LATE PLEISTOCENE SALAMANDER (AMBYSTOMATIDAE; CAUDATA; AMPHIBIA) FROM TÉRAPA, SONORA, MEXICO

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Abstract—Fifty-seven Late Pleistocene, Rancholabrean Land-Mammal "Age," localities are known in Sonora, Mexico. Most reports are preliminary descriptions that mention the recovery of bison, horse, proboscideans, and an occasional glyptodont. Rarely are there details about the recovery of microfaunal taxa, especially the herpetofaunal species. Exceptions to this include Rancho la Brisca, La Playa, and Térapa. In contrast to the former two localities, Térapa is situated along the Río Moctezuma that today enters the robust riverine system of the Río Bavispe/Yaqui (with its headwaters in southeastern-most Arizona and in the Sierra Madre Occidental). Amphibian remains recovered from Térapa are voluminous yet dominated by anurans. Only 17 remains are identifiable as salamander and recovered from an apparent carnivore scat. The specimens indicate that *Ambystoma* sp. did inhabit the Río Moctezuma valley (albeit rare) during the Late Pleistocene, where it is not recorded today. This is the first reported fossil salamander of Late Pleistocene age from Sonora, Mexico.

INTRODUCTION

The extant amphibians and reptiles of Sonora, Mexico have received much attention since the middle of the nineteenth century largely due to its proximity to adjacent Arizona and New Mexico (Lemos-Espinal and Rorabaugh, 2015). Although the Pleistocene fossil record of mammals is fairly-well understood for these USA states (Arizona: Mead et al., 2005; New Mexico: Harris, 2005; Morgan and Lucas, 2005; Morgan and Harris, 2015) and is beginning to be understood for parts of Sonora (Arroyo-Cabrales et al., 2002; White et al., 2010), the fossil herpetofauna, especially amphibians, is largely unstudied. Presented here from the Térapa local fauna is the description of the first fossil salamander from Sonora, México.

Sonora is the second largest Mexican state, with Chihuahua the largest and adjacent to the east. With Arizona and New Mexico bordering Sonora to the north, one might expect that the extant herpetofauna species are the same across the political border. Both Enderson et al. (2009) and Lemos-Espinal and Rorabaugh (2015) categorize the herpetofauna of Sonora into nine and seven (respectively) biotic assemblages. As shown by Smith and Lemos-Espinal (2015) and Brennan and Babb (2015), species richness of the herpetofaunas has Arizona and New Mexico most closely paired, then Sonora and Chihuahua form their own pair. Considering just the salamanders (with non-native species excluded), Sonora and Chihuahua form a distinct cluster and are more distantly related to Arizona, New Mexico, and other Mexican states (Smith and Lemos-Espinal, 2015, fig 13.2).

Sonora and Arizona hold critical physiographic positions in that they are at the latitudinal transition between the present Neotropical and Nearctic biotic zones found from the high Sierra Madre Occidental and Madrean Sky Island mountains (Madrean Archipelago of Lowe, 1992; Bezy and Cole, 2014) to the low Sonoran Desert (detailed discussion in Lemos-Espinal and Rorabaugh, 2015). The climate today in northern Sonora varies from hot and arid in the western deserts, transitioning to cool and moist in the mountains to the east (Brown, 1982). Description of the varied vegetation and biotic communities of Sonora was provided in Lemos-Espinal and Rorabaugh (2015, and references within). Most rivers in Sonora begin in the northern part of the state and flow south and west to the Sea of Cortés. Only the Colorado River and a few small streams with headwaters in extreme southeastern Arizona (that reach the Río Bavispe/Yaqui system) enter Sonora from Arizona. The Santa Cruz and San Pedro rivers travel through northern-most Sonora and then enter Arizona to add to the Colorado River system.

