



A New Species of Mud Turtle of Genus *Kinosternon* (Testudines: Kinosternidae) from the Pacific Coastal Plain of Northwestern Mexico

JESÚS A. LOC-BARRAGÁN^{1,2,3}, JACOBO REYES-VELASCO⁴, GUILLERMO A. WOOLRICH-PIÑA¹, CHRISTOPH I. GRÜNWARD^{3,4}, MYRIAM VENEGAS DE ANAYA^{5,6}, JUDITH A. RANGEL-MENDOZA⁷ & MARCO A. LÓPEZ-LUNA^{7,8*}

¹Tecnológico Nacional de México Campus Zacapoaxtla, Posgrado en Ciencias Ambientales. División de Biología. Laboratorio de Ecofisiología y Zoología. Carretera Acuaco-Zacapoaxtla Km 8. Col. Totoltepec, Zacapoaxtla, Puebla, México. C. P. 73680.

✉ gwoolrich@live.itsz.edu.mx; <https://orcid.org/0000-0002-3421-7246>

²Red Mesoamericana y del Caribe para la Conservación de Anfibios y Reptiles (MesoHerp).

✉ biolocbarragan@gmail.com; <https://orcid.org/0000-0001-6851-054X>

³Biodiversa, Comité Nacional para la Conservación de Ecosistemas Mexicanos A.C. Avenida de la Ribera no. 203, C.P. 45900, Chapala, Jalisco, México.

✉ cgruenwald@switaki.com; <https://orcid.org/0000-0001-5994-555X>

⁴Herp.mx A.C. Villa de Álvarez, Colima, México.

✉ jacobo.reyes@nyu.edu; <https://orcid.org/0000-0002-8787-9980>

⁵Universidad Tecnológica de Panamá, Campus Víctor Levi Sasso. Avenida Universidad Vía Puente Centenario, Ancón, Republic of Panamá.

✉ miryam.venegas@utp.ac.pa; <https://orcid.org/0000-0003-4287-0162>

⁶Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancón, Republic of Panamá.

⁷División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco. Carr. Villahermosa-Cárdenas km 0.5, 86039 Villahermosa, Tabasco, México.

✉ jurannmen@gmail.com; <https://orcid.org/0000-0003-1189-9835>

⁸Instituto de Neuroetología, Universidad Veracruzana. Av. Dr. Luis Castelazo, Col. Industrial Ánimas, 91190 Xalapa-Enríquez, Veracruz, México. Current address.

✉ marco.lopez.luna@gmail.com; <https://orcid.org/0000-0003-2259-544X>

*Corresponding author

Abstract

We describe a new species of mud turtle of the genus *Kinosternon* from the Pacific Coastal Plain of the Mexican states Sinaloa and Nayarit. The new species shares morphological characters with the recently described *Kinosternon vogti*, which are unique to these two turtles and separate them from the other species of the genus. The new species differs from *K. vogti* by skin coloration, size, and the scutellation of both carapace and plastron. We also present a molecular phylogeny of the family Kinosternidae based on two mitochondrial and four nuclear loci. Our results show that the new species is most closely related to *K. vogti*, and together they form the sister group to the *K. hirtipes* and *K. integrum* species groups of *Kinosternon*.

Key words: Reptilia; freshwater turtle *sp. nov.*; endemic; Sinaloa; Nayarit; Pacific Coastal Plain

RESUMEN

Describimos una nueva especie de tortuga casquito del género *Kinosternon* de la Llanura Costera del Pacífico Mexicano en los estados de Sinaloa y Nayarit. La nueva especie comparte caracteres morfológicos con *Kinosternon vogti*, separandolas de las otras especies del género. Las diferencias entre la nueva especie y *K. vogti* incluyen la coloración, tamaño, y proporciones en los escudos del caparazón y el plastrón. También presentamos una filogenia molecular de la familia Kinosternidae basada en dos genes mitocondriales y cuatro nucleares. Nuestros resultados muestran que la nueva especie está más emparentada con *K. vogti*, y juntos estas especies forman el grupo hermano de los grupos de especies *K. hirtipes* y *K. integrum*.

Palabras claves: Reptilia; Tortuga de agua dulce *sp. nov.*; endémica; Sinaloa; Nayarit; Llanura Costera del Pacífico

INTRODUCTION

The herpetofauna of northwestern Mexico has been studied for at least 150 years (Goldman 1951, Hardy and McDiarmid 1969). The most extensive collections formed the basis for a study undertaken by E. W. Nelson and E.A. Goldman between 1892 and 1906 (Flores-Villela et al. 2004). Additional expeditions, mainly in the mid-twentieth century, added to the knowledge of the herpetofauna of Jalisco, Nayarit and Sinaloa. Those studies have painted a detailed picture of the herpetofaunal biodiversity of the region (Van Denburgh 1897, Hardy and McDiarmid 1969, García 2006, Chávez-Ávila et al., 2015, Woolrich-Piña et al., 2016). However, some groups remained poorly studied, such as freshwater turtles of the genus *Kinosternon*, with eight species distributed along the Pacific versant in Mexico, of the total of 16 that inhabit Mexico (Legler and Vogt 2013, TTWG 2017, López-Luna et al. 2018). This genus has been under-studied in this region, potentially due to their aquatic habits, and the difficulty in differentiating among species (Legler and Vogt 2013). Thus, questions remain about the diversity of the genus *Kinosternon* in the northwestern Mexico. For example, the morphologically distinctive dwarf species *Kinosternon vogti* López-Luna et al. 2018 was only recently described from the Bahía de Banderas region of Jalisco. Specimens of this species were misidentified as *Kinosternon chimalhuaca* Berry et al. 1997 for almost two decades (Cupul-Magaña and Rubio-Delgado 2003) before the species was properly described (López-Luna et al. 2018). A similar situation occurred in the state of Nayarit, when on 23 August 1962 an unidentified turtle was collected 11 km S of Acaponeta, which was later reported as a juvenile female of *Kinosternon chimalhuaca* (Webb 2001). Based on the morphological characteristics of this individual detailed by Webb (2001), López-Luna et al. (2018) entertained the possibility of it belonging to a more northern population of *Kinosternon vogti*. The recent observation and capture of other individuals in southern Sinaloa with the same characteristics prompted the reexamination of the original specimen, deposited in the Herpetology Collection of the University of Texas at El Paso (UTEP 3908). We confirmed that the newly collected specimens and the original individual from Nayarit are conspecific, and that these specimens represent a second, un-described dwarf species of kinosternid turtle from the Pacific Coastal Plain and foothills of southern Sinaloa and northern Nayarit, which we describe herein.

MATERIALS AND METHODS

Initially, in a night-driving survey looking for amphibians and reptiles in southern Sinaloa, we found a single road-killed (DOR) turtle, now designated as holotype of our new species. About a month later we collected two turtles of interest in the field with the use of chicken wire funnel traps (Iverson 1979a) baited with canned tuna. Traps were left both day and night for no more than eight hours at a time for five days. With the exception of UTEP 3908, all specimens were collected in seasonal ponds near La Concepción, Sinaloa during the summer rainy season. The two captured individuals (designated as paratypes), were humanely euthanized with a Pentobarbital solution following the AVMA guidelines for the Euthanasia of Animals (Underwood and Anthony 2020). We took muscle tissue samples for molecular analysis and preserved them in 96% ethanol. We fixed specimens in 10% buffered formalin and then transferred them to 70% ethanol for permanent storage in scientific collections. We recorded the coloration in life based on notes taken on individuals in the field, and also from high quality digital photographs.

All measurements were taken by one of us (MALL) using digital calipers (ROK ®) to the nearest 0.1 mm, and we provide means \pm standard deviation. UTEP 3908 was photographed in the UTEP herpetological collection, and the photographs were sent with metric and standard color references. We calculated this individual's measurements with the Rulerswift® app (<http://www.tangyc.top/>). The criteria for measurements and nomenclature for turtle specimens and comparison with other species were taken from the general descriptions in Legler and Vogt (2013), as well as the descriptions of *Kinosternon* from Mexico (Berry and Iverson 1980, Berry et al. 1997, López-Luna et al., 2018). We measured eighteen morphological character states, and list the abbreviations used in parentheses: CL (maximum carapace length); CW (carapace width at level marginal scutes 5-6); CH (maximum carapace height); HW (head width at level of jaw articulation); AHW (width of anterior plastral lobe at anterior hinge); PHW (width of posterior plastral lobe at posterior hinge); BRL (length of bony bridge); HL (maximum length of plastral hind-lobe); LPH (length of interposterior humeral scute seam) FL (maximum length of plastral forelobe); FEL (length of interfemoral scute seam); PL (maximum length of plastron); PS1 (midline length of plastral scute 1); PS6 (mid-line length of plastral scute 6); AIC (axillary-inguinal contact, + or -); M2C (contact between second marginal scute and

first vertebral scute, + or -); V1-V5 (maximum width and length of vertebral scutes 1-5); and M1-M11 (length and height of marginal scutes 1-11). We calculated the plastral formula as described by Legler and Vogt (2013).

