

***Kinosternon scorpioides* (Linnaeus 1766) – Scorpion Mud Turtle**

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SUMMARY. – *Kinosternon scorpioides*, the Scorpion Mud Turtle (Family Kinosternidae), is a medium to large-sized mud turtle, with adult males in some populations regularly exceeding 200 mm in carapace length. The species occurs from the Mexican state of Tamaulipas in Gulf of Mexico drainages, southward throughout the Isthmus of Tehuantepec and the Yucatan Peninsula in Mexico, and throughout most of Central and South America in both Atlantic and Pacific drainages at least to the upper Río Paraná in northern Argentina. Four subspecies are currently recognized, which vary in morphology: *K. s. scorpioides*, *K. s. abaxillare*, *K. s. albogulare*, and *K. s. cruentatum*. Maximum size in various populations ranges from 150 to over 200 mm carapace length. Mature females lay up to five clutches of 1–8 eggs during an extended annual reproductive season. The species is exploited in parts of its range for tourist trinkets, pet trade, medicine, and food, but the greatest threats to its survival are from habitat degradation and alteration. Conservation measures should include expanded studies of the status of the species throughout its range, as well as detailed studies of its life history, habitat utilization, diseases, and the effects of habitat modification on individuals and populations across its range.

DISTRIBUTION. – Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Trinidad, Venezuela. Northeast and eastern Mexico through Central America and across northern and central South America to northern Argentina.

SYNONYMY. – *Testudo scorpioides* Linnaeus 1766, *Emys scorpioides*, *Chersine scorpioides*, *Uronyx scorpioides*, *Terrapene scorpioides*, *Cinosternon scorpioides*, *Clemmys (Cinosternon) scorpioidea*, *Cinosternon scorpioideum*, *Kinosternum scorpioides*, *Cinosternum scorpioides*, *Thyrosternum scorpioides*, *Swanka scorpioides*, *Kinosternon scorpioides*, *Kinosternon scorpioides scorpioides*, *Testudo tricarinata* Retzius in Schoepff 1792, *Terrapene tricarinata*, *Testudo retzii* Daudin 1801, *Emys retzii*, *Kinosternon longicaudatum* Spix 1824, *Kinosternum longicaudatum*, *Cinosternon longicaudatum*, *Swanka longicaudata*, *Kinosternon brevicaudatum* Spix 1824, *Cinosternon brevicaudatum*, *Kinosternon shavianum* Bell 1825, *Cinosternon shavianum*, *Cinosternum shavianum*, *Thyrosternum shavianum*, *Monoclista retziana* Rafinesque 1832, *Cinosternum scorpioides integrum brasiliense* Siebenrock 1907, *Kinosternon scorpioides seriei* Freiberg 1936, *Kinosternon scorpioides pachyurum* Müller and Hellmich 1936, *Kinosternon panamensis* Schmidt 1946, *Kinosternon scorpioides carajasensis* da Cunha 1970.

SUBSPECIES. – Four are currently recognized: 1) *Kinosternon scorpioides scorpioides* (Scorpion Mud Turtle) (distribution: eastern Panama to northern South America and the Amazon basin to northern Argentina); 2) *Kinosternon scorpioides abaxillare* (Central Chiapas Mud Turtle) (synonymy: *Kinosternon abaxillare* Baur in Stejneger 1925) (distribution: central Chiapas, Mexico); 3) *Kinosternon scorpioides albogulare* (White-throated Mud Turtle) (synonymy: *Cinosternon albogulare* Duméril and Bocourt 1870, *Cinosternum albogulare*, *Kinosternon cruentatum albogulare*) (distribution: Honduras and El Salvador through Nicaragua and Costa Rica to western Panama); and 4) *Kinosternon scorpioides cruentatum* (Red-cheeked Mud Turtle) (synonymy: *Cinosternon cruentatum* Duméril and Bibron in Duméril and Duméril 1851, *Kinosternum cruentatum*, *Kinosternon cruentatum*, *Swanka cruentata*, *Thyrosternum cruentatum*, *Kinosternon cruentatum*, *Kinosternon cruentatum cruentatum*, *Kinosternum mexicanum* LeConte 1854, *Cinosternon mexicanum*, *Kinosternon mexicanum*, *Swanka mexicana*, *Kinosternum triliratum* LeConte 1859, *Cinosternon triliratum*, *Swanka trilirata*, *Cinosternum triliratum*, *Kinosternon cruentatum consors* Stejneger 1941) (distribution: Tamaulipas, Mexico, to southern Guatemala).

STATUS. – IUCN 2011 Red List: Not Listed (Least Concern, LR/lc) (assessed 1996, needs updating); CITES: Not Listed; Colombia Red Book of Endangered Reptiles: Vulnerable (D2).