These river systems provide the needed corridors for dispersing species that require a riparian environment or more tropical habitats. Thirty-eight species of amphibians are recorded in Sonora, and all require some moist conditions for reproduction; most have an aquatic larval stage (Lemos-Espinal and Rorabaugh, 2015). Today only two families of salamanders are reported as indigenous to Sonora (Rorabaugh and Lemos-Espinal, 2016). Two species within Ambystomatidae are found in the state: *Ambystoma rosaceum* (Tarahumara salamander; ajolote Tarahumara), the more common salamander, and the much-less common *A. mavortium* (barred tiger salamander; ajolote tigre; once within *A. tigrinum*). The single Sonoran species within Plethodontidae (*Pseudoeurycea bellii*; ajolote de tierra, tlaconete pinto) has a restricted presence up in the Sierra Madre Occidental on the far eastern side of the state and into Chihuahua (Lowe et al., 1968; Lowe and Holm, 1989; Van Devender et al., 1989; Bezy et al., 2004).

Seven assemblages of extant reptiles and amphibians are recognized in Sonora by Lemos-Espinal and Rorabaugh (2015). Of these seven, salamanders are recorded from only the Montane/Foothills assemblage (*Ambystoma rosaceum, Pseudoeurycea bellii*) and the Grassland assemblage (*Ambystoma mavortium*), i.e., caudates are highly restricted in their Sonoran geographic distribution today.

Sixty-four fossil localities of Neogene age (Miocene, Pliocene, Pleistocene) are represented in Sonora with the bulk of them, 57, dating to the Late Pleistocene (Rancholabrean Land Mammal Age) and not described in detail (Arroyo-Cabrales et al., 2002; Ferrusquía-Villafranca et al., 2010; White et al., 2010). Of these, only two have detailed descriptions and related chronological sequences: Rancho la Brisca (Van Devender et al., 1985) and San Clemente de Térapa (=Térapa; Mead et al., 2006).

FOSSIL LOCALITY

The fossil outcrops at Térapa are located along the Río Moctezuma. The drainage begins just north of the town of Nacozari and flows south through Moctezuma and Térapa to join the Río Bavispe and Río Yaqui, which even today empties still into the Sea of Cortés between Guaymas and Ciudad Obregón. The basaltic Tonibabi lava flow forced the Río Moctezuma farther west within its valley and created a catchment basin that proceeded to in-fill with side-streams from the east and possibly

occasional over-the-back flow from the river. The impoundment created a short-lived marsh and open-water environment. Stratigraphy was described in Mead et al. (2006). The recovery of *Bison* (Bovidae) places the locality within the Rancholabrean Land-Mammal "Age." Analyses using infrared stimulated luminescence (IRSL), amino acid racemization (AAR), and radiocarbon (14C) show the impounding basalt and fossiliferous sediments formed 43,000 to 40,000 years ago (Bright et al., 2010). About 20 fossil outcrops comprise the Térapa local fauna in an area of approximately 1 by 2 km. To date the following taxa or analyses have been described: crocodilian (Mead et al., 2006), birds (Steadman and Mead, 2010; Oswald and Steadman, 2011), shrews and bats (Czaplewski et al., 2014), glyptodont and pampathere (Mead et al., 2007), ostracodes and isotopes (Nunez et al., 2010; Bright et al., 2016), dire wolf (Hodnett et al., 2009), proboscideans (Mead et al., 2019), additional ungulates and carnivores (Short et al., in press), and an incipient description of horse and bison (Carranza-Castañeda and Roldán-Quintana, 2007). Rodents, mollusks, anurans, fish, and squamates are being studied.

SALAMANDER

The most abundant vertebrate remains from the Térapa local fauna include fish, amphibians, and turtles, all yet to be fully described. Of the thousands of amphibian remains, anurans predominate and include multiple taxa. Only 17 elements are identifiable as salamander. The clump of salamander specimens were recovered in 2004 by Marci Hollenshead from the Beto outcrop at Térapa within the upper marsh organic clay unit (Bp2), which represents the end of the impounded marsh habitat before being covered by river gravels of the Ruíz Phase (Mead et al., 2006). All salamander elements (and fragments of an unidentifiable rodent skeleton) appear to be from a single individual. Specimens are highly etched, and fragmented with cavities filled with a white, chalky-carbonate substance giving the appearance of bones observed in carnivore scats. Other faunal remains (but not chalky or etched) in the immediate area of the "scat" include abundant fish and anuran remains along with ground sloth, turtles, and capybara. All fossil samples removed from the numerous outcrops at Térapa are currently housed at The Mammoth Site (Hot Springs, South Dakota) and are assigned specimen numbers (TERA) in a system used exclusively for the locality. When the fauna is completely studied, all specimens will be returned to México.

