# FIRST RECORD OF FOSSIL CHELYDRID AND TRIONYCHID TURTLES (TESTUDINES) FROM THE PLEISTOCENE OF SONORA, MEXICO

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Abstract—The late Pleistocene of northern Mexico is relatively poorly understood, and represented by only a few fossil localities. One such locality is Térapa, located in east-central Sonora. The deposit dates to between 43,000 and 40,000 years old (Rancholabrean) and yields a rich fossil fauna of over 60 identified taxa, dominated by birds and large mammals. Geologic evidence at the site indicates a marshland with permanent sources of calm freshwater, which is supported by the presence of fossil remains of freshwater invertebrates, fishes, frogs, crocodilians and turtles. Previous studies have reported fossil turtles representing two families: Emydidae and Kinosternidae. Both of these families are represented in the extant fauna of Sonora. Here, we present the remains of two additional families of turtles from Térapa, Chelydridae and Trionychidae, both of which are absent today in the naturally-occurring fauna of Sonora. The extralimital presence of these families at Térapa indicates a significant biogeographical shift between the late Pleistocene and the present day. Previous studies have noted the similarly unusual discovery of crocodilians at Térapa, and proposed that its presence might be the result of dispersal into Sonora via coastal and riparian routes. We suggest a similar migration pattern might explain the presence of chelydrids and trionychids at the site, with the turtles dispersing into Sonora either from the north or from the south, and we discuss evidence for both scenarios.

# INTRODUCTION

San Clemente de Térapa, commonly called Térapa, is a rich fossil locality in east-central Sonora, Mexico. The fossil site is located in Sonora at Municipio de Moctezuma, San Clemente de Térapa, Río Moctezuma, 13.7 km (by air) SSE of Moctezuma at 29.67861°N 109.6525°W, with an elevation of 580 meters above sea level, 23 km SSW of the Sierra de la Madera, and 37 km W of the Río Bavispe (Fig. 1). The Rio Bavispe is a major tributary of the Río Yaqui. The fossil site is located between two lobes of the Tonibabi Lava Flow, which likely dammed the river, creating a marsh. The site dates to the Rancholabrean land mammal "age" (LMA) between 43,000 and 40,000 years old (Bright et al., 2010), and as such is one of the few intensely studied late Pleistocene fossil localities in northwestern Mexico. This locality yields a rich fossil fauna of over 60 taxa, listed in full by Mead et al. (2006) and White et al. (2010), including numerous species of fish, frogs, reptiles, birds, and mammals. The geology of the site, described in detail by Mead et al. (2006), indicates a short-lived marshland environment with permanent ponds or streams, an interpretation supported by the presence of many water-loving fossil taxa including fishes, frogs, and aquatic reptiles. Fossil remains of large herbivores at the site have been used to infer the presence of grassland adjacent to the marshland (Mead et al., 2006, 2007), although large mammals can travel long distances and are often poor indicators of vegetation. Isotopic studies performed by Nunez et al. (2010) and avian faunal analysis by Steadman and Mead (2010) corroborate these interpretations, implying that the environment surrounding Térapa consisted of marshland, woodland and grassland habitats. Mead et al. (2006) also reported on the surprising recovery of crocodilian and capybara remains, suggesting a more tropical component to the late Pleistocene climate of the region. In contrast to the subtropical marshland-woodland-grassland habitats inferred for Térapa, the modern environment in this region of Sonora is called matorral espinoso de piedemonte (foothill thornscrub) and is considered tropical (Martínez-Yrízar et al., 2010; Van Devender et al., 2013b). The only other major Rancholabrean-aged fossil locality in Sonora that has been discussed in detail in the literature is Rancho La Brisca (Van Devender et al., 1985), located about 100 km northwest of Térapa (Fig. 1A). In addition to being generally similar in age and geographic position, Rancho La Brisca shares a number of faunal similarities with Térapa (White et al., 2010). However, one of the most notable differences between the sites is that crocodilian remains are absent from Rancho La Brisca. With a unique location and an extensive fossil record, Térapa represents a rare opportunity for a detailed glimpse into the Rancholabrean of northwestern Mexico.