Taxonomy. – The Scorpion Mud Turtle was first described by Linnaeus in 1766 as *Testudo scorpioides*, but has an extensive list of synonyms (see above). Gray (1831)

was the first to use the currently recognized combination of *Kinosternon scorpioides*. The phylogenetic relationships of *K. scorpioides* to other kinosternids have been studied via



Figure 1. Adult female *Kinosternon scorpioides scorpioides* from Cojedes, Venezuela. Photo by John Iverson.

karyotype analysis (Sites et al. 1979), biochemical analysis of serum (Crenshaw 1962; Frair 1972) and other tissue proteins (Seidel et al. 1986), cladistic analysis of neural bones (Iverson 1988a) and other characters (Iverson 1991), as well as general morphology (Berry 1978; Smith and Smith 1979; Iverson and Berry 1979; Berry and Iverson 1980; Berry and Legler 1980).

The most recent and comprehensive analysis of geographic variation within *K. scorpioides* was that of Berry

(1978), who recognized six subspecies based on a phenetic analysis of external morphological characteristics: *K. s. scorpioides* (eastern Panama to northern Peru and Brazil), *K. s. abaxillare* (restricted to the central valley of Chiapas, Mexico and adjacent Guatemala), *K. s. albogulare* (Honduras and El Salvador to Panama), *K. s. carajasensis* (central Brazil near the Serra dos Carajás), *K. s. cruentatum* (Tamaulipas, Mexico to Honduras and El Salvador), and *K. s. serei* (Río Paraná drainages in northern Argentina, northwestern Paraguay, and



Figure 2. Top: Adult *Kinosternon scorpioides cruentatum* female from Manuel, Tamaulipas, Mexico. **Bottom:** *Kinosternon scorpioides albogulare* female from Rio Corobizi, Guanacaste, Costa Rica. Photos by John Iverson.



Figure 3. Top: Adult *Kinosternon scorpioides cruentatum* female from Muna, Campeche, Mexico. **Bottom:** *Kinosternon scorpioides albogulare* female from Rio Corobizi, Guanacaste, Costa Rica. Photos by John Iverson.



Figure 4. Distribution of *Kinosternon scorpioides* in Central and South America; dotted lines delimit the distribution of subspecies: *K. s. cruentatum* from Mexico to Guatemala, *K. s. abaxillare* as an enclave in central Chiapas, Mexico, *K. s. albogulare* from Honduras and El Salvador to Panama, and *K. s. scorpioides* from Panama to Argentina. Red dots = museum and literature occurrence records of native populations based on Iverson (1992), plus more recent and authors' data; green shading = projected native distribution based on GIS-defined hydrologic unit compartments (HUCs) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al. 2009), and adjusted based on authors' data.

southeastern Bolivia). This classification was subsequently followed by Ernst and Barbour (1989) and Iverson (1986b, 1991, 1992), among others. However, Cabrera and Colantonio (1997) recommended that *K. s. carajasensis* and *K. s. serei* be placed into synonymy with *K. s. scorpioides* based on extensive overlap in key characteristics. The current classification with four subspecies was followed by Berry and Iverson (2001), among others. However, some popular European accounts have elevated *cruentatum* to species status without justification (Schilde 2001; Artner 2003; Vetter 2005). In addition, numerous authors have mistakenly used the name *K. s. cruentatum* for specimens from Costa Rica (e.g., Acuña-Mesén and Merchán-Fornelino 2003; review

in Iverson 2010), whereas only *K. s. albogulare* occurs in Costa Rica (Berry 1978; Berry and Iverson 2001; among many others).

According to Iverson's (1991) phylogenetic analysis of relationships within the genus *Kinosternon* based on morphology, *K. scorpioides* is a member of a closely-related group of Mexican and Central American species which includes *K. integrum*, *K. alamosae*, *K. oaxacae*, *K. acutum*, *K. creaseri*, and, perhaps, *K. leucostomum*. Several other authors have previously noted the close relationship of *K. scorpioides* to *K. integrum*, *K. alamosae*, and *K. oaxacae* based on morphological characteristics and geographic distribution (e.g., Berry 1978; Berry and Iverson 1980;



Figure 5. Left: *Kinosternon scorpioides scorpioides* female from Cojedes, Venezuela. Middle: *Kinosternon scorpioides albogulare* female from Rio Corobizi, Guanacaste, Costa Rica. Right: *Kinosternon scorpioides cruentatum* male from Dzibalchen, Campeche, Mexico. Photos by John Iverson.



Figure 6. *Kinosternon scorpioides abaxillare* from Tuxtla Gutiérrez, Chiapas, Mexico. Photo by Nora López-León.

Berry and Legler 1980; Iverson and Berry 1979). Iverson (1998) combined morphology and mitochondrial DNA data to suggest that the genus *Kinosternon* includes at least three clades: a *flavescens-subrubrum* group, a *leucostomum-dunni* group, and a *scorpioides-integrum-hirtipes* group. These clades were also confirmed by Reid et al. (2011).