DNA extraction, sequencing and phylogenetic analyses

Tissues from the holotype (JALB-391, MZFC-HE 35627) were preserved in 96% EtOH. We isolated genomic DNA of sample using a Qiagen DNeasy extraction kit (Qiagen, Inc., Valencia, CA, USA). We used polymerase chain reaction (PCR) to amplify a fragment of the mitochondrially-encoded Cytochrome Oxidase B (Cytb), as well as the rRNA loci 12s and 16s. Additionally, we sequenced four nuclear loci, R35, TB01, PSMC1 and KIAA0398, which have been used previously to infer evolutionary relationships in the family Kinosternidae (Iverson et al. 2013; Spinks et al. 2014). The PCR products were sequenced in both directions by BGI Life Technologies, Hong Kong. We used the primers and PCR conditions used by Iverson et al. (2013) and Spinks et al. (2014). In the case of *Kinosternon vogti* we used the sequences of the mitochondrial gene Cytochrome b (Cyt b), obtained by López-Luna *et al.* (in prep). Unfortunately, we were not able to include nuclear data for *K. vogti*. All sequences are deposited and available at NCBI's Genbank (Table S1).

Phylogenetic analyses

We edited the raw sequence chromatograms using the program Geneious v6.1.6 (Biomatters Ltd., Auckland, NZ) and aligned the edited sequences using MAFFT (Katoh and Stanley, 2013). We then manually trimmed the 5' and 3' ends of each sequence to reduce columns with high levels of missing data. We concatenated all genes using the program SequenceMatrix (Vaidya *et al.*, 2011). We included multiple species of the family Kinosternidae obtained from Genbank (Table S1). The final data set consisted of 4892bp (1945bp of three mtDNA genes, and 2947bp of five nuclear loci).

We selected best-fit models of evolution for each loci and codon position for the alignment based on the Bayesian Information Criterion (BIC) implemented in PartitionFinder v1.1.1 (Lanfear et al., 2012). The best-fit partition scheme for the alignment is shown in Table 1. We used this best-fit partition scheme and set of substitution models to estimate phylogenetic relationships among members of the family Kinosternidae using Bayesian Markov Chain Monte Carlo (MCMC) simulation in MrBayes v3.2.1 (Ronquist *et al.* 2012), which we implemented on the CIPRES science gateway server (Miller et al., 2010). The MrBayes analyses consisted of four independent runs, each of 10^7 MCMC generations with four chains (one cold and three heated), sampling every 1,000th generation. We then confirmed convergence among runs based on overlap in likelihoods and parameter estimates, as well as effective sample size (ESS) and potential scale reduction factor value estimates (PSRF) for each parameter, which were evaluated in Tracer v1.6 (Rambaut *et al.* 2014). Based on the PSRF values, individual runs had converged by 10^5 generations (ESS > 200 for all parameters), and we discarded the first 10^5 samples as burn-in. We then combined the 4 independent MCMC samples (post burn-in) and computed a maximum clade credibility tree using TreeAnnotator v1.8.2 (Rambaut and Drummond 2014).

TABLE 1. Best-fit models of evolution for each locus and codon position.

Loci	Origin	Codon position	Substitution model
A17367	Nuclear Intron	-	HKY + gamma
A22519	Nuclear Intron	-	HKY + gamma
R35	Nuclear Intron	-	HKY + gamma
TB01	Nuclear Intron	-	HKY + I
12s	mitochondrial rRNA	-	GTR + I + gamma
16s	mitochondrial rRNA	-	GTR + I + gamma
Cyt b	protein-coding mtDNA	1st codon	GTR + I + gamma
Cyt b	protein-coding mtDNA	2nd codon	GTR + I + gamma
Cyt b	protein-coding mtDNA	3rd codon	GTR + I + gamma

SYSTEMATICS

Order: Testudines

Suborder: Cryptodira

Family: Kinosternidae

Kinosternon cora sp. nov.

(Figs. 1,2,3,5,6)

Cora Mud Turtle, Casquito cora, Chacuanita cora

Holotype—(JALB-391, MZFC-HE 35627) (Fig. 1), an adult female from Mexico: Sinaloa: Ejido La Concepción (La Concha), Municipio de Escuinapa (22.531758°, -105.450767°; datum WGS 84; elev. 10 masl) collected on 4 September 2017 by J. A. Loc-Barragan. (Fig. 4)

Paratypes—(3): An adult female (JALB-412, MZFC-HE 35628) (Fig. 2A) and juvenile male (JALB-411, MZFC-HE 35629) (Fig. 3) from Mexico: Sinaloa: Ejido La Concepción (La Concha), Municipio de Escuinapa (22.531758°N, -105.450767°W; datum WGS 84; elev. 10 masl) (Fig. 4) collected on 15 October 2017 by J. Loc-Barragan, M. A. López-Luna and A. H. Escobedo-Galván; an adult female (UTEP 3908) (Fig. 2B) from Mexico: Nayarit: 11 km S of Acaponeta on Hwy. 15 (Fig. 4) collected on 23 August 1962 by R. G. Webb, D. W. Tinkle, W. Auffenberg, W. Auffenberg Jr., L. Irwin, W. Milstead and D. Patten.

Diagnosis—A small *Kinosternon*, the largest known specimen is a female (CL=107.7 mm). This species is unique among *Kinosternon* of western Mexico, except *K. vogti*, of which it is a sister species, by possessing a very reduced and weakly kinetic plastron; a narrow bridge; and a proportionally wide carapace. We describe the diagnostic characteristics of *Kinosternon cora* with the species present on the Mexican Pacific versant (Table 2).

Kinosternon cora differs from *K. chimalhuaca*, Berry, Seidel and Iverson 1997, with which it was originally confused, by the following characters (character states of *K. chimalhuaca* in parentheses): A greater relative carapace width, average CW/CL ratio > 71% (< 70%); a very small plastron; average PHW/CW < 49% (> 49%); a narrow bridge, average BRL/CL < 13% (>13%); and a relatively large axillary scute, > 60% of the size of the inguinal scute (< 60% of the size of the inguinal scute).

Kinosternon cora differs from the broadly sympatric *K. integrum* LeConte 1854, by the following characters (character states of *K. integrum* in parentheses): A greater relative carapace width, average CW/CL ratio > 71% (< 70%); a very small plastron, average PHW/CW < 49% (> 55%); a long interfemoral scute seam, average FEL/HL > 40% (< 40%); a narrow bridge, average BRL/CL < 13% (>18%); and a relatively large axillary scute > 60% of the size of the inguinal scute (< 35% of the size of the inguinal scute).

Kinosternon cora differs from the southern species, *Kinosternon oaxacae* Berry and Iverson 1980, by the following characters (character states of *K. oaxacae* in parentheses): A greater relative carapace width, average CW/CL ratio > 71% (< 70%); a very small plastron, average PHW/CW < 49% (> 53%); a long interfemoral scute seam, average FEL/HL > 40% (< 40%); a narrow bridge, average BRL/CL < 13% (>18%); a relatively large axillary scute, > 60% of the size of the inguinal scute (< 40% of the size of the inguinal scute); and the first vertebral scute not in contact with M2 (first vertebral scute in contact with M2).

Kinosternon cora differs from the southernmost Mexican coastal species, *Kinosternon scorpioides cruentatum* (Duméril and Bibron 1851), by the following characters (character states of *K. s. cruentatum* in parentheses): A greater relative carapace width, average CW/CL ratio > 71% (< 70%); a very small plastron, average PHW/CW < 49% (> 60%); a long interfemoral scute seam, average FEL/HL > 40% (< 20%); a narrow bridge, average BRL/CL < 13% (>25%); a relatively large axillary scute, > 60% of the size of the inguinal scute (< 40% of the size of the inguinal scute).

Kinosternon cora differs from the northern Pacific coastal species, *Kinosternon alamosae* Berry and Legler 1980, by the following characters (character states of *K. alamosae* in parentheses): A greater relative carapace width, average CW/CL ratio > 71% (< 70%); a very small plastron, average PHW/CW < 49% (> 70%); a long interfemoral scute seam, average FEL/HL > 40% (< 35%); a narrow bridge, average BRL/CL < 13% (>30%); and axillary and inguinal scutes in broad contact, separating the abdominal and marginal scutes (Axillary and inguinal scutes never in contact, abdominal and marginals in contact).

Kinosternon cora differs from the northernmost Mexican coastal species *Kinosternon stejnegeri* Hartweg 1938 (formerly *K. arizonense* Gilmore 1923), by the following characters (character states of *K. stejnegeri*): A very small plastron, average PHW/CW < 49% (> 70%); a long interfemoral scute seam, average FEL/HL > 40% (< 35%); a narrow bridge, average BRL/CL < 13% (>25%); a relatively broad axillary scute, less than twice as long as wide (narrow axillary scute, three times longer than wide)

Kinosternon cora is a member of the *K. hirtipes/integrum* group. The subspecies of *K. hirtipes* (Wagler 1830), closest geographically to *Kinosternon cora* is *K. h. chapalaense* Iverson 1981. *Kinosternon cora* differs from *K. h. chapalaense*, by the following characters (character states of *K. h. chapalaense* in parentheses): A greater relative plastron width, average AHW/CL ratio > 40% (< 35%); a very small plastron, average PHW/CW < 49% (> 50%); a long interfemoral scute seam, average FEL/HL > 40% (< 35%); and a narrow bridge, average BRL/CL < 13% (>18%).