It is also noted that another Pleistocene fossil site in Sonora, from



FIGURE 1. The location of Térapa and the modern distribution of North American Chelydridae and Trionychidae. A, location of Térapa and the nearby site of Rancho La Brisca. Térapa sits alongside the present course of the Rio Moctezuma just west of the Sierra Madre Occidental mountain range. Modified from Mead et al. (2006). B, distribution of Chelydridae and Trionychidae across North America. Shaded area: Chelydrid distribution. Hatched area: Trionychid distribution. Both turtle families are widespread across North America, but neither occurs naturally in Sonora. Chelydrids are represented in North America by the genera *Chelydra* and *Macrochelys*. New World trionychids all belong to the genus Apalone. Note that the disjoint southwestern portion of the trionychid range represents introduced, but established, populations (discussed in text). Turtle distribution information from Bonin et al. (2006), Conant and Collins (2008), Ernst (2008) and Ernst and Lovich (2009).

the early to middle Pleistocene (Irvingtonian LMA), is known from Golfo de Santa Clara in northwestern Sonora (Croxen et al., 2007). It is found near the northern extent of the Gulf of California, and is part of the Colorado River Delta, with its fossil vertebrate fauna commonly called the El Golfo local paleobiota or El Golfo local fauna (Shaw, 1981; Croxen et al., 2007). Its Irvingtonian vertebrate fauna currently consists of over 80 taxa, including some potentially more southern taxa such as the giant anteater (*Myrmecophaga tridactyla*) and boa constrictor (*Constrictor constrictor*) (Shaw, 1981; Shaw and McDonald, 1987; Croxen et al., 2007).

Previous reports on the fossil fauna of Térapa focused on mammals and birds (Mead et al., 2007; Nuńez et al., 2010; Steadman and Mead, 2010; Oswald and Steadman, 2011), whereas turtles have received comparatively little attention. Mead et al. (2006) noted that turtles dominated the reptilian remains at the site and reported the presence of "pond turtles." White et al. (2010) provided further assessment of the turtle fossils, identifying three taxa from the site belonging to the families Emydidae (*Trachemys* and *Terrapene*) and Kinosternidae (*Kinosternon*). Here, we report fossil material belonging to the turtle families Chelydridae and Trionychidae. Neither chelydrids nor trionychids have previously been reported from either Térapa or Rancho La Brisca, nor does either family occur naturally in Sonora today (e.g., Rorabaugh, 2008; Enderson et al., 2009, 2010; Van Devender et al., 2013a). Thus, we report the first known natural occurrence of chelydrids and trionychids in Sonora, Mexico.

**Institutional abbreviations: ETVP**, East Tennessee State University Vertebrate Paleontology Lab, Johnson City, Tennessee, USA; **TERA**, Térapa fossil material, currently at East Tennessee State University, Johnson City, Tennessee, USA.

# METHODS AND MATERIALS

The fossils from Térapa (TERA) are temporarily cataloged and held at the Vertebrate Paleontology Laboratory of East Tennessee State University, Johnson City, Tennessee, USA, until a permanent repository in Mexico can be identified. Identification of materials was accomplished primarily through comparison with the extensive modern comparative collection of turtles housed at ETVP (see Appendix 1).

### SYSTEMATIC PALEONTOLOGY TESTUDINES Linnaeus, 1758 CRYPTODIRA Cope, 1868 POLYCRYPTODIRA Gaffney and Meylan, 1988 CHELYDRIDAE Grey, 1831 Chelydridae indeterminate Fig. 2

Chelydrid material recovered from Térapa consists of plastral The two best-preserved of these fragments (TERAfragments. 150 and TERA-275) represent the distal portion of the hypoplastron (Fig. 2). These elements are assignable to Chelydridae based on the characteristic robust anterodistal hypoplastral projections and similar overall morphology. It should be noted that various turtles, including members of the Emydidae, may have similar-looking plastral projections and have similar morphology of the distal portions of the hyo- and hypoplastra, particularly in juveniles. However, the fossil material we present here may be distinguished from emydids and other non-chelydrid turtles by a number of characters. First, other turtles often have scute sulci present; in the case of emydids and others these sulci are associated with the axillary and inguinal scutes/buttresses. No sulci are present on TERA-150 or TERA-275. Second, while chelydrid shell material commonly has distinct sculpturing composed of irregularconnected furrows, these furrows are more prominent medially on the hyo- and hypoplastra, but absent laterally. The distal portions of the hyo- and hypoplastra in modern chelydrids have proximodistallyoriented striations, a trait also seen in TERA-150 and TERA-275. The striations may travel farther away from the sutural contacts near the anterior surface on the hyoplastron, but not posteriorly, and vice-versa for the hypoplastron. In emvdids these striations tend to be restricted near the sutural contacts. Third, the sutural projections in emydids also tend to become smaller moving toward the middle of the bridge, while these projections in chelvdrids tend to remain more similar in size, the latter condition also present in TERA-150 and TERA-275. Finally, the emydid bridge tends to be fairly robust medially, and becomes more gracile moving toward the middle of the bridge. A similar condition is found in chelydrids, including TERA-150 and TERA-275, but to a lesser degree than in emydids. The morphology of these projections, sculpturing, and lack of pitting help to distinguish these remains from