Description. — *Kinosternon scorpioides* is a medium to large-sized mud turtle, with adult males in some populations regularly exceeding 200 mm in carapace length (CL). There is considerable geographic variation in body size, with some populations with small body size having females slightly larger than males, to other populations with larger overall body size having males slightly larger than females (Acuña-Mesen et al. 1993; Acuña-Mesen and Arturo 1994; Iverson 2010, among others). However, the ratio of mean male size to mean female size is not correlated with mean adult size (Iverson 2010), as expected from the results of Berry and Shine (1980). Record CL (in mm) for males and females, respectively, of each subspecies is: *abaxillare*, 166 and 148; *albogulare*, 179 and 166; *cruentatum*, 166 and 148; and *scorpioides*, 205 and 175 (Iverson 2010; Iverson, unpubl. data). Hatchlings are 23–37 mm CL (Goode 1994; Iverson 2010).

Males are characterized by a considerably longer, prehensile tail, which is tipped by a much larger terminal spine than in females (Pritchard and Trebbau 1984). Females tend to have a somewhat larger plastron and more domed carapace than do males (Berry 1977, 1978; Berry and Shine 1980; Pritchard and Trebbau 1984). The back of the hind legs of male *K. scorpioides* lack the roughened “clasp organs” found in many members of the genus (Iverson and Berry 1979).

The carapace of *K. scorpioides* typically has three prominent longitudinal keels, although older individuals with worn shells may have these keels reduced or absent. The central (vertebral) scutes bear a distinctive posterior notch in all but the oldest, largest individuals. The first vertebral scute is wider than long. The tenth marginal scutes are higher than the ninth, and usually (73%) higher than the eleventh. The shape of the carapace is approximately oval; the margins are distinctly flared outward in some populations (e.g., *K. s. scorpioides*), but only slightly flared or not flared at all in



Figure 7. *Kinosternon scorpioides scorpioides* (MVZ 71379) from Colombia; note the distinctive plastron. Photo by John Iverson.

other populations (e.g., *K. s. cruentatum* and *albogulare*). Coloration of the shell is highly variable both within and among populations, with color varying from tan, olive, or brown to black. The shells of lighter colored individuals may have darker spots or interlaminal seams. In hatchlings carapace color varies from light to dark brown, often with darker interlaminal seams.

The plastron typically has two well-developed hinges, although the anterior hinge (between the hyoplastron and epiplastron bones) may be somewhat more kinetic than the posterior (hypoplastron/xiphiplastron) hinge. Adults in some semi-terrestrial populations have a longitudinal hinge between the xiphiplastra which permits midline kinesis of the posterior lobe of the plastron, creating an exceptionally tight seal, presumably for predator protection (Bramble et al., 1984; Iverson 1991). Berry (1977, 1978) suggested that an extensive plastron would help prevent desiccation in those *K. scorpioides* populations subject to periodic drought, which appears to be the case in Central America (Acuña-Mesén 1990). The plastron rarely bears a posterior notch (except in South America), but if present it is deeper in adult males than females. The interanal scute seam is long, averaging 30% of carapace length (19–39%), and the interpectoral seam is short or occasionally (27%) absent. The plastron is usually lighter in color than the carapace, varying from yellow to brown in adults. Hatchlings may have a cream to orange to reddish plastron (May 2009).

Skin color varies from gray to brown to nearly black, often with yellow, orange, or red vermiculations on the head and neck. The subspecific name *cruentatum* (meaning “besmirched with blood”) refers to the bright red vermiculations on the head and neck of adults in some populations of *K. s. cruentatum* and *K. s. albogulare* in Mexico and Central America. The name *albogulare* (meaning “white throated”) refers to the pale chin of some individuals. The name *abaxillare* (“without an axillary”) refers to the lack of that scute in most individuals in that subspecies (Iverson 2008 described variation in this trait). The name *scorpioides* (“like a scorpion”) presumably refers to the long, prehensile, spine-tipped tail of large male specimens.

The karyotype (2N = 56) includes 11–13 pairs of macrochromosomes, and 15–17 pairs of microchromosomes

(Barros et al. 1972; Killebrew 1975; Bickham and Baker 1976; Sites et al. 1979).

The four subspecies can be identified by the following characters. *Kinosternon s. scorpioides* has a moderately to strongly tricarinate carapace that is somewhat depressed (shell height is 35% of CL in males, 38% in females). Head markings consist of yellow, pale gray, or pale brown dots or reticulations on a darker brown, gray, or olive background. The plastron is intermediate to small in size, and does not completely close the ventral openings of the shell (width of posterior plastral lobe averages 38% of CL in males, 41% in females; bridge length averages 24% of CL in males, 27% in females; and interabdominal seam length averages 26% of CL in males, 29% in females). Axillary scutes are in contact with the inguinal scutes. The posterior plastral lobe bears a shallow posterior notch that is more emarginate in males than in females.