Kinosternon cora is the sister species of geographically proximate *K. vogti* (Fig. 4) with which it shares several characters that distinguish them both from the other species. However, *Kinosternon cora* differs from *K. vogti* by the following characters (character states of *K. vogti* in parentheses): a more robust body (body small); darker gray skin coloration (skin coloration pale grayish); a nuchal scale that is two to three times width than long (nuchal scale as wide as long; Figs. 5 A, B); marginal scale 11 half as high as marginal 10 (marginal 11 almost as high, or just a little shorter than marginal 10; Figs. 5 C, D); posterior plastral lobe not notched posteriorly (posterior plastral lobe notched; Figs. 5 E, F); plastron length smaller, average PL/CL ratio 80% (average PL/CL ratio 90%); bridge length shorter, average BRL/CL ratio 11% (average BRL/CL ratio 19%); rostral shield less conspicuous, V-shaped (rostral shield large and rounded); rostral shield the same color as the dorsal head coloration (rostral shield different color than coloration than head, bright yellow in males, pale yellowish in females Figs. 5 G, H); and males without yellow reticulations on head (males with small yellow reticulations on head).

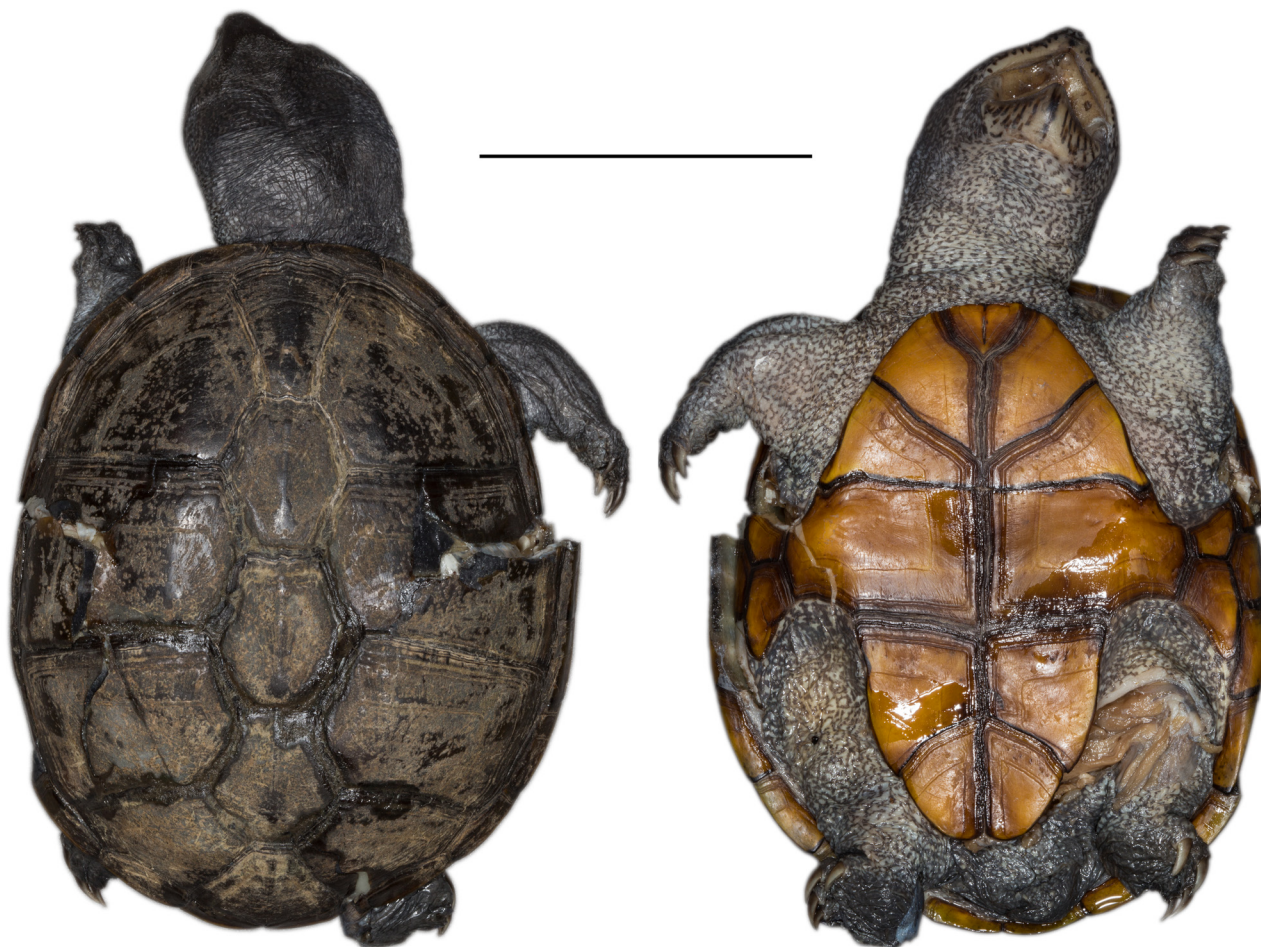


FIGURE 1. Holotype (adult female) of *Kinosternon cora* sp. nov. MZFC-HE 35627. Dorsal and ventral view. Black line represents 50 mm. Photo by M. A. López-Luna.

TABLE 2. Characters* useful in distinguishing females of *Kinostemon* species along Pacific Coastal Mexico

Species	N	CL (mm)	CW/CL	CH/CL	CH/CW	PL/CL	FL/CL	HL/CL	BRL/CL	PS1/CL	PS6/CL	AIC	M2C
<i>K. cora</i>	3	99.6 (92.1–107.7)	0.79	0.40	0.51	0.81	0.31	0.27	0.11	0.10	0.19	3/3 (100%)	0/3 (0%)
<i>K. vogti</i>	3	92.2 (89.4–94.4)	0.75	0.41	0.55	0.90	0.38	0.28	0.19	0.12	0.22	3/3 (100%)	0/3 (0%)
<i>K. chimalhuaca</i>	57	108.1 (99–127)	0.70	0.38	0.54	0.91	0.29	0.36	0.22	0.14	0.22	54/54 (100%)	6/54 (11.1%)
<i>K. stejnegeri</i>	21	134 (110.7–157.7)	0.70	0.40	0.57	0.95	0.34	0.34	0.25	0.34	0.23	7/22 (31.8%)	0/22 (0%)
<i>K. atamosae</i>	16	113 (89–126)	0.67	0.40	0.59	0.96	0.29	0.30	0.30	0.17	0.24	0%	0%
<i>K. sonoriense</i>	100	120 (92.6–155)	0.66	0.37	0.56	0.90	0.31	0.35	0.25	0.17	0.19	+50%	+50%
<i>K. integrum</i>	6	134.2 (103–163)	0.66	0.40	0.6	0.95	0.33	0.35	0.27	0.17	0.25	3/6 (50%)	5/6 (83.3%)
<i>K. oaxacae</i>	2	128 (126–130)	0.67	0.36	0.54	0.93	0.31	0.35	0.25	0.17	0.22	18/18 (100%)	17/17 (100%)
<i>K. scorioides</i>	49	124.2 (105–138)	0.71	0.48	0.68	0.97	0.32	0.37	0.31	0.17	0.32	1/24 (4.2%)	19/24 (79.2%)
CL	Carapace length												
CW	Carapace width												
CH	Carapace height												
PL	Length of plastron												
FL	Length of forelobe												
HL	Length of plastral hindlobe												
BRL	Length of bony bridge												
PS1	Length of plastral scute 1 (midline)												
PS2	Length of plastral scute 6 (midline)												
AIC	Axillary-inguinal contact												
M2C	Contact between second marginal scute and first vertebral												

*With the exception of *K. cora* and *K. vogti*, the data were compiled from Berry & Berry (1984), Berry & Iverson (1980), Berry & Legler (1980), Berry et al. (1997), Huise (1976), Iverson (1981), and Legler & Vogt (2013).

