responsibility of O.C.-C.

Authors' contributions. Z.J.T., A.P.-C., X.W., O.C.-C., J.J.A.-G. and H.T. conducted fieldwork and acquired data; A.P.-C. and H.T. performed laboratory preparation; Z.J.T., X.W., O.C.-C. and J.J.A.-G. analysed the data; Z.J.T., X.W. and O.C.-C. wrote the paper, and J.J.A.-G., A.P.-C. and H.T. revised content. All authors approved the final version of the paper and agreed to be accountable for all aspects of the work.

Competing interests. We have no competing interests.

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