Kinosternon s. cruentatum has a strongly tricarinate carapace in all but the oldest, largest individuals. The shell is relatively high (shell height averages 43% of CL in males, 46% in females). Head markings consist of yellow, orange, or red dots or reticulations on a darker brown, gray, or olive background. The plastron is extensive, and usually completely closes the ventral openings of the shell (width of posterior plastral lobe averages 47% of CL in males, 48% in females; bridge length averages 29% of CL in males, 31% in females; and interabdominal seam length averages 26% of CL in males, 28% in females). Axillary scutes are rarely in contact with inguinal scutes. The posterior plastral lobe bears only a tiny posterior notch, or more typically none at all.

Kinosternon s. abaxillare has a strongly tricarinate carapace in all but the oldest, largest individuals. The shell is somewhat depressed (shell height averages 38% of CL in males, 39% in females). Head markings consist of yellow, cream, or pale gray dots or reticulations on a gray or olive background. The plastron is extensive, and usually completely closes the ventral openings of the shell (width of posterior plastral lobe averages 48% of CL in males, 48% in females; bridge length averages 28% of CL in males, 30% in females; and interabdominal seam length averages 31% of CL in males, 33% in females). Axillary scutes are usually absent, or the axillary-abdominal scute seam is incomplete in most individuals (Iverson 2008). The posterior plastral lobe bears only a tiny posterior notch, or more typically none at all.

Kinosternon s. albogulare has a moderately to strongly tricarinate carapace, with a relatively high shell (shell height is 41% of CL in males, 46% in females). Head markings consist of yellow, cream pink, or orange dots or reticulations on a brown or gray background. The plastron is extensive, and usually completely closes the ventral openings of the shell (width of posterior plastral lobe averages 47% of CL in males, 50% in females; bridge length averages 25% of CL in males, 28% in females; and interabdominal seam length averages 28% of CL in males, 30% in females). Axillary and inguinal scutes are usually (86% of individuals) in contact.

The posterior plastral lobe bears only a tiny posterior notch, or more typically none at all.

Distribution. — *Kinosternon scorpioides* occurs in a variety of permanent, semipermanent, and temporary aquatic habitats, primarily at lower elevations throughout its range. It apparently reaches its northernmost limit in the Río Soto la Marina drainage in Tamaulipas, Mexico (Iverson and Berry 1979), occupying Gulf of Mexico drainages southward to the Isthmus of Tehuantepec and the Yucatan Peninsula of Mexico and Belize (Lee 1980, 1996, 2000), and on Isla Cozumel (Duellman 1965). Iverson and Berry (1979) noted that in northeastern Mexico *K. scorpioides* occurs in Gulf drainages only seaward of the Sierra Madre Oriental mountain range, but is replaced by *K. integrum* in the upper reaches of Gulf drainages on the Mexican Plateau. It also occurs in Caribbean drainages in Honduras and Nicaragua, but not in those in Costa Rica or Panama, and on Isla de San Andrés, Colombia. However, Dunn and Saxe (1950) and Pritchard and Trebbau (1984) hypothesized that the San Andrés population may be the result of human introduction based on the lack of differentiation from mainland populations, also demonstrated morphometrically by Berry (1978). In Pacific drainages, it apparently occurs from the Río Tehuantepec southward throughout Central America to Panama (Berry 1978; Berry and Iverson 1980; Iverson 1986b, 1992). The species apparently reaches its highest elevation in Costa Rica, but does not occur above 1425 m (Savage 2002).

In South America, *K. scorpioides* is apparently restricted to Atlantic drainages (Berry 1978; Pritchard and Trebbau 1984; Iverson 1986b, 1992; Rueda-Almonacid et al. 2007). It is common in many coastal lowland drainages in northern and eastern South America, and although it ranges throughout most of the Amazon basin, it is apparently rare at most inland localities (Pritchard and Trebbau 1984, in general; Duellman 1978, in Ecuador; Dixon and Soini 1977, in Peru; Vogt 2008, in Brazil).

One notable inland population occurs on Serra Norte, a 700 m plateau in the Serra dos Carajas in Pará, Brazil (da Cunha 1970, as *K. s. carajasensis*). Pritchard and Trebbau (1984) speculated that this population may have reached the plateau carried in the talons of predatory birds.

The most extensive inland population is that in the upper Río Paraná basin (Gran Chaco) of northern Argentina (Freiberg 1936, 1967, as *K. s. serei*; Cei 1993), southern Bolivia (Richard 1990; Müller and Hellmich 1936, as *K. s. pachyurum*), and northwestern Paraguay (Norman 1994; Artnr 1997). Pritchard and Trebbau (1984) suggested that the present disjunct distribution of *K. scorpioides* in South America may reflect remnants of a larger post-Pleistocene distribution that was largely extirpated by forest expansion during the most recent pluvial period.