FIGURE 2. Chelydridae indeterminate, **A-B**, TERA-150, distal portion of right hypoplastron in ventral (A) and dorsal (=visceral) (B) views. **C-D**, TERA-275, distal portion of left hypoplastron in dorsal (=visceral) (C) and ventral (D) views. Bar scales = 5 mm.

otherwise similar features present on the shells of Trionychidae as well. Unfortunately, these fragments alone do not provide enough detailed features to allow for identification of this material beyond family level.

## TRIONYCHIDAE Fitzinger, 1826 Trionychidae indeterminate Fig. 3

One small carapace fragment (TERA-276) has been identified as trionychid (Fig. 3). TERA-276 represents a small bone fragment with relatively fine pitting and shallow sutural projections. While the fragment does have fine pitting, it does not agree in morphology with the texturing and pitting that can be present in kinosternid specimens. Kinosternids, such as Kinosternon and Sternotherus, may have fine pitting and texturing on their shells, which tends to become more pronounced around sutural surfaces, particularly around the bridge. However, even when investigating the entire shell, the texturing in kinosternids is almost completely made up of furrows, with very little pitting. The texturing of TERA-276, however, is almost exclusively pitting, with only a few furrows present. Exposed emydid trabeculae can also have pitting that is superficially similar, although the surface sculpturing of TERA-276 is preserved outer surface and not altered by weathering or erosion, therefore not representative of emydid trabeculae. In trionychids, especially on the carapace, texturing is typically made up of more pitting proximally near and on the neurals, while these pits tend to coalesce and more furrows are present distally near the outer rim of the carapace. Crocodilians can also possess pitting on various skeletal elements and, as mentioned above, are also known from the Térapa site. However, in juvenile and younger individuals, crocodilians generally exhibit smaller and deeper pitting, these pits becoming wider and shallower through ontogeny (Buffrénil, 1982). Were TERA-276 a crocodilian, the small size of the specimen would imply it would have belonged to a juvenile; however, the small pits with gracile and thin walls between the pits do not agree with the morphology present in iuvenile crocodilians either.

Ornamentation can also be found on the bone surface of some fish, including catfish, however this ornamentation is less uniform than that present on TERA-276, and the ornamentation tends to be made up for the most part of furrows and ridges. This is in contrast to the ornamentation present on TERA-276, which is made up mostly of pitting with only a few very short furrows. The break on the internal surface of the specimen appears to represent the breakage of the rib, implying it is a partial costal and not a part of the bridge that is more strongly textured in kinosternids. The two small pits present on the ventral surface are thought to be fenestrae or foramina, but may also



FIGURE 3. Trionychidae indeterminate. TERA-276, proximal portion of ?costal 5 in ventral (=visceral) (A) and dorsal (B) views. Abbreviation: rb, rib breakage. Bar scale = 2 mm.

be pathologic. Their placement potentially near the attachment of a rib would agree with a possible location for nutrient foramina. Additionally, the interdigitating sutural teeth are quite shallow, but this condition has been found in some trionychids we have examined (example ETVP 9217). The sutural teeth tend to be larger and more pronounced along the anterior and posterior sutural surfaces of the costals, but shallower and less pronounced medially with the contact between the costals and neurals.