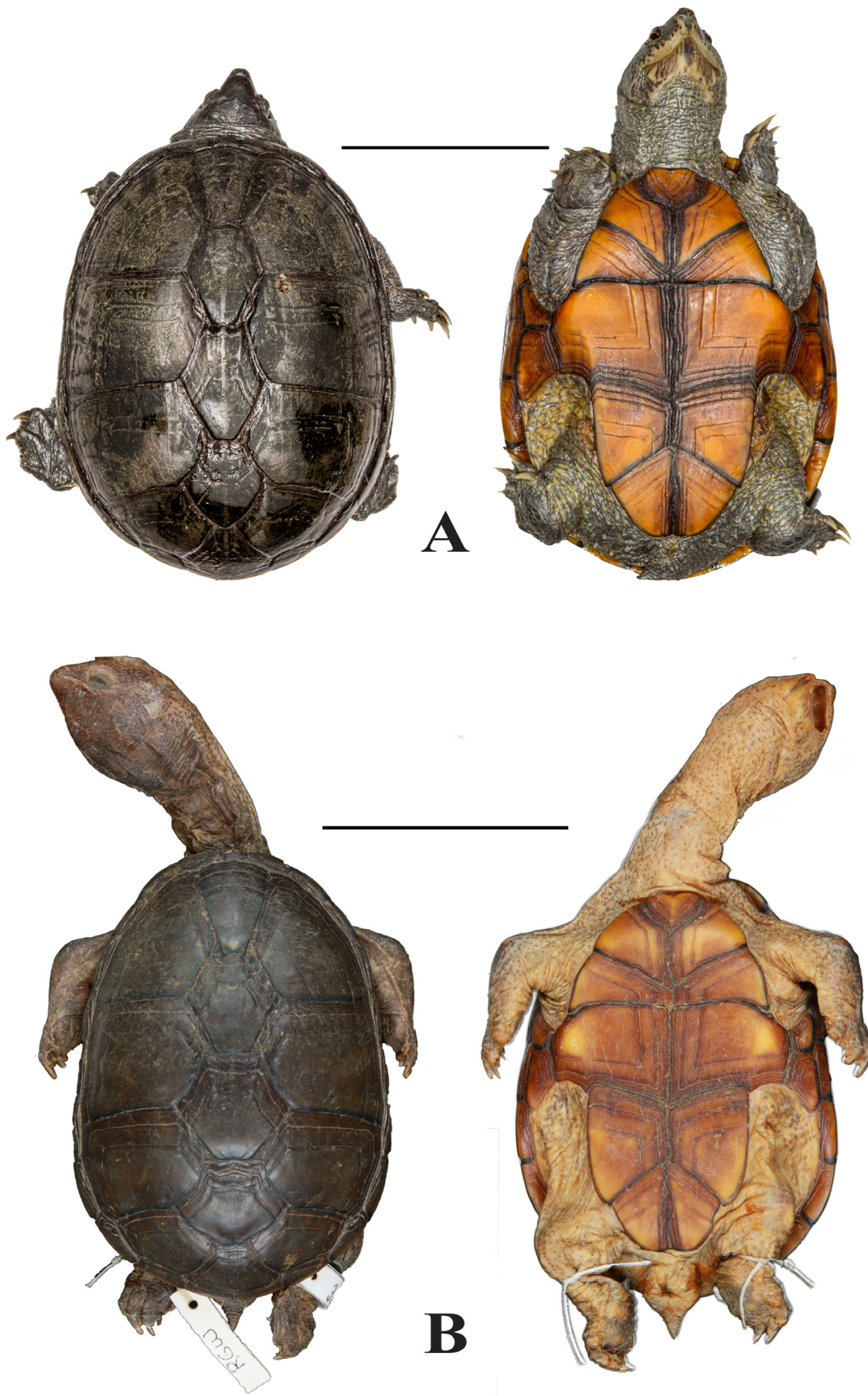


FIGURE 2. Female paratypes of *Kinosternon cora* sp. nov. **A** MZFC-HE 35628 **B** UTEP 3908. Dorsal and ventral views. Black lines represent 50 mm. Photo **A** by M. A. López-Luna, Photo **B** by Muriel M. Norman and Daniela Dominguez.



FIGURE 3. Male paratype of *Kinosternon cora* sp. nov. MZFC-HE 35629. Dorsal and ventral view. Black line represents 50 mm. Photo by M. A. López-Luna.

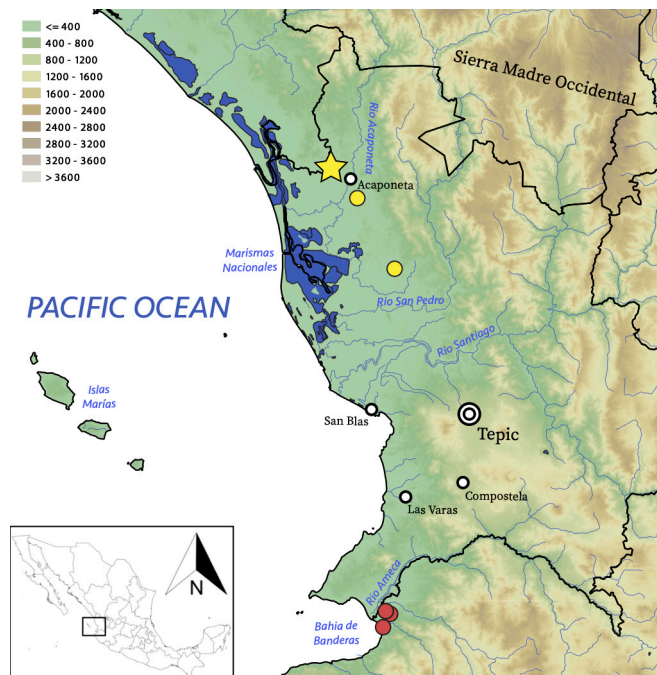


FIGURE 4. Known distribution of *Kinosternon cora* sp. nov. in Sinaloa and Nayarit. Yellow star represents the type locality, yellow dots represent additional records. Red dots represent the records of the sister species *Kinosternon vogti*.

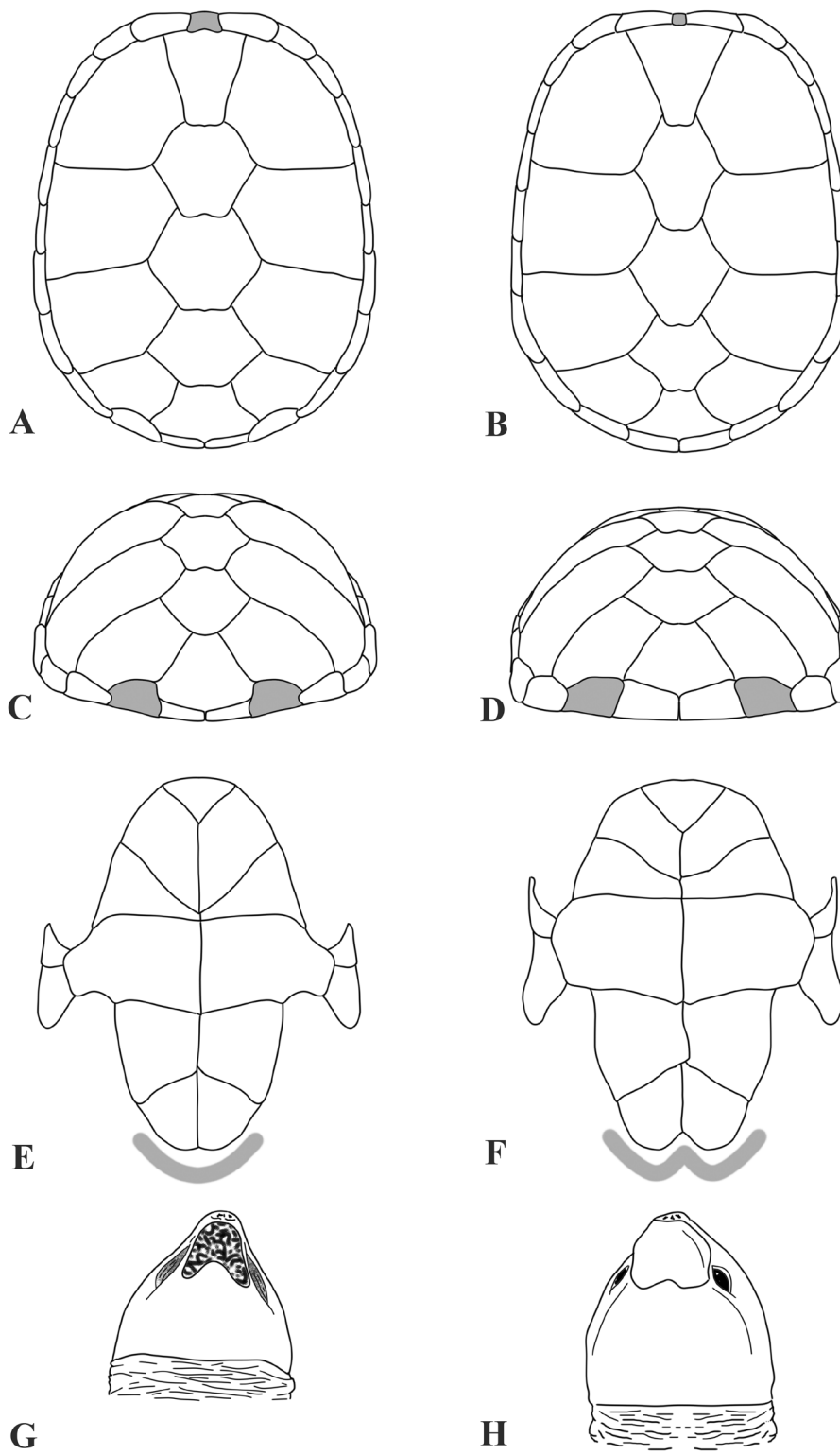


FIGURE 5. Diagnostic differences between *Kinosternon cora* sp. nov. (A, C, E, G) and *Kinosternon vogti* (B, D, F, H). A, B: proportions of the nuchal shield; C, D: ratio of the height of the M10 to the adjacent shields; E, F: absence / presence of a notch in the anal shields; G, H: shape and patterning of nasal shield.



FIGURE 6. Head patterns of *Kinosternon cora* sp. nov. **A:** Female holotype, MZFC-HE 35627, **B:** Male paratype, MZFC-HE 35629. Unscaled images. Photo by M. A. López-Luna.