Fossil material apparently attributable to *K. scorpioides* is only known from the Pleistocene of Yucatan, Mexico (Kuhn 1964; Langebartel 1953; Mlynarski 1976 [apparently referring to Langebartel 1953]).

Habitat and Ecology. — The Scorpion Mud Turtle occurs in a variety of permanent, semi-permanent, and

temporary aquatic environments. It usually prefers quiet backwaters and isolated ponds to the main channels of major rivers, although Pritchard (1979) discussed reports that it occupied “rivers and streams” in Chiapas, Mexico, where it could be seen basking on rocks. Hartweg and Oliver (1940) collected specimens from seepage pools of the Río Tehuantepec, and from a “very filthy watering hole” near the village of Tehuantepec. Dean (1980) found them in coastal freshwater “esteros” immediately adjacent to the coast. In Chiapas, Mexico, Alvarez del Toro (1982) reported that *K. s. cruentatum* occupied rivers and streams where it was difficult to observe, and that *K. s. abaxillare* occurred in virtually every river or swamp, even when water was nearly absent. Duellman (1965) reported specimens from a partly dried marsh on Isla Cozumél, and from limestone sinkholes (“cenotes”), lakes and water holes on the Yucatan Peninsula, Mexico. Iverson (1988b) reported *K. scorpioides* from roadside ditches near cenotes in Yucatan, where it was microsympatric with its congeners *K. creaseri* and *K. leucostomum* (see also Moll 1990). Lee (1996, 2000) found them to be common to abundant in a variety of aquatic habitats on the Yucatan Peninsula of Mexico, Belize, and Guatemala. Dundee et al. (1986) found a specimen adjacent to a freshwater spring run in a mangrove swamp. *Kinosternon scorpioides* is also microsympatric with *K. acutum* in Belize (University of Utah voucher specimens) and with *K. herrerae* in Veracruz (Artner 2009). It is apparently parapatric with *K. oaxacae* and *K. integrum* (Iverson and Berry 1979; Iverson 1986a). It has also been found to occur microsympatrically with the Emydidae (Dean 1980; Moll 1990; McCranie et al. 2006; Barreto et al. 2009), Geoemydidae (Iverson, R. Vogt, pers. obs.), Podocnemididae (Stanton and Dixon 1977), and Chelidae (Métrailler 2003; Rhodin et al. 2009; R. Vogt, pers. comm.), but not apparently the Dermatemydidae or Chelydridae.

Stuart (1935) reported them as common in water holes and open savannas during the rainy season in Guatemala. In Honduras, Meyer and Wilson (1973) recorded *K. scorpioides* in and around ponds, streams, and inundated areas from sea level to 900 m elevation in tropical and subtropical moist and arid forests. Meyer (1966) collected an Honduran specimen in a pool of water beneath a grain mill. Teska (1976) reported specimens leaving a marsh area adjacent to the Río Tempisque in Costa Rica. The species has been collected in Costa Rica from near sea level to 1425 m elevation (Savage 2002) in lakes and swamps, where it prefers aquatic habitats with abundant organic material and decomposing vegetation, and high CO₂ concentrations (Acuña-Mesen et al. 1983; Savage 2002).

Medem (1958, 1960) described the habitat of *K. scorpioides* in South America (primarily Colombia) as streams, small pools, lakes, swamps, and marshes. Pritchard and Trebbau (1984) described the habitat of *K. scorpioides* in Venezuela as drainage ditches, roadside ditches, and other human-altered or anthropogenic habitats, ponds with ample organic material, and in the moving waters of a creek (see also Larrea 1948 and Sexton 1960), ponds and slow-moving

bodies of water in Trinidad (Murphy 1997), from drainage ditches near sugar cane fields in Guyana (Pritchard and Trebbau 1984), and temporary ponds in evergreen forests in central Brazil (Vogt et al. 2009). Kearney (1972) described finding specimens in a small ditch littered with trash in Trinidad. Fretey (1977) found the species in roadside ditches, forests, impoundments, and rice fields in French Guiana. Barreto et al. (2009) identified coastal lagoons in Brazil as preferred habitat. In Brazil, as elsewhere throughout its range, it can successfully inhabit temporary ponds (Pereira et al. 2007; Vogt 2008).

The species is primarily restricted to fresh water, although it has been recorded from mildly saline conditions in Costa Rica (Acuña-Mesen et al. 1983). Pritchard (1989) reported a freshly dead specimen from an open sea beach in the Northwest District of Guyana, but offered no explanation as to how it got there. Forero-Medina et al. (2007) reported *K. s. albogulare* from both freshwater ponds and mangroves, presumably brackish, on Isla de San Andrés, Colombia. Dean (1980) estimated an aquatic home range of 450 m² in coastal Chiapas.