Based on the morphology of the sutural surfaces on this fragment, we tentatively identify this specimen as the proximal end of the fifth costal. The sculpturing preserved on the dorsal surface of this fragment is consistent with the carapace sculpturing patterns characteristic of trionychids. The sculpturing is composed of numerous small pits, some of which have become elongate near the sutural surfaces. Fine sculpturing on such a small fragment may represent a juvenile. Keeping in mind that sculpturing can vary within a single trionychid taxon based on location on the shell (Holman and Case, 1988; Gardner and Russell, 1994; Jasinski, 2013), the identified fragment cannot be definitively assigned to the genus Apalone, the only currently recognized native trionychid genus in North America (Bonin et al., 2006; Ernst and Lovich, 2009), although it is superficially similar based on its sculpturing. However, Apalone often have relatively larger pits, potentially showing distinction from the specimen. No trionychid material is available from Térapa that displays any features that would allow identification beyond the family level.

# DISCUSSION

The presence of Chelydridae and Trionychidae at Térapa represents a significant range extension during the Pleistocene of both families. These families are not known from any previous fossil material in Sonora, nor do they occur naturally in the Sonora region today, although one trionychid taxon, Apalone spinifera, has been introduced to Sonora (Rorabaugh, 2008; Enderson et al., 2009, 2010). Mead et al. (2006) interpreted the paleoenvironment of this locality to include a freshwater marshland, so it is not surprising that chelydrids and trionychids would be able to live there; modern members of both families prefer to dwell in calm, freshwater habitats with muddy or sandy bottoms (Finkler and Kolbe, 2008; Ernst and Lovich, 2009). However, the geographical separation between Térapa and the modern ranges of these families is more surprising. Today, chelydrids in North America, represented largely by the common snapping turtle Chelydra serpentina, are distributed across nearly the entire eastern and central United States, and from the Mexican border north into Canada (Bonin et al., 2006; Ernst, 2008). Disjoint populations of chelydrids occur in Central America, but none live in Mexico. The most widespread of the North American trionychids is *Apalone spinifera*, which overlaps C. serpentina across much of its range in the eastern United States. Apalone spinifera extends farther south than C. serpentina, ranging into northern Mexico,

and populations of the species are known as far west as New Mexico, with introduced populations in Arizona and California (Bonin et al., 2006; Ernst and Lovich, 2009). The distribution of North American chelydrids and trionychids is shown in Figure 1B. While Chelydridae extends into the southernmost United States, and Trionychidae ranges into northern Mexico, the main extent of these natural populations is separated from Sonora by the Sierra Madre Occidental mountain range. Both families are previously known from the Pleistocene fossil record, but no known fossil records exist of these turtles from any site nearer to Sonora than southwestern Kansas (Holman, 1987) or southern Nevada (Van Devender and Tessman, 1975). The presence of both families in Sonora approximately 43,000 – 40,000 years ago at Térapa indicates a drastic biogeographical shift in turtle distribution between the Late Pleistocene and the present, and warrants discussion.

Chelydridae and Trionychidae are not the first unusual reptile families to be found at Térapa. Mead et al. (2006) described crocodilian teeth from Térapa, and noted that they are significant, as no sustained populations of crocodilians are present in Sonora today. The authors stressed that these isolated teeth did not allow them to make a definitive identification beyond "crocodilian," and cautiously assigned the teeth to the American crocodile (Crocodylus acutus) based on historical reports of the presence of these animals in this region (Mead et al., 2006). Nabhan (2003) reported that C. acutus was historically present in Sonora and the adjacent Gulf of California, and Baegert (1952) reported the presence of "alligators of considerable size" in the mouth of the Colorado River in the 1700s. Today, C. acutus is restricted to the tropics (Alderton, 1992), but these historical records farther north might represent populations or individuals migrating north along the coast of the Gulf of California. Mead et al. (2006) hypothesized that crocodiles might have had access to Térapa during the Rancholabrean in the same way, by following the coast north and then migrating up the Yaqui River east into interior Sonora, as the Río Moctezuma is a northwestern tributary of the Río Yaqui. Additionally, it is of note that fresh or brackish water mangrove swamps are present as far north as the Infiernillo Strait between Tiburón Island and the adjacent Sonoran mainland. As discussed above, a more tropical component and environment in this region would imply that these mangrove swamps may have been found farther north and been more common during the "Sangamon" interglacial and portions of the Pleistocene.

#### Down from the North

Unlike the crocodilians, modern trionychids are not known from the tropics of the New World, but modern trionychid populations (*Apalone spinifera*) inhabit eastern North America, including much of the eastern United States (introduced populations are also known from Arizona and California), and northeastern Mexico (Fig. 1B). It seems reasonable that a more western and southern extension of this distribution might have inhabited Térapa during the Rancholabrean.