Description of holotype—An adult female (JALB-391, MZFC-HE 35627), road-killed, with the carapace broken along the lateral plane, involving the costal scutes 2 and 4 on the right side, and costal scutes 2 and 3 on the left side. The marginal shields 5, 6, 7 on the right side, and 5 on the left side are fractured. The right abdominal is fractured in the region adjacent to the bridge. Although the fractures cracked the carapace and part of the plastron, the seam and proportions of the scutes remain in good condition. Characteristics and measurements are as follows: CL= 99.0 mm; CW= 89.4 mm; CH= 36.6 mm; HW= 27.0 mm; HL= 28.3 mm; AHW= 47.8 mm; LPH= 14.9 mm; FL= 30.0 mm; PHW= 36.0 mm; carapace relatively compressed and wide (CW/CL= 90 %); unicarinate with longitudinal keel slightly evident; growth rings evident on plastral and carapacial scutes; scutes imbricate; V1 very narrow, not in contact with M2; M1-9 aligned; M10 twice as high as M9 and M11; M11 slightly shorter than M9; V1, V2 and V3 longer than wide (22 x 17 mm, 23.3 x 20 mm, 23.9 x 20 mm), V4 as long as wide (21.3 x 22 mm), and V5 wider than long (12.4 x 23.1 mm). Plastron small (PL/CL= 80%), flat, with two kinetic hinges; anterior hinge straight and freely movable; posterior hinge flat anteriorly and not movable; posterior plastral lobe entire, not notched; axillary and inguinal scutes very wide and in full contact; axillary extends from middle M5 to middle M6; inguinal scute extending from middle M6 to posterior M7. Plastral formula 4>6>2>5>1>3. Head relatively wide (HW/CL= 27%), rostral shield large, furcate v-shaped, dark grayish; maxillary sheath hooked. Diameter of the tympanic membrane as large as the eye socket. One pair of small chin barbels elongated and conspicuous. Dorsal and lateral surfaces of the neck smooth. Tongue papillose. Jaw sheaths yellowish, streaked with dark brown. Manus and pes muscled and fully webbed; digital claws well developed. Keratinized patches on the posterior thigh and crus (clasping organs) poorly developed in the only known juvenile male; presumed to be well-developed in adult males. Falciform scales on antebrachium and heel typically kinosternine, keratinized. Tail very short, protruding slightly from the marginal shields and with a very small “claw” on the tip; with 4 dorsolateral longitudinal rows of poorly developed papillae.

Color of holotype in preservative: Coloration of carapace dark brown-olive with the edge of scutes black. Color of plastron orange with annuli proximal to midventral line dark brown; edges of the plastral scutes dark brown. Head grayish, with a reticulated pattern in buff or whitish, strongly reticulated laterally and ventrally. Overall, soft body parts with the same pattern. Figs. 1 and 6A show the holotype in preservative.

Variation—Including the holotype and three paratypes. The first measure corresponds to the average of three adult females, and the second measure to the only juvenile male collected; CL = 92.1–107.7 mm ($\mu=99.6 \pm 7.6$ mm), 75 mm; CW = 63.7–89.4 mm ($\mu=68.8 \pm 13.5$ mm), 58.6 mm; CH = 36.6–45.2 mm ($\mu=39.9 \pm 4.6$ mm), 30.4 mm; HW = 22.6–27.0 mm ($\mu=25.5 \pm 2.5$ mm), 20.0 mm; HL = 24.0–29.0 mm ($\mu=27.1.9 \pm 2.7$ mm), 23.3 mm; AHW = 37.0–48.1 mm ($\mu=44.3 \pm 6.3$ mm), 34.2 mm; LPH = 10.0–15.0 mm ($\mu=13.3 \pm 2.9$ mm), 14.7 mm; FL= 30.0–33.4 mm ($\mu=31.1 \pm 2$ mm), 25.3 mm; PHW = 30.0–39.6 mm ($\mu=35.2 \pm 4.8$ mm), 27.0 mm; carapace compressed and wide (CW/CL = 70–90%, $\mu = 80\%$), 70%; Scutellation and color of carapace are similar to holotype. Proportion PL/CL = 80–84% ($\mu = 81\%$), 86%. Plastral formula: 4>6>2>5>1>3 (50%), 4>2>6>5>1>2 (25%), 4>6>5>2>1>3 (25%). Relative head width (HW/CL) 25–27%; Rostral shield V-shaped on the supranasal region with a dark gray pattern color in all females, same shape in the male, but the color pattern of rostral shield dark, and slightly reticulated with yellow. Chin barbels and neck papillae similar to holotype. Characteristics of the females’ tail, similar to holotype; tail of juvenile male longer, reaching up to half of the M9, prehensile, the “claw” of the tail, inconspicuous to the eye, but hardened to the touch.

Color of paratypes in life: Coloration of carapace varies from olive-green to dark brown. The edges of scutes are invariably black. Color of plastron yellowish to bright orange, with dark brown outlines on the scutes, and with deep and dark interlaminar seams. Dorsal surfaces of head dark gray, with a pale yellow or whitish reticulations which become more dense laterally and ventrally. Reticulations become orange laterally on some individuals. An indistinct but dark-bordered and conspicuous pale yellow stripe on head, which runs from the posterior region of the beak, down to tympanic membrane. Jaw sheaths yellow-streaked or reticulated with dark brown. Lateral and ventral neck pale gray, but conspicuously reticulated (Fig. 6 A, B). Color of muscled manus, pes and tail gray-brownish above; thighs and forearm pale gray with reticulations.

Geographic distribution and habitat—*Kinosternon cora* inhabits low elevations from 10–30 m asl on the Pacific Coastal Plain adjacent to the foothills of the Sierra Madre Occidental. The predominant type of vegetation is tropical deciduous forest, with trees of 15–25 m in height. Along riparian areas tropical semi-deciduous forest is present, with *Enterolobium* sp., *Ficus* sp. and *Taxodium mucronatum* trees, which may reach a height of 30 m or more. Many trees and shrubs carry epiphytes and parasites. *Eucalyptus* crops have been planted in a large area near the type locality of *Kinosternon cora* (Fig. 7).

Etymology—The specific epithet is derived from the name “Cora”, the Native-Mexican ethnic group that is most widespread in Nayarit. The ethnic Cora population is concentrated in the municipalities of El Nayar, Acaponeta, Rosamorada and Ruiz, all of which are in Nayarit, the state where this new species was first discovered in 1962.

Additional observations—An adult male (Fig. 8 A) was photographed from “just E of Rosamorada” on Rosamorada–San Juan Bautista Hwy., Municipio de Rosamorada by J. Loc-Barragán in September of 2013. A juvenile female (Fig. 8 B) was photographed at “a farm near Chilapa”, Municipio de Rosamorada (22.031930°, -105.227922°; datum WGS 84; elev. 30 masl) by Jorge Larios Luquín in October of 2019. Photographs of both individuals appear to be *K. cora* based on the diagnostic characteristics of the plastron and the carapace. We consider these sightings important as they extend the known distribution of this species.



FIGURE 7. Aerial photograph (above) of the type locality of *Kinosternon cora*. A small temporary lake with affluent streams, surrounded by secondary vegetation (below), and invasive eucalyptus plantations originally planted for forest management.

Phylogenetic relationships and genetic distinctiveness

We recovered *Kinosternon cora* as the sister taxon of *K. vogti*, with strong support (posterior probability (pp) = 1; (Fig. 9). These two species were recovered as sister to *K. sonoriense* LeConte 1854, but with low support (pp = 0.51), and all three species formed a well-supported clade with *K. chimalhuaca* + *K. hirtipes* with strong support

(pp = 1). Together, these five species can be considered to belong to the *K. hirtipes* group. *Kinosternon integrum*, *K. scorpioides* (Linnaeus 1766), and *K. oaxacae* form the *K. scorpioides* group. The *K. hirtipes* species group and the *K. scorpioides* species group are sister to each other. *Kinosternon alamosae* appears to be basal to both the *K. hirtipes* and *K. scorpioides* species groups.

The remaining relationships in our phylogeny are mostly in concordance with previous phylogenies of the family Kinosternidae (Iverson et al. 2013; Spinks et al. 2014), which is not surprising as the majority of the sequences used here were previously used in those studies. However, some interesting differences must be noted. We recovered *Sternotherus* as sister to all *Kinosternon*, similar to the results of Spinks et al. (2014), with strong support (pp = 1). Iverson et al. (2013) had recovered *Sternotherus* as nested within *Kinosternon*, which led them to describe a new genus *Cryptochelys* for some of the species of *Kinosternon*, which are also recovered as reciprocally monophyletic with respect to other *Kinosternon* in our analysis. Another difference in our phylogeny is the position of *K. leucostomum* (Duméril, Bibron and Duméril 1851), and *K. dunnii* Schmidt 1947, which with *K. angustipons* Legler 1965, are sister to *K. herrerae* Stejneger 1925, *K. acutum* Gray 1831a, and *K. creaseri* Hartweg 1934. This is similar to the results given by Iverson et al. (2013), while Spinks et al. (2014) recovered *K. leucostomum* and *K. dunnii* as sister to a much bigger clade that includes all *Kinosternon* (with the exclusion of the *K. flavescens* Agassiz 1857, *K. stejnegeri*, *K. durangoense* Iverson 1979b, *K. baurii* (Garman 1891), and *K. subrubrum* Bonnaterra 1789). Furthermore, we recovered *K. flavescens* as sister to *K. baurii* and *K. subrubrum* (similar to Iverson et al., 2013), while Spinks et al. (2014) found *K. flavescens* to be sister to *K. stejnegeri* and *K. durangoense*.

Natural history observations

The holotype, an adult female, was recently road killed when collected on 4 September 2017. With the plastron and carapace broken, enlarged ovarian follicles of four different sizes were visible outside of the body. This suggests *K. cora* may be capable of producing multiple clutches each year. The paratype female MZFC- HE 35628 collected in mid-October, was kept alive in captivity, and laid two eggs in the water on 30 January 2018. One of the eggs was broken by the female, and the other remained intact (29 mm x 18 mm) but experienced no development. We observed that the pond at the type locality dries completely during the dry season. Although uncertain, this suggests that the population in that area may estivate during the dry season. *Kinosternon cora* is micros sympatric with *K. integrum*. Two of the paratypes were captured together in the same trap, along with four *K. integrum*. Further ecological data are unknown at this time.