Many populations show a propensity for partial terrestriality, particularly when aquatic habitats begin to dry (Stuart 1935 [Guatemala]; Stafford and Meyer 2000, Moll 1990 [Belize]; Berry 1978 [Nicaragua and general]; Teska 1976, Acuña-Mesén 1990, Acuña-Mesén et al. 1983, Mudde and van Dijk 1984 [Costa Rica]; Larrea 1948 [Venezuela]; Norman 1994, Cabrera 1998, Schilde 2001 [South American Chaco]). Both Stuart (1935) and Acuña-Mesén (1990) reported movements of *K. scorpioides* in front of brush fires which apparently threatened their terrestrial refugia. Teska (1976) found individuals in pastures and forests as far as 500 m from the nearest marsh, and observed movements of up to 175 m. On San Andrés Island, Forero-Medina and Castaño-Mora (2011) found a mean two-day actual distance traveled terrestrially by adults of 68 m (maximum 380 m), and a mean net two-day displacement of 35 m (maximum 300 m). Interestingly, Buskirk (2007) observed that when disturbed in shallow water in Paraguay this species fled onto land toward dense vegetation, and Sanderson (1941) recorded finding them in trees.

During times of drought or dry season, individuals are known to burrow beneath drying mud or leaf litter where they may remain in a semi-dormant condition (Ernst and Barbour 1989 [general]; Duellman 1965 [Isla Cozumél, Mexico]; Stafford and Meyer 2000 [Belize]; Lee 1996, 2000 [Yucatan Peninsula of Mexico, Belize, and Guatemala]; Berry 1978, Legler 1990 [Caribbean Nicaragua]; Teska 1976, Acuña-Mesén 1990, Leender 2001, Savage 2002 [Costa Rica]; Lacépède 1788 [French Guiana]; Larrea, 1948 [Venezuela]; Vogt 2008 [Brazil]; Buskirk 2007 [Paraguay]). Berry (1977, 1978) suggested that the large, kinetic plastron of some *K. scorpioides* populations is an adaptation to periodic drought conditions, although this adaptation may also serve for predator protection (Bramble et al. 1984; Iverson 1991).

The primary activity period of *K. scorpioides* is probably crepuscular (Cabrera 1998, Argentina), although Pritchard

and Trebbau (1984) noted that it was active at night in Trinidad (Kearney 1972), and during the day in French Guiana (Fretey 1977). Larrea (1948), Duellman and Salas (1991), and Kohler et al. (2006) reported it as nocturnal in Venezuela, Peru, and El Salvador, respectively. However, Vogt (2008) reported that it can be active at any time in Brazil, although the period of greatest activity is dusk. Forero-Medina and Castaño-Mora (2006) found the species to be primarily nocturnal in freshwater ponds on San Andrés Island, but frequently diurnal in mangrove swamps. Stafford and Meyer (2000) stated that it is chiefly nocturnal in Belize, but may be found on land in the day during the rainy season. Most turtles entered traps overnight in coastal Chiapas, but they could have entered them in the evening (Dean 1980). During field work on the Yucatan peninsula, Iverson (unpubl. data) trapped and hand-captured the species during daylight hours, but did not sample after dark.

Lacher et al. (1986) noted that basking is rare in Brazil and that body temperatures were similar to water temperatures. Contrary to the observations of Pritchard (1979) in the same state (Chiapas), Dean (1980) never observed *K. scorpioides* to bask. Dale Jackson (pers. comm.) has observed occasional basking in captives. Hofer (1999) reported that captive females increase their basking time in the weeks prior to nesting.

Kinosternon scorpioides is primarily a carnivorous predator and scavenger in nature (Pritchard and Trebbau 1984), feeding on insects and their larvae, spiders, snails, worms, crabs, shrimp, fishes, frog eggs, tadpoles, adult frogs, snake scales, bird eggshells, and parts of mammals, the latter three probably as carrion (Fretey 1977; Vanzolini et al. 1980; Castillo-Centeno 1986; Monje-Nájera and Moreva-Brenes 1987; Moll 1990; Lee 1996, 2000; Acuña-Mesén 1998; Cabrera 1998; Savage 2002; dos Santos et al. 2006; Forero-Medina and Castaño-Mora 2006; Rueda-Almonacid et al. 2007; Vogt 2008; Carvalho et al. 2008). However, plant materials, including algae, fruits, nuts, seeds, flowers, and aquatic plants such as *Paspalum* and *Elodea*, are also eaten (Vanzolini et al. 1980; Himmelstein 1981; Alvarez del Toro 1982; Métrailler and Le Gratiét 1996; Buskirk 2007; Carvalho et al. 2008). In captivity it is primarily carnivorous, though sometimes accepting plant matter, and may even attack other members of its species (Pritchard and Trebbau 1984; Ernst and Barbour 1989). The species can apparently feed terrestrially as well as aquatically (Forero-Medina and Castaño-Mora 2006).