Trionychid populations are clearly able to survive in the southwestern United States, directly north of Sonora (although these populations, while established, are introduced), and may have had a more western distribution in the past. This population might have migrated south along the coast of the Gulf of California and gained access to interior Sonora by following the Yaqui River to Térapa. Both Apalone spinifera and A. ferox (native to Florida) are known to be able to survive in brackish waters (Bonin et al., 2006), albeit not continuously, but a migration along the coast is feasible. Late Pleistocene climatic transitions may have forced these turtles out of Sonora as the marshland habitats of Térapa gave way to the modern semiarid shrub land, and resulted in their more restricted modern distribution. However, permanent bodies of water are still present in the region, although these turtles are not naturally present. Unfortunately, no fossil record of trionychids exists from the Pleistocene of the arid southwest United States to lend support to this hypothesis. Even so, their presence in the watershed of the Gulf of California may provide a probable means for them to extend farther south.

It may be that this scenario could be used to explain the chelydrid presence at Térapa as well. This is complicated by the fact that the modern range of Chelydridae is blocked from western extension by the mountainous and desert environments of the arid southwest United States. While no modern chelydrid populations have been reported from west of the Rocky Mountains, there has been one report of chelydrid fossils from southern Nevada (Van Devender and Tessman, 1975; Ernst, 2008). The presence of chelydrids in the Basin and Range Province in the Rancholabrean lends some support to the hypothesis of chelydrid populations extending south into Térapa.

Nevertheless, a southern push of vertebrates during glacial periods could force some more northern taxa to move farther south during these episodes. The Rancho la Brisca fauna includes Bison, a northern element (Van Devender et al., 1985). As approximately 90% of the Pleistocene experienced glacial conditions, interglacials, whether they were or were not more tropical, would have represented much shorter periods. Northern aquatic species that expanded southward during glacials surely could have lingered during interglacials. Additionally, as Chelydra was previously reported from the Colorado River drainage in southern Nevada in the Rancholabrean west of the Continental Divide (Van Devender and Tessman, 1975; Ernst, 2008), it is more likely that it somehow got from the Pecos River/Rio Grande drainage in the Gila River system, and then into the Río Yaqui. Part of the headwaters of the Río Yaqui are in southwestern New Mexico and southeastern Arizona. While the western record for trionychids is not currently known, they likely could have followed a similar dispersal scenario.

#### Up from the South

Alternatively, considering that there are chelydrid populations living today in the tropics of Central America (Fig. 1B), it may be that chelydrids had a broader tropical distribution during the Late Pleistocene, and that their range, like that of the crocodilians, extended into Sonora along the coast from the tropics in the south. It might also be that the moist tropical environments of Central America and Mexico would have been more easily traversed by these turtles than the more northern plains. Both North American genera of Chelydridae (Chelydra and Macrochelys) can inhabit brackish water (Bonin et al., 2006; Ernst, 2008), albeit not continuously, and would be capable of migrating along coastal habitats. Additionally, the presence of mangrove swamps in the region may have provided relatively close "stepping stones" that the turtles could have utilized in traveling north. However, this would require chelydrids to have been rare throughout this range, and/or become extinct throughout this range. Today, Chelydridae overlaps with Crocodylus acutus in both Central America and southern Florida, and, in fact, Chelydra serpentina will sometimes share dens with crocodilians (Ernst, 2008); it would not be surprising if these two reptiles shared distribution patterns and associations in the past as well.

Additionally, this southern tropical distribution scenario could be proposed for the trionychids as well. *Apalone spinifera* extends today into eastern Mexico, ranging south to much lower latitudes than Térapa. Furthermore, trionychid fossils are known from the Miocene-Pliocene of Central America and South America (Wood and Patterson, 1973; Laurito et al., 2005). In contrast to the "down from the north" hypothesis described above, it might be that the geographical barriers of the southwestern United States prevented trionychids from migrating into the southwestern states in the past, as seems to have been the case for chelydrids. In that scenario, a broader tropical distribution of trionychids might have extended west across Mexico and north along the Gulf of California, from there following riverine passages into both interior Sonora and the southwestern United States. This would require a large range extension and a great deal of subsequent extinction within that range, to explain the lack of extant presence. Climatic shift and resulting environmental changes at the end of the Pleistocene would have removed suitable habitats from Sonora and tropical Mexico and restricted the turtles of both families to their more limited modern distributions. In this scenario, the disjunct population of trionychids in the southwestern United States would represent a remnant population of a former distribution extending from the south, rather than a distribution extending west across the United States, as Conant and Collins (1998) suggested. The presence of some southern taxa at El Golfo (Croxen et al., 2007) may also lend some credence to an up from the south dispersal for these two turtle groups as well.