TERA-470A (Fig. 1) is the ventral portion of a fragmented left exoccipital with occipital condyle and a portion of the otic capsule. No parasphenoid is attached. The otic capsule is expanded as in ambystomatids and not small and enclosed as in plethodontids (e.g., Wake, 1963, 1966). Width across the expanded otic capsule for TERA-470A is approximately 6.5 mm (due to fragmentation). Width across the otic capsule of select comparative species: *Pseudoeurycea belli* (3.5 mm; svl=85 mm, snout vent length), *Ambystoma rosacea* (~4.5 mm), *A. mavortium* (6.2 mm; svl=110), *A. tigrinum* (6.0-6.5 mm, n=3, Michigan), *A. mexicanum* (6.5 mm; partially transformed adult). Because of the preserved morphology and comparable size, TERA-470A is identified as *Ambystoma* sp.

TERA-470B is the distal half of a right dentary with highly eroded tooth pedicels. TERA-470C is distal segment of left dentary with tooth pedicels preserved. Both dentary fragments are from a large salamander consistent with *Ambystoma* and distinctly larger than those within Plethodontidae.

TERA-470D includes four fragmented mid-trunk vertebrae. No transverse processes are preserved. Three have the spinal nerve foramen exposed on the vertebra consistent with *Ambystoma* and other ambystomids (Edwards, 1976), and unlike plethdontids. Two have centrum lengths (2.7, 2.8 mm) consistent with *Ambystoma* with a svl of 110 mm. Poor preservation negates obtaining standard and detailed measurements. Two have an overall morphology of a high neural arch as found in *Ambystoma* and are not the more flattened, smaller vertebrae of *Pseudoeurycea* and other plethodontids. Three have the continuous notochord opening within the centrum indicating larval or neotenic growth stages. These characters permit the identification to be *Ambystoma* sp., likely neotenic.

TERA-470E includes two ribs. TERA-470F is a small, fragmented caudal vertebra. TERA-470G includes two metaphodials. TERA-470H includes five phalanges. TERA-470E-H are the size of fairly large *Ambystoma* but exhibit no morphological traits constrained to this genus.

DISCUSSION AND CONCLUSIONS

The overall analysis of the 17 recovered salamander fossils is that *Ambystoma* sp. did inhabit the Río Moctezuma valley during the Late Pleistocene (albeit rare so far in the fossil record), and it is not recorded there today. The specimens represent a single individual most likely from a carnivore scat. This is the first record of a fossil salamander from Sonora, México. The fossil record of the region is not known well enough yet to determine if salamanders were common or uncommon (rare?) in the local biotic community during the Late Pleistocene.

Two species of *Ambystoma* live today in Sonora, México. *Ambystoma mavortium* is a large-sized (terrestrial adult svl ≤165 mm), widespread species within the USA. Having a larval stage in ontogeny, members of this family rarely occur beyond regions receiving less than 500 mm annual precipitation (Duellman