Natural predators of this mud turtle are poorly documented. However, adults are killed by coyotes, jaguars, and other large cats (Acuña-Mesén and Arturo 1994; Acuña-Mesén 1998; Savage 2002), raptors (Pritchard and Trebbau 1984), and owls (Pereira et al. 2007); juveniles are eaten by coyotes, cats, raptors and vultures, and green iguanas (Acuña-Mesén 1998); and coyotes eat the eggs (Acuña-Mesén 1998; Savage 2002). These predators seem not to be deterred by the pungent musk produced by these turtles. Moll (1990) reported that *K. scorpioides* is also eaten by the larger kinosternid *Staurotypus* (presumably *S. triporcatus*).

Because of its extensive terrestrial activity, *K. scorpioides* is often parasitized by ticks (Acuña-Mesén 1998; Guerra et al. 2000; Burrige and Simmons 2003; Buskirk 2007; Pereira et al. 2007; Dantas-Torres et al. 2010). Other parasites include hemogregarines (Plimmer 1913), nematodes (Alho 1965; Bursey and Brooks 2011), protozoans (Lainson and Shaw 1971), and trematodes (Hughes et al. 1941, 1942; Zerecero 1948; Caballero and Brenes 1958; Yamaguti 1958; Caballero and Zerecero 1954; Caballero et al. 1957, 1959; Mané-Garzon and Holcman-Spector 1968; Salazar 2004). Leeches have not been reported on this species.

There is no published record of copulation in the field; however, mating behavior of captive *K. scorpioides* is typically kinosternine, and has been described by Sexton (1960), Fretey (1976), Pritchard and Trebbau (1984), Ernst and Barbour (1989), Savage (2002), Vogt (2008), May (2009), Nickl (2011), and the authors' unpublished data. The male generally approaches the female from the rear, often biting her hind limbs, tail, or carapace. The male usually mounts from the rear, clasping the edges of the female's carapace with his forelimbs and hind limbs. The male often waves his head laterally in a rapid fashion, and may bite the female's shell and head, apparently to force her head into the shell which exposes her cloaca. The male forces his prehensile tail beneath the female's carapace, and attempts intromission. Females may be receptive, or may attempt to escape or even attack the male. Berry and Shine (1980) characterized *K. scorpioides* as a "bottom walking" species which regularly utilizes "forced insemination" as a mating strategy. Mertens (1972) reported the successful captive reproduction of a *K. s. scorpioides* from Panama (as "*panamensis*") with one from Colombia.

Growth has been poorly studied in *K. scorpioides*; no field study of growth based on mark and recapture is known. However, based on plastral scute annuli, Pritchard and Trebbau (1984) reported five unsexed Venezuelan *K. s. scorpioides* with 102–135 mm CL that they estimated were only 5 to 6.5 yrs old. Iverson (2008) used the same technique for *K. s. abaxillare* and speculated that it would take 8–10 yrs for females to reach maturity at about 122 mm CL. Iverson (2010) later estimated that female *K. s. cruentatum* on the Yucatan peninsula require 9–10 yrs to reach maturity at about 100–105 mm CL. In captivity, Goode (1991, 1994) raised female *K. s. albogulare* from hatching to maturity at 122–132 mm CL in 4–5 yrs.

Females of *K. s. cruentatum* on the Yucatan Peninsula and in Belize mature at small body sizes (100–105 mm CL), and remain small (<141 mm CL) even as adults (Iverson 2010). However, females of the same subspecies in Tamaulipas and Veracruz, Mexico, apparently mature at a larger size (>125 mm CL) and grow at least as large as 148 mm CL (Iverson 2010). In comparison, female maturity in *K. s. abaxillare* occurs between 120 and 130 mm CL, and that for *K. s. albogulare* apparently at 122 to 132 mm CL (Goode 1994). The reproductive anatomy of adult females was reviewed by Machado Júnior et al. (2006), and male reproductive anatomy was described in detail by Carvalho et al. (2010).

Based on a recent review by Iverson (2010), the nesting season of *K. scorpioides* extends for up to 10 months a year. For *K. s. cruentatum* and *K. s. albobugulare* oviposition may begin as early as August and extend to the following May or June, followed by ovarian recrudescence during June to August. Although nesting is possible during this long period, it may not be continuous if interrupted by cold weather or drying up of the aquatic habitat. The nesting season for *K. s. abaxillare* may be shorter, with available data suggesting that it might extend only from January to May. The nesting season for *K. s. scorpioides* is less well understood because most of the available information comes from captives; captive nesting records extend from January to at least September (Sexton 1960; Costa et al. 2009; Iverson 2010), suggesting that timing in South America is fundamentally different than farther north. Field studies of reproduction in South America are sorely needed.