Unfortunately, no fossil record of either Chelydridae or Trionychidae exists from any localities farther south than Térapa during the Pleistocene, so the "up from the south" hypothesis is lacking support from the Rancholabrean fossil record, and for that matter, so is the "down from the north" hypothesis. Either scenario suggests that both chelydrids and trionychids have been more widely distributed over the past 40,000 years than is currently understood. However, an up from the south scenario implies that populations of these turtles would have died out in hundreds of aquatic environments along the west coast of Mexico. Both turtles are very adaptive, and evidence of remnant populations should be scattered throughout western Mexico. Indeed, they are ecologically quite distinct from Crocodylus acutus, which thrives in brackish water. This seems to make the up from the south scenario less likely. Regardless, the fossil record of turtles will need to be further explored in Mexico and the United States before the biogeographical history of these animals can be explained any further. Indeed, it is of note that further analysis of the emydids and kinosternids is needed to determine whether the taxa at Térapa represent northern or southern forms as well.

## CONCLUSIONS

This study represents the first report of Chelydridae and Trionychidae from Sonora, Mexico. The presence of both families in Sonora during the Rancholabrean LMA supports the evidence for an environmental shift from a wetter, likely tropical marshland in the past to the arid scrubland of modern Sonora. Furthermore, the presence of these turtles at Térapa implies a dramatic change in the geographical distribution of both families between the late Pleistocene and today. We propose that the presence of chelydrids and trionychids at Térapa might imply an extensive tropical distribution of one or both of these families during the late Pleistocene, from which the turtles might have migrated north along the Gulf of California into Sonora, and upriver into Térapa. The same scenario has been proposed in the past to explain the presence of crocodilian and capybara remains at Térapa. No fossil evidence is known of either chelydrids or trionychids occurring in such a southern distribution during the Pleistocene, although today, chelydrids are known to live in the tropics of Central America and northern South America. The alternative hypothesis is that the turtles in Sonora represent a southern extension of a past distribution occurring in the western United States. This hypothesis is supported by the presence of trionychids in New Mexico and by the presence in Nevada of chelydrids in the Rancholabrean, but is complicated, as with the previous hypothesis, by a lack of significant fossil evidence for these families in that region of North America during that time interval. Either scenario demonstrates that these turtles were more widely distributed in the late Pleistocene than is presently understood, and that their past distribution differs drastically from their modern range. More fossil evidence will be needed to further elucidate the Pleistocene evolution and biogeography of these turtles.

# ACKNOWLEDGMENTS

We thank J. Mead, S. Swift, and A. Baez for providing us with the fossil material we used in this study, and for informative discussions about the Térapa locality. We would like to thank B. Schubert for offering helpful advice and useful references. And we thank all those who participated in the excavations at Térapa, without whom none of this material would be available for study. R. White and an anonymous reviewer provided helpful reviews on an earlier version of this manuscript. A. Lichtig, S. Lucas, and an anonymous reviewer also provided helpful reviews that improved this manuscript as well.