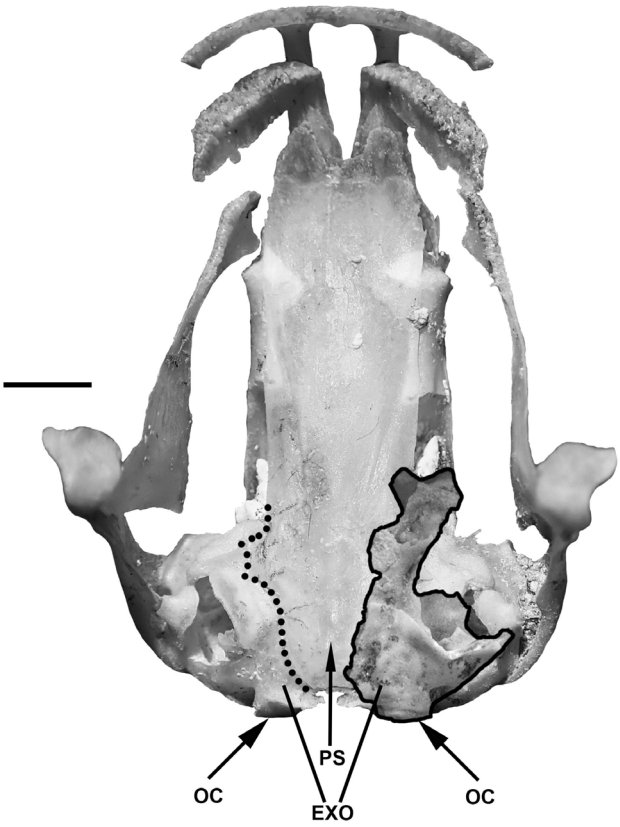

FIGURE 1. Extant *Ambystoma tigrinum* skull in ventral view with mandibles removed; anterior at top. Fossil fragment of exoccipital, TERA-470A, outlined in black placed over same exoccipital region on extant specimen. Abbreviations: EXO, exoccipital; OC, occipital condyle; PS, parasphenoid. See text for description. Scale bar equals 2 mm.

and Sweet, 1999). *Ambystoma mavortium* can survive arid regions by undergoing facultative neoteny (retention of larval characteristics, such as external gills, at sexual maturity) (Pedersen, 1993). *Ambystoma* in Sonora, Arizona, and New Mexico today occupy a wide variety of habitats provided there is tranquil, fishless water nearby for breeding, including wetlands and semi-desert grasslands, and range from desertscrub up to higher elevation spruce-fir forests (Degenhardt et al., 1996; Rorabaugh and Lemos-Espinal, 2016). A small population of *A. m. stebbinsi* is restricted to the San Rafael Valley at the border with Sonora; whether this is a distinct species (Jones et al., 1988) or a hybrid form between *A. mavortium* and *A. nebulosum* is still unresolved (Irschick and Shaffer, 1997). Although found state-wide in Arizona and New Mexico, in Sonora this species is restricted to the northeastern part of the state along the border with the USA. It is not recorded from along the Río Moctezuma or nearby drainages (Rorabaugh and Lemos-Espinal, 2016; pers. comm. J. Rorabaugh 10/2018).

Smaller than typical *Ambystoma mavortium*, *A. rosaceum* (adult svl≤ 85 mm) lives in slow-moving streams associated with grasslands but can occur in faster-moving waters in oak and pine-oak woodlands at higher altitudes, and to a lesser extent in foothills with thornscrub (Anderson, 1978; Rorabaugh and Lemos-Espinal, 2016). Rarely do adults of this species retain gills and remain as an aquatic form. Although presently found in higher altitude mountains (>1000 m altitude) near the northeastern border with the USA, this species is not known to occur in the USA.

Conspecific individuals of *Ambystoma* sp. may present differing morphologies that complicate fossil identifications. The condition of neoteny within fossil vertebrae can be inferred by well-ossified trunk vertebrae with open notochordal canals (Tihen, 1942, 1958; Holman, 1975; Rogers, 1985; Holman, 2006). Another condition found in the living forms of *Ambystoma* is that of skull growth variation due to cannibalistic behavior (e.g., Rose and Armentrout, 1976; Pedersen, 1993); this morphology has not been evaluated in terms of skeletal identification issues related to each species. Thus, it is my contention here that it is questionable that isolated vertebrae and possibly other skeletal remains of *Ambystoma* from Sonora, Arizona, New Mexico and possibly elsewhere in the Arid Southwest can be satisfactorily identified to species level given the large variation in individual size and shape of larval and terrestrial forms. Identifications of fossil mole salamanders from the Pleistocene of Sonora, Arizona, and New Mexico should be conservative and be viewed as *Ambystoma* sp. until more descriptive apomorphies can be found in both extant forms.