DISCUSSION

Our study shows that *Kinosternon cora* is the sister species of *K. vogti*, from which it can easily be distinguished by morphological characters. Our phylogenetic analysis shows that these two species are nested within the *Kinosternon hirtipes* group, but show significant morphological and molecular differences from the species in those groups. The presence of clasping organs in a juvenile individual of *K. cora* also suggests that *K. cora* is part of the *K. hirtipes* group, as the presence of clasping organs is a character that defines the group (with the exception of *K. chimalhuaca*, which lacks them). It is possible that the ancestor of *Kinosternon vogti* and *K. cora* invaded the lowlands of western Mexico after splitting from an ancient *K. hirtipes* group stock, and later diverged from each other. At some other point, the ancestor of *K. chimalhuaca* also invaded the Pacific lowlands, presumably from the Mexican Plateau.

The five species of continental turtles described in Mexico during the last 20 years, four in the last 10 years, have all been discovered along the west coast of the country (Murphy et al., 2011; Edwards et al. 2016; López-Luna et al., 2018; this paper). They include three species of the genus *Kinosternon*: *K. chimalhuaca*, *K. vogti* and now *K. cora*. *Kinosternon* is prone to endemism within one or a few biogeographic regions, and thus several species have reduced ranges (Legler and Vogt, 2013). Large areas of the west coast of Mexico have received little attention when it comes to studies of freshwater turtles, the possibility remains that the ranges of the latter three species may be more extensive, and the Pacific Coast may harbor additional undescribed, localized, cryptic species.



FIGURE 8. Further observations of *Kinosternon cora* sp. nov. Series of photographs above: Adult male observed near Rosamorada, Municipio de Rosamorada, Nayarit. Photos by J. A. Loc-Barragán. Series of photographs below: Juvenil female observed near Chilapa, Municipio de Rosamorada, Nayarit. Photos by Jorge Larios Luquín.

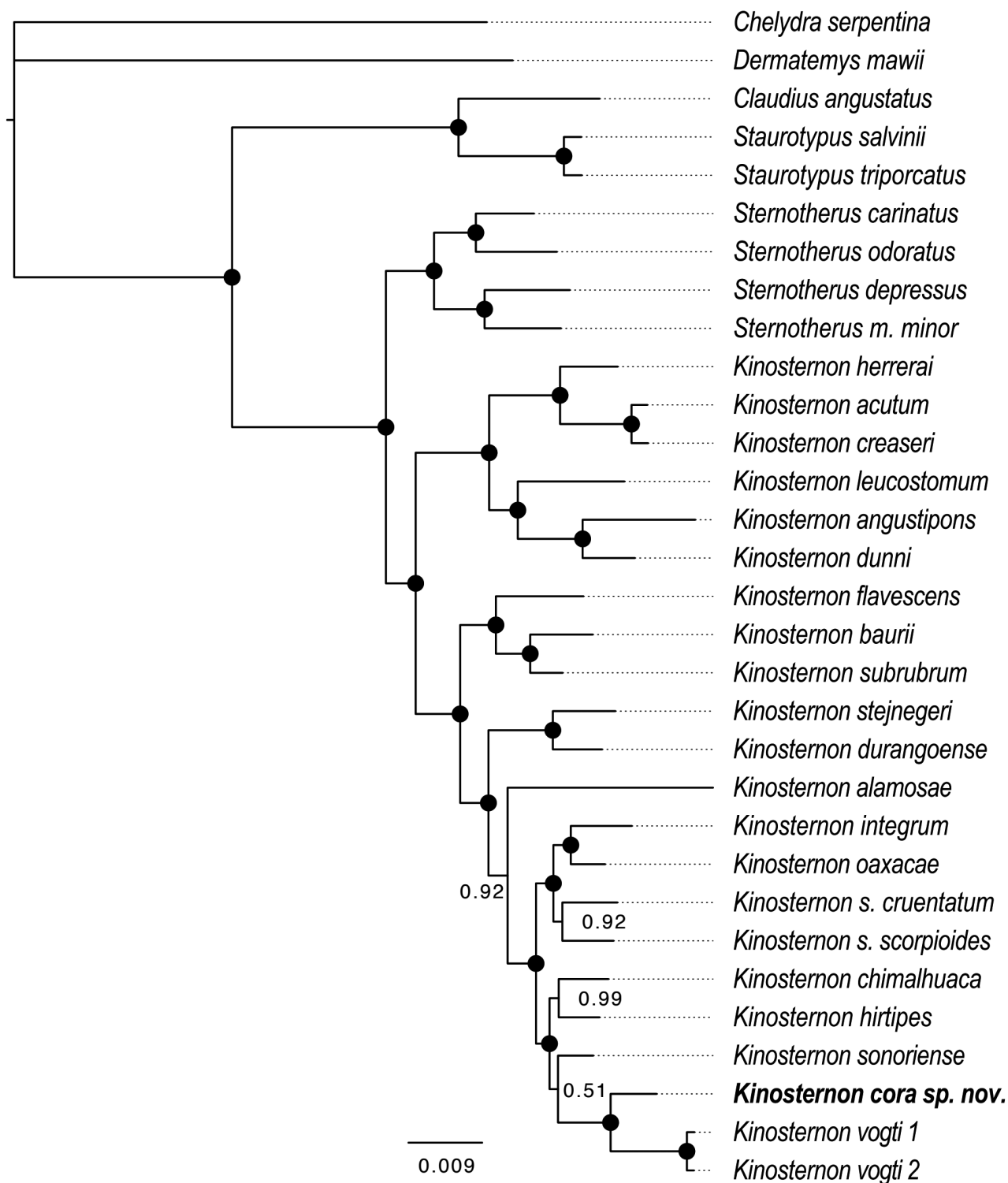


FIGURE 9. Phylogenetic tree showing the relationships of Kinosternidae, and the position of *Kinosternon cora* sp. nov., based on three mitochondrial and four nuclear loci. Bayesian posterior probabilities of each node are reported; solid circles indicate 1.0 support.

The Pacific coastal lowlands between and beyond the known ranges of *K. cora* and *K. vogti* have not been thoroughly sampled for freshwater turtles. This includes the area between Rosamorada and San Blas, as well as the area around the town of Las Varas, Nayarit. In addition, the coastal lowlands between Río San Nicolas and Puerto Vallarta, near the town of Tomatlán, Jalisco, have not been sampled for *Kinosternon*, and could potentially harbor another undescribed species. This region was not sampled by Berry, Seidel, and Iverson when they sampled the southern

coast of Jalisco before describing *K. chimalhuaca* (J. B. Iverson and J. F. Berry personal communications). Further south, along the coastal lowlands of Colima, Michoacán and Guerrero, few collections exist for *Kinosternon*, and all apparently represent *K. integrum* which is more commonly collected than either *K. cora* or *K. vogti*. Hence, it would not be surprising to find novel taxa in those areas see Zarza et al. 2011 and 2019 for analogous studies of the diversity within another lowland Pacific coast species complex: *Ctenosaura pectinata* (Wiegmann 1834).

Currently, the Mexican Pacific Versant is home to 20 species of continental turtles, being more diverse and with more endemism than along the coastal plain of the Gulf of Mexico with 14 species, the latter considered as the primary region of diversity and endemism of continental turtles in Mexico (Ippi and Flores 2001). We suggest that new analyses of diversity and endemism in Mexico, highlighting the coastal region of the western and Pacific northwest of Mexico are warranted.

Conservation—The conservation status of *K. cora* cannot currently be assessed, because only six specimens are known from an area of approximately 500 km². Our data demonstrate that this species is sympatric with *Kinosternon integrum* and probably *Trachemys ornata* (Gray 1831b). *Kinosternon integrum* is the most abundant species on the Pacific Coastal Plain, and in capture surveys using funnel traps *K. integrum* represented more than 85% of the freshwater turtles captured (Loc-Barragan, unpublished data). Human exploitation of the freshwater turtles in the area is minimal, except for sporadic illegal collection for pets. *Kinosternon cora* could come under collection pressure from wildlife traffickers, so we propose to include it in the Mexican laws (NOM 059) as a protected species, so that appropriate and legal conservation programs can be established. Most bodies of water within the known range of *K. cora* have been modified to some degree for agricultural purposes. Streams and small ponds have been dredged for use as water reservoirs. Large amounts of water are used for irrigation of crops in the area (e.g., mango, sorghum and soy). Local farmers and ranchers use chemicals to control weeds, which pollutes ponds and waterways, causing some intoxication or death of cattle (Loc-Barragan, personal observation). This extensive agricultural use of water results in rapid reductions in water as the dry season begins. Furthermore, during the dry season when mud turtles may be in estivation, it is common for ranchers to burn the edges of ponds to make them more accessible for cattle when the rains come. The impact of these activities on the freshwater turtles in the area is unknown, although it is possible that these artificial water basins can help turtles. As suggested for *Kinosternon stejnegeri* and *K. durangoense*, these reservoirs are very important during dry seasons, and are frequently used by these species (Iverson 1989). Unfortunately, the range of *K. cora* suffers from social and drug-related conflicts and it is not possible to safely monitor populations at this time.