### 166

# REFERENCES

- Alderton, D., 1992, Crocodiles and Alligators of the World: United Kingdom, Blandford, 190 p.
- Baegert, J.J., 1952, Observations in Lower California: translated from the original German with an introduction and notes by M. M. Brandenburg and Carl L. Baumann: Berkeley, University of California Press, 218 p.
- Bonin F., Deveaux, B. and Dupré. A., 2006, Turtles of the World: Baltimore, The Johns Hopkins University Press, 416 p.
- Bright, J., Kaufman, D.S., Forman, S.L., McIntosh, W.C., Mead, J.I. and Baez, A., 2010, Comparative dating of a *Bison*-bearing late-Pleistocene deposit, Térapa, Sonora, Mexico: Quaternary Geochronology, v. 5, p. 631–643.
- Buffrénil, V.de., 1982, Morphogenesis of bone ornamentation in extant and extinct crocodilians: Zoomorphology, v. 99, p. 155–166.
- Conant, R. and Collins. J.T., 1998, A Field Guide to Reptiles and Amphibians of Eastern and Central North America, Third ed. Expanded: New York, Houghton Mifflin, 616 p.
- Croxen, F.W., III, Shaw, C.A. and Sussman, D.R., 2007, Pleistocene geology and paleontology of the Colorado River Delta at Golfo de Santa Clara, Sonora, Mexico; *in* Reynolds, R.E., ed., Wild, scenic & rapid-a trip down the Colorado River trough, The 2007 Desert Symposium field guide and abstracts from proceedings California State University, Desert Studies Consortium and LSA Associates, Inc., p. 84–89.
- Enderson, E.F., Quijada-Mascareñas, A., Turner, D.S., Rosen, P.C. and Bezy, R.L., 2009, The herpetofauna of Sonora, Mexico, with comparisons to adjoining states: Check List, v. 5, p. 632–672.
- Enderson, E.F., Quijada-Mascareñas, A., Turner, D.S., Bezy, R.L. and Rosen, P.C., 2010, Una sinopsis de la herpetofauna con comentarios sobre las prioridades en investigación y conservación; *in* Molina-Freaner, F.E. and Van Devender, T.R., eds., Diversidad biológica de Sonora; Mexico, Universidad Nacional Autonóma de México, p. 357–383.
- Ernst, C.H., 2008, Systematics, Taxonomy, and Geographic Distribution of the Snapping Turtles, Family Chelydridae; *in* Steyermark, A.C., Finkler, M.S. and Brooks, R.J., eds., Biology of the Snapping Turtle (*Chelydra serpentina*); Baltimore, The Johns Hopkins University Press, p. 5–13.
- Ernst, C.H. and Lovich, J.E., 2009, Turtles of the United States and Canada; Baltimore, The Johns Hopkins University Press, 827 p.
- Finkler, M.S. and Kolbe, J.J., 2008, Physiology and ecology of hatchling snapping turtles; *in* Steyermark, A.C., Finkler, M.S., and Brooks, R.J., eds., Biology of the Snapping Turtle (*Chelydra serpentina*); Baltimore, The Johns Hopkins University Press, p. 158–167.
- Gardner, J.D. and Russell, A.P., 1994, Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa: Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen, v. 193, p. 209–244.
- Holman, J.A., 1987, Climatic significance of a late Illinoian herpetofauna from southwestern Kansas: Contributions from the Museum of Paleontology, University of Michigan, v. 27, p. 129–141.
- Holman, J.A. and Case, G.R., 1988, Reptiles from the Eocene Tallahatta Formation of Alabama: Journal of Vertebrate Paleontology, v. 8, p. 328– 333.
- Jasinski, S.E., 2013, Review of the fossil Trionychidae (Testudines) from Alabama, including the oldest record of trionychid turtles from eastern North America: Bulletin of the Alabama Museum of Natural History, v. 31, p. 46–59.
- Laurito, C., Valerio, A.L., Z., Gómez, L.D., Mead, J.I., Pérez, E.A., G., and Pérez, L.G., 2005, A Trionychidae (Reptilia: Testudines, Cryptodira) from the Pliocene of Costa Rica, southern Central America: Revista Geológica de América Central, v. 32, p. 7–11.
- Martínez-Yrízar, A., Felger, R.S. and Búrquez, A., 2010, Los ecosistemas terrestres: un diverso capital natural; *in* Molina-Freaner, F.E. and Van