Rancholabrean-age *Ambystoma* in Arizona are reported from just three localities. (1) Papago Springs Cave specimens (*A*. cf. *A. tigrinum*; in the Canelo Hills at the north end of San Rafael Valley, Sonora border) include vertebrae and limb bones from sedimentary units dating greater than 172,000 yr B.P. (Czaplewski et al., 1999). (2) Specimens from a preliminary study at a quarry locality near Show Low in east-central part of the state are not accurately dated but were recovered in association with extinct peccary, *Platygonus*, and other extra local species not in that region today, thus a latest Pleistocene age is assumed (Murray et al., 2005). (3) A maxilla and postcranial skeletal elements of *Ambystoma* sp. were recovered from the Bear Pit red matrix in Pyeatt Cave, located on the south end of the Huachuca Mountains, southeastern Arizona at the border with Sonora. Accurate age assignment of the salamander remains in Pyeatt Cave may not be possible, but specimens were associated with material dated to approximately 17,450 cal B.P. (Czaplewski et al., this volume). The record of Late Pleistocene *Ambystoma* in New Mexico is much more robust and better documented than in Arizona (see overview in Darcy et al., this volume).

Although mentioned above that a minimum of 57 fossil localities of Rancholabrean age are known in Sonora, most descriptions merely mention the recovery of bison, horse, proboscideans, and an occasional glyptodont; rarely are there details about the recovery of microfaunal taxa, especially herpetofaunal species. Three exceptions to this include (1) Rancho la Brisca, (2) La Playa, and (3) Térapa.

(1) Rancho La Brisca occurs along the Río Santo Domingo tributary of the Río San Miguel, which combines with the Río Sonora. The fossil deposit is a spring- and stream-fed marsh and lacustrine deposit perched above the present canyon bottom. Today, water does not consistently reach to the Sea of Cortés, and it is uncertain how much flow the river had in the Pleistocene. The locality produced a wealth of microfaunal remains, especially anurans, but no salamanders were recovered (Van Devender et al., 1985). The fossil fish (five taxa) and the wealth of anuran species at Rancho la Brisca indicate that at least near its headwaters south of Cananea there was abundant water to support a diverse aquatic environment.

(2) West of Rancho la Brisca are the sedimentary units at La Playa – a valley-bottom alluvial deposit along the Río de las Pedradas (a tributary of the Río Magdalena and Río de la Asunción). The locality produced some smaller taxa (the grassland prairie dog, *Cynomys*: Mead et al., 2010), but only limited testing was completed and more should be attempted.

Both of the above localities and their river drainages are located well into the more arid desert region of northwestern Sonora. The volume of permanent water that flowed to the sea through these channels during the Late Pleistocene is unknown.

(3) In contrast to these two localities, Térapa is situated along a sustainable river today and enters the robust riverine system of the Río Bavispe/Yaqui (with its headwaters in mountainous southeasternmost Arizona and in the Sierra Madre Occidental). The taxa identified as fossils from this locality are distinct from those of the other two well-known sites with the occurrence of *Crocodylus*, the extinct capybara (*Neochoerus*: Mead et al., 2018), abundant aquatic birds (Steadman and Mead, 2010; Oswald and Steadman, 2011), and other taxa with certain subtropical, savanna, and riparian forest affinities. With the current known list of taxa from these three Late Pleistocene sites, it appears reasonable that a salamander has not been recovered from Rancho la Brisca or La Playa yet has at Térapa. Further work is needed on the Térapa deposit with the hope to recover additional remains of *Ambystoma,* including well-preserved cranial material.

Additional research is also needed to better understand the cranial and postcranial morphology through ontogeny (including neoteny) of extant *Ambystoma tigrinum*, *A. mavortium*, and *A. rosaceum*, if not other species within the complex throughout their current distribution. A first step to the understanding would be to root the study with a comprehensive molecular assessment, then proceed to skeletal morphology. Considering the study of Sonoran salamanders presented here, the ultimate goal is to be able to identify fossil remains to better appreciate past geographic distributions of two closely-related ambystomatid salamanders, in addition to the plethodontid, *Pseudoeurycea*. Additional cienega (spring), paludal, and lacustrine localities of Late Pleistocene age need to be assessed in detail via micromesh sieving in northern and eastern, mountainous Sonora in the search for the needed microfaunal deposits.

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