Acknowledgments

We thank Uri O. Garcia-Vazquez for allowing us to use his collection permit SEMARNAT (SGPA/DGVS/ 0475/19), and Leticia Ochoa, Oscar A. Flores-Villela and Israel Solano-Zavaleta of the Colección de Herpetología de la Facultad de Ciencias de la Universidad Nacional Autónoma de México, for facilitating the deposit of type specimens and, for their effort to reviewing *Kinosternon* specimens in the collection. We thank Mingna Zhuang, University of Texas El Paso Biodiversity Collections Manager, for facilitating the remote review of specimens, and Muriel M. Norman and Daniela Dominguez for taking detailed photographs of the UTEP 3908. We are deeply grateful to John Iverson, James Berry, and Richard C. Vogt for reviewing the initial draft of this manuscript and for their invaluable suggestions and insightful comments. The participation of MAL-L, JAR-M and MVA would not have been possible without the support of Armando H. Escobedo-Galván of the Centro Universitario de la Costa, of the Universidad de Guadalajara and Global Wildlife Conservation, Turtle Conservation Fund and Turtle Conservancy that supported this work (Grant 5271.008-0272; TCF 0754). We want to greatly thank to José Ascensión Loc Avena, for allowing us to conduct safe field surveys. We greatly appreciate to Jorge Larios Luquín for the information and images of specimens of *Kinosternon cora* that he provided us for this work. We thank Biencom Real Estate for generously providing funds to support the fieldwork and publish this manuscript.

Literature Cited

Agassiz, L. (1857) *Contributions to the Natural History of the United States of America. Vol. 1*. Little, Brown & Co., Boston, lii + 452 pp.

<https://doi.org/10.5962/bhl.title.12644>

- Berry, F.J. & Berry, C.M. (1984) A re-analysis of geographic variation and systematics in the Yellow Mud Turtle, *Kinosternon flavescens* (Agassiz). *Annals of Carnegie Museum of Natural History*, 53 (7), 185–206.
[<https://www.biodiversitylibrary.org/item/216357#page/203/mode/1up>]
- Berry, J.F. & Iverson, J.B. (1980) A new species of mud turtle, genus *Kinosternon*, from Oaxaca, Mexico. *Journal of Herpetology*, 14 (4), 313–320.
<https://doi.org/10.2307/1563684>
- Berry, J.F. & Legler, J.M. (1980) A new turtle (genus *Kinosternon*) from northwestern Mexico. *Contributions in Science, Natural History Museum of Los Angeles County*, 325, 1–12.
[<https://www.biodiversitylibrary.org/item/214422#page/29/mode/1up>]
- Berry, J.F., Seidel, M.F. & Iverson, J.B. (1997) A new species of mud turtle (genus *Kinosternon*) from Jalisco and Colima, Mexico, with notes on its natural history. *Chelonian Conservation and Biology*, 2 (3), 329–337.
- Bonnaterre, P.J. (1789) *Tableau encyclopédique et méthodique des trois règnes de la nature. Erpétologie*. Panckoucke, Paris, xxviii + 71 pp.
<https://doi.org/10.5962/bhl.title.11660>
- Chávez-Avila, S.M., Casas-Andreu, G., García-Aguayo, A., Cifuentes-Lemus, J.L. & Cupul-Magaña, F.G. (2015) *Anfibios y reptiles del estado de Jalisco. Análisis espacial, distribución y conservación*. Universidad de Guadalajara, Puerto Vallarta, 101 pp. ISBN: 978-607-742-318-8. [<http://www.cuc.udg.mx/sites/default/files/publicaciones/2015%20-%20Anfibios%20y%20reptiles%20del%20estado%20de%20Jalisco.pdf>]
- Cupul-Magaña, F.G. & Rubio-Delgado, A. (2003) Distribución de dos especies de tortugas dulceacuícolas, *Kinosternon chimalhuaca* y *Chelydra serpentina* (Testudines), en Puerto Vallarta, Jalisco; México. *Boletín de la Sociedad Herpetológica Mexicana*, 11 (1), 49–50.
- Duméril, A.M.C. & Duméril, A.H.A. (1851) *Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle de Paris*. Gide et Baudry/Roret, Paris, 224 pp.
- Edwards, T., Karl, A., Augh, M., Rosen, P., Meléndez-Torres, C. & Murphy, R.W. (2016) The desert tortoise trichotomy: Mexico hosts a third new sister-species of tortoise in the *Gopherus morafkai*-*G. agassizii* group. *Zookeys*, 562, 131–158.
<https://doi.org/10.3897/zookeys.562.6124>
- Flores-Villela, O., Smith, H.M. & Chiszar, D. (2004) The history of herpetological exploration in Mexico. *Bonner Zoologische Beiträge*, 3 (4), 311–335.
- García, A. (2006) Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biological Conservation*, 130 (1), 25–46.
<https://doi.org/10.1016/j.biocon.2005.11.030>
- Garman, S. (1891) On a tortoise found in Florida and Cuba, *Cinosternon baurii*. *Bulletin of Essex Institute, Salem, Massachusetts*, 23, 141–144
- Gilmore, C.W. (1923) A new fossil turtle, *Kinosternon arizonense*, from Arizona. *Proceedings of the United States National Museum*, 62 (2451), 1–8.
<https://doi.org/10.5479/si.00963801.62-2451.1>
- Goldman, E.A. (1951) Biological investigations in Mexico. *Smithsonian Miscellaneous Collections*, 115, 1–476.
<https://www.biodiversitylibrary.org/item/80431#page/7/mode/1up>
- Gray, J.E. (1831a) *Synopsis Reptilium or short descriptions of the species of reptiles. Part I. Cataphracta, tortoises, crocodiles, and enaliosaurians*. Treuttel, Wurz & Co., London, 85 pp.
<https://doi.org/10.5962/bhl.title.4697>
- Gray, J.E. (1831b) *A synopsis of the species of Class Reptilia. In: Griffith, E & E. Pidgeon: The animal kingdom arranged in conformity with its organisation by the Baron Cuvier with additional descriptions of all the species hither named, and of many before noticed. Vol. 9*. Whittaker, Treacher and Co., London, 481 + 110 pp.
- Hardy, L.M. & McDiarmid, R.W. (1969) The amphibians and reptiles of Sinaloa, Mexico. *University of Kansas Publications, Museum of Natural History*, 18 (3), 39–252.
<https://doi.org/10.5962/bhl.part.19990>
- Hartweg, N. (1934) Description of a new kinosternid from Yucatan. *Occasional Papers of the Museum of Zoology, University of Michigan*, 277, 1–2.
<https://deepblue.lib.umich.edu/handle/2027.42/56716>
- Hartweg, N. (1938) *Kinosternon flavescens stejnegeri*, a new turtle from northern Mexico. *Occasional Papers of the Museum of Zoology, University of Michigan*, 371, 1–5.
- Hulse, A.C. (1976) Growth and morphometrics of *Kinosternon sonoriense* (Reptilia, Testudines, Kinosternidae). *Journal of Herpetology*, 10 (4), 341–348.
<https://doi.org/10.2307/1563072>
- Ippi, S. & Flores, V. (2001) Las tortugas neotropicales y sus áreas de endemismo. *Acta Zoológica Mexicana*, 84, 49–63.
- Iverson, J.B. (1979a) Another inexpensive turtle trap. *Herpetological Review*, 10 (2), 55.
- Iverson, J.B. (1979b) A taxonomic reappraisal of the yellow mud turtle, *Kinosternon flavescens* (Testudines: Kinosternidae). *Copeia*, 1979 (2), 212–225.
<https://doi.org/10.2307/1443406>