- Mead, J.I., Baez, A., Swift, S.L., Carpenter, M.C., Hollenshead, M., Czaplewski, N.J., Steadman, D.W., Bright, J. and Arroyo-Cabrales, J., 2006, Tropical marsh and savanna of the late Pleistocene in northeastern Sonora, Mexico: The Southwestern Naturalist, v. 51, p. 226–239.
- Mead, J.I., Swift, S.L., White, R.S., McDonald, H.G. and Baez, A., 2007, Late Pleistocene (Rancholabrean) Glyptodont and Pampathere (Xenarthra, Cingulata) from Sonora, Mexico: Revista Mexicana de Ciencias Geológicas, v. 24, p. 439–449.
- Nabhan, G.P., 2003, Singing the turtles to the sea: the Seri art and science of reptiles: Berkeley, University of California Press, 350 p.
- Nuńez, E.E., Macfadden, B.J., Mead, J.I. and Baez, A., 2010, Ancient forests and grasslands in the desert: diet and habitat of late Pleistocene mammals from north-central Sonora, Mexico: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 297, p. 391–400.
- Oswald, J.A. and Steadman D.W., 2011, Late Pleistocene passerine birds from Sonora, Mexico: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 301, p. 56–63.
- Rorabaugh, J.C., 2008, An introduction to the herpetofauna of mainland Sonora, México, with comments on conservation and management: Journal of the Arizona-Nevada Academy of Science, v. 40, p. 20–65.
- Shaw, C.A., 1981, The middle Pleistocene El Golfo local fauna from northwestern Sonora, Mexico. Master Thesis, Long Beach, California State University, 282 p.
- Shaw, C.A. and McDonald, H.G., 1987, First record of giant anteater (Xenarthra, Myrmecophagidae) in North America: Science, v. 236, p. 186–188.
- Steadman, D.W. and Mead, J.I., 2010, A late Pleistocene bird community at the northern edge of the tropics in Sonora, Mexico: American Midland Naturalist, v. 163, p. 423–441.
- Van Devender, T.R., Rea, A.M. and Smith, M.L., 1985, The Sangamon interglacial vertebrate fauna from Rancho La Brisca, Sonora, Mexico: Transactions San Diego Society of Natural History, v. 21, p. 23–55.
- Van Devender, T.R. and Tessman, N.T., 1975, Late Pleistocene snapping turtles (*Chelydra serpentina*) from southern Nevada: Copeia, v. 1975, p. 249–253.
- Van Devender, T.R., Enderson, E.F., Turner, D.S., Villa, R.A., Hale, S.F., Ferguson, G.F. and Hedgcock, C., 2013a, Comparison of Preliminary Herpetofaunas of the Sierras la Madera (Oposura) and Bacadéhuachi with the Mainland Sierra Madre Occidental in Sonora, Mexico; *in* Gottfried, G.J., Ffolliott, P.F., Gebow, B.S., Eskew, L.G. and Collins, L.C., eds., Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III; Fort Collins, United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Proceedings, RMRS-P-67, p. 110–116.
- Van Devender, T.R., Yanes-Arvayo, G., Reina-Guerrero, A.L., Valenzuela-Yánez, M., de la Paz Montańez-Armenta, M. and Silva-Kurumiya, H., 2013b, Comparison of the tropical floras of the Sierra la Madera and the Sierra Madre Occidental, Sonora, Mexico; *in* Gottfried, G.J., Folliott, P.F., Gebow, B.S., Eskew, L.G. and Collins, L.C., eds., Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III; Fort Collins, United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Proceedings, RMRS-P-67, p. 240–242.
- White, R.S., Mead, J.I., Baez, A. and Swift, S.L., 2010, Localidades de vertebrados fósiles del Neógeno (Mioceno, Plioceno y Pleistoceno): una evaluación preliminar de la biodiversidad del pasado; *in* Molina-Freaner, F.E. and Van Devender, T.R., eds., Diversidad biológica de Sonora: Mexico, Universidad Nacional Autonóma de México, p. 51–72.
- Wood, R.C. and Patterson, B., 1973, A fossil trionychid turtle from South America: Brevoria, v. 405, p. 1–10.

# APPENDIX

Modern specimens housed at the East Tennessee State University Vertebrate Paleontology Lab (ETVP) used for comparisons. Specimens are listed taxonomically by family, then alphabetically, and finally numerically.

Chelydridae		Trionychidae	
Chelydra sp.	ETVP 9892	Trionychidae indet	ETVP 9217
Chelydra serpentina	ETVP 138	Trionychidae indet	ETVP 9474
Chelydra serpentina	ETVP 531	Trionychidae indet	ETVP 9836
Chelydra serpentina	ETVP 7984	Apalone ferox	ETVP 2989
Chelydra serpentina	ETVP 8793	Apalone ferox	ETVP 94352
Chelydra serpentina	ETVP 9886		
Chelydra serpentina	ETVP 9888		
Chelydra serpentina	ETVP 9889		
Chelydra serpentina	ETVP 9891		
Chelydra serpentina	ETVP 9893		
Chelydra serpentina	ETVP 9899		
Chelydra serpentina	ETVP 9900		
Chelydra serpentina	ETVP 9901		
Chelydra serpentina	ETVP 14313		
Macrochelys sp.	ETVP 9950		

168