- Iverson, J.B. (1981) Biosystematics of the *Kinosternon hirtipes* group (Testudines, Kinosternidae). *Tulane Studies of Zoology and Botany*, 23 (1), 1–74.
[<https://www.biodiversitylibrary.org/item/30378#page/17/mode/1up>]
- Iverson, J.B. (1989) The Arizona mud turtle, *Kinosternon flavescens arizonense* (Kinosternidae), in Arizona and Sonora. *The Southwestern Naturalist*, 34 (3), 356–368.
<https://doi.org/10.2307/3672164>
- Iverson, J.B., Le, M. & Ingram, C. (2013) Molecular phylogenetics of the mud and musk turtle family Kinosternidae. *Molecular Phylogenetics and Evolution*, 69 (3), 929–939.
<https://doi.org/10.1016/j.ympev.2013.06.011>
- Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in performance and usability, *Molecular Biology and Evolution*, 30 (4), 772–780.
<https://doi.org/10.1093/molbev/mst010>
- Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29 (6), 1695–1701.
<https://doi.org/10.1093/molbev/mss020>
- LeConte, J. (1854) Description of four new species of *Kinosternum*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7, 180–190.
[<https://www.biodiversitylibrary.org/item/17735#page/202/mode/1up>]
- Legler, J. (1965) A new species of turtle, genus *Kinosternon*, from Central America. *University of Kansas Publications, Museum of Natural History*, 15 (13), 615–625.
<https://doi.org/10.5962/bhl.part.7292>
- Legler, J. & Vogt, R.C. (2013) *Turtles of Mexico: Land and Freshwater Forms*. University of California Press, Berkeley, 402 pp.
<https://doi.org/10.1525/9780520956896>
- Linnaeus, C. (1766) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio duodecima, reformata*. Laurentii Salvii, Stockholm, Holmiae, 532 pp.
<https://doi.org/10.5962/bhl.title.68927>
- López-Luna, M.A., Cupul-Magaña, F.G., Escobedo-Galván, A.H., González-Hernández, A.J., Centenero-Alcalá, E., Rangel-Mendoza, J.A., Ramírez-Ramírez, M.M. & Cazares-Hernández, E. (2018) A distinctive new species of Mud Turtle from Western México. *Chelonian Conservation and Biology*, 17 (1), 2–13.
<https://doi.org/10.2744/CCB-1292.1>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *2010 Gateway Computing. Environments Workshop GCE*, 2010, 1–8.
<https://doi.org/10.1109/GCE.2010.5676129>
- Murphy, R.W., Berry, K.H., Edwards, T., Leviton, A.E., Lathrop, A. & Riedle, J.D. (2011) The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. *ZooKeys*, 113, 39–71.
<https://doi.org/10.3897/zookeys.113.1353>
- Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v1.6, Available from <http://beast.bio.ed.ac.uk/Tracer> (accessed 28 August 2020)
- Rambaut, A. & Drummond, A.J. (2014) TreeAnnotator. Version 1.8.2. Available from <https://beast.community/treeannotator> (accessed 28 August 2020)
- Ronquist, F., Teslenko, M., Mark, P. van der, Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61 (3), 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Schmidt, K.P. (1947) A new kinosternid turtle from Colombia. *Fieldiana: Zoology*, 31 (13), 109–112.
<https://doi.org/10.5962/bhl.title.3075>
- Spinks, P.Q., Thomson, R., Muge, G. & Shaffer, H.B. (2014) Multilocus phylogeny of the New-World Mud Turtles (Kinosternidae) supports the traditional classification of the group. *Molecular Phylogenetics and Evolution*, 76, 254–260.
<https://doi.org/10.1016/j.ympev.2014.03.025>
- Stejneger, L.H. (1925) New species and subspecies of American turtles. *Journal of Washington Academy of Sciences*, 15 (20), 462–463.
[<https://www.biodiversitylibrary.org/item/123269#page/552/mode/1up>]
- Turtle Taxonomy Working Group [Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B. & van Dijk, P.P.] (2017) *Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status. 8th Edition*. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Pritchard, P.C.H. & Mittermeier, R.A. (Eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs*, 7, pp. 1–292.
<https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017>
- Underwood, W. & Anthony, R. (2020) *AVMA Guidelines for the Euthanasia of Animals: 2020 Edition*. Retrieved 30 March

2020, 2020-01. Available from <https://www.avma.org/sites/default/files/2020-01/2020-Euthanasia-Final-1-17-20.pdf> (accessed 28 August 2020)

- Vaidya, G., Lohman, D.J. & Meier, R. (2011) SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, 27 (2), 171–180.
<https://doi.org/10.1111/j.1096-0031.2010.00329.x>
- Van Denburgh, J. (1897) Reptiles from Sonora, Sinaloa and Jalisco, Mexico, with a description of a new species of *Sceloporus*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 49, 460–64.
<https://www.jstor.org/stable/4062303>
- Wagler, J.G. (1830) *Natürliches System der Amphibien, mit vorangehender Classification der Säugetiere und Vögel. Ein Beitrag zur vergleichenden Zoologie*. Cotta, München, Stuttgart, and Tübingen, 354 pp.
<https://doi.org/10.5962/bhl.title.58730>
- Webb, R.G. (2001) The Jalisco Mud Turtle, *Kinosternon chimalhuaca*, in northern Nayarit, Mexico. *Herpetological Review*, 32 (2), 87–88.
- Wiegmann, A.F.A. (1834) *Herpetologia Mexicana, seu descriptio amphibiorum novae hispaniae, quae itineribus comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede im Museum Zoologicum Berolinense Pervenerunt. Pars prima, saurorum species*. Berlin, Lüderitz, iv + 54 pp.
<https://doi.org/10.5962/bhl.title.119131>
- Woolrich-Piña, G.A., Ponce-Campos, P., Loc-Barragán, J.A., Ramírez-Silva, J.P., Mata-Silva, V., Johnson, J.D. & Wilson, L.D. (2016) The herpetofauna of Nayarit, Mexico: composition, distribution, and conservation. *Mesoamerican Herpetology*, 3 (2), 376–448.
- Zarza, E., Reynoso, V.H. & Emerson, B.C. (2011) Discordant patterns of geographic variation between mitochondrial and microsatellite markers in the Mexican black iguana (*Ctenosaura pectinata*) in a contact zone. *Journal of Biogeography*, 38 (7), 1394–1405.
<https://doi.org/10.1111/j.1365-2699.2011.02485.x>
- Zarza, E., Reynoso, V.H., Faria, C.M. & Emerson, B.C. (2019) Introgressive hybridization in a Spiny-Tailed Iguana, *Ctenosaura pectinata*, and its implications for taxonomy and conservation. *PeerJ*, 7, e6744.
<https://doi.org/10.7717/peerj.6744>

Table S1. Genbank accession numbers for sequences used in this study

Species	mtDNA			Nuclear				
	12	16s	Cytb	R35	TB01	PSMCI	KIAA0398	
<i>Cheyledra serpentina</i>	DQ256378	DQ256378	-	JN860577	GU085697	-	GU085621	
<i>Claudius angustatus</i>	KF301254	KF301323	KF301358	KJ582915	KJ583006	KJ582833	KJ582789	
<i>Dermatemys mawii</i>	KF301255	KF301322	KF301357	KJ582913	KJ583005	KJ582832	KJ582786	
<i>Kinosternon acutum</i>	KF301263	KF301331	KF301366	KJ582917	KJ583008	KJ582835	KJ582790	
<i>Kinosternon alamosae</i>	KF301265	KF301333	KF301368	-	-	-	-	
<i>Kinosternon angustipons</i>	-	KF301334	KF301369	-	-	-	-	
<i>Kinosternon baurii</i>	KF301267	KF301336	KF301371	AY339642	KJ583011	-	KJ582794	
<i>Kinosternon chimalhuaca</i>	KF301268	KF301337	KF301372	KJ582922	KJ583013	KJ582838	KJ582795	
<i>Kinosternon cora</i> sp. nov.	MW035845	MW035844	MW026700	MW026703	MW026704	MW026701	MW026702	
<i>Kinosternon creaseri</i>	KF301269	KF301338	KF301373	KJ582924	KJ583015	KJ582840	KJ582797	
<i>Kinosternon dummi</i>	KF301270	KF301339	KF301374	KJ582925	KJ583016	KJ582841	KJ582799	
<i>Kinosternon durangoense</i>	KF301271	KF301340	KF301375	KJ582927	KJ583017	KJ582844	KJ582800	
<i>Kinosternon flavescens</i>	KF301272	KF301341	KF301376	KJ582929	KJ583019	KJ582846	KJ582803	
<i>Kinosternon herrerai</i>	KF301273	KF301342	KF301377	KJ582932	KJ583021	KJ582847	KJ582805	
<i>Kinosternon hirtipes</i>	KF301275	KF301344	KF301379	KJ582935	KJ583022	KJ582849	KJ582806	
<i>Kinosternon integrum</i>	KF301276	KF301345	KF301380	KJ582936	KJ583025	KJ582852	KJ582807	
<i>Kinosternon leucostomum</i>	KF301279	KF301348	KF301383	KJ582938	KJ583026	KJ582853	KJ582809	
<i>Kinosternon oaxacae</i>	KF301280	KF301349	KF301384	KJ582939	KJ583029	KJ582856	KJ582810	
<i>Kinosternon s. cruentatum</i>	KF301284	KF301352	KF301387	KJ582944	KJ583032	KJ582859	KJ582815	
<i>Kinosternon s. scorpoides</i>	KF301283	KF301353	KF301388	KJ582943	KJ583030	KJ582857	KJ582812	
<i>Kinosternon sonorense</i>	KF301285	KF301354	KF301389	KJ582946	-	KJ582862	KJ582817	
<i>Kinosternon stejnegeri</i>	KF301287	KF301335	KF301370	KJ582919	KJ583010	KJ582837	KJ582792	
<i>Kinosternon subrubrum</i>	KF301266	KF301355	KF301390	KJ582948	KJ583037	-	KJ582818	
<i>Kinosternon vogti</i> 1	-	-	MW192515	-	-	-	-	
<i>Kinosternon vogti</i> 2	-	-	MW192516	-	-	-	-	

...continued on the next page

Table S1. (continued)

Species	mtDNA				Nuclear			
	12	16s	Cytb	R35	TB01	PSMC1	KIAA0398	
<i>Staurotypus salvinii</i>	KF301256	KF301324	KF301359	KJ582956	KJ583046	KJ582871	KJ582827	
<i>Staurotypus triporcatus</i>	KF301257	KF301325	KF301360	KJ582958	KJ583047	KJ582873	KJ582829	
<i>Sternotherus carinatus</i>	KF301258	KF301326	KF301361	KJ582949	KJ583039	KJ582864	KJ582820	
<i>Sternotherus depressus</i>	KF301259	KF301327	KF301362	KJ582952	KJ583041	KJ582866	KJ582823	
<i>Sternotherus minor minor</i>	KF301260	KF301329	KF301363	KJ582954	KJ583042	KJ582867	KJ582824	
<i>Sternotherus odoratus</i>	KF301262	KF301330	KF301365	KJ582955	KJ583044	KJ582869	GU085633	