The extended reproductive season in this species facilitates the production of multiple annual clutches, both in captivity and in the field. Internesting intervals in captivity are generally one to two months (review in Iverson 2010), although Hofer (1999) reported a female that laid two clutches of 4 eggs each only 16 days apart. Maximum annual clutch frequency for females in captivity is at least four, based on an annual mean of 3.25 in some years (Goode 1994). The production of five (or more) clutches per year in the field is possible based on field dissections (Iverson 2010). Annual clutch frequency apparently increases with body size and age (Goode 1994).

Nesting *K. scorpioides* construct a small body pit below which the eggs are deposited in a shallow nest chamber (photos in Rudloff 1990 and May 2009). Mean depth to the top of the eggs is 2.1 cm (range, 0–3 cm) and mean depth to the bottom of the eggs is 4.6 cm (range, 2–7 cm), although they are sometimes dropped on the surface (Castillo-Centeno 1986). Cei (1993) and Norman (1994) suggested that they are also sometimes deposited just under the leaf litter. Castillo-Centeno (1986; see also Savage 2002) reported that nests are usually constructed among the roots at the base of clumps of grasses, but occasionally at the base of trees. Nests have been found from 5 to 191 m (mean, 62 m) from the water, and typically to the north of the closest water (Castillo-Centeno 1986).

Across the species' range, clutch size has been confirmed to vary from 1 to 8 eggs (Iverson 2010), with maximum clutch size for *K. s. cruentatum* of 3 eggs (e.g., Merchán and Fournier 2004), for *K. s. abaxillare*, 5 eggs, for *K. s. albobugulare*, 8 eggs, and for *K. s. scorpioides*, 6 eggs. Exaggerated reports of clutch sizes of 12–16 eggs (Freiburg 1981; repeated by Ernst and Barbour 1989), 10 eggs for *K. s. cruentatum* in Mexico (Alvarez del Toro 1982; repeated by several authors), and 6–12 eggs for *K. s. abaxillare* (Alvarez del Toro 1982) have been perpetuated in the literature, but are surely in error. Ernst and Barbour (1989) suggested that these high numbers may represent counts of enlarged follicles rather than shelled eggs. Clutch size tends to increase with female body size (Goode 1994; Iverson 2010).

Eggs average 34 mm in length (range 23–41), 18 mm in width (range 14–26), and 6.7 g (range 2.5–11.8), and tend to increase in average size from north to south (Iverson 2010). Eggs in Mexico and northern Central America are typically only 5–6 g, whereas those in South America are typically 8–10 g. Relative egg mass ($[\text{egg mass} \times 100]/[\text{gravid body mass} - \text{clutch mass}]$) averages only about 1.9 (Iverson 2010), compared to typical values of 2.4–3.1 for other kinosternid species (Iverson 1999). Relative clutch mass ($[\text{clutch mass} \times 100]/[\text{gravid body mass} - \text{clutch mass}]$) for *K. scorpioides* from the Yucatan averages about 4.9 and that for captive females apparently from Honduras averages about 5.3 (Good 1994; Iverson 2010). Mean relative clutch mass for other kinosternids averages 6.0 (Iverson 1999). To summarize, relative to congeners, *K. scorpioides* produces very few, relatively small eggs, with low investment per clutch, but this is offset by the production of more clutches per year than most other species (Iverson 1999, 2010).

Kinosternon scorpioides also exhibits embryonic diapause (Ewert 1985, 1991), where early development is delayed until the diapause is broken by an environmental cue (e.g., warming temperatures after a chilling period). It also exhibits embryonic estivation (Ewert 1985, 1991), where full-term embryos have a reduced metabolism until hatching is stimulated by the environment (e.g., immersion of eggs during rainfall). These mechanisms serve to synchronize hatching to the beginning of the summer rainy season, even if the eggs were laid as much as nine months earlier (Castillo-Centeno 1986; Iverson 2010). As a result, the total incubation period is not correlated with incubation temperature (Ewert 1985), and has been recorded to last from 78 days (presumably lacking diapause and estivation; Ewert 1985) to 266 days (Rocha and Molina 1990; see review of all records in Iverson 2010).

The species exhibits temperature-dependent sex determination (TSD), with some populations apparently exhibiting TSD pattern II (low-temperature females, mid-temperature males, and high-temperature females; Ewert and Nelson 1991), and others apparently exhibiting pattern Ia (mid-temperatures producing mostly males, and high temperature producing all females; Ewert et al. 2004). This unusual variation clearly deserves further study.

The species is long-lived. Slavens and Slavens (1994) reported a *K. s. abaxillare* captured as an adult and still alive in captivity after 26 years and one month, and a *K. s. cruentatum* kept in captivity for 24 years and seven months. Dale Jackson (pers. comm.) has a kyphotic *K. s. cruentatum* that is still alive at this writing (2011), 24 years after its capture by him, JBI, and Mike Ewert as an adult in 1987 in Quintana Roo, Mexico.

Kyphosis has also been reported in an adult from French Guiana (Métrailler and Le Gratiot 1996), and JBI collected an additional kyphotic specimen (two total) in Quintana Roo in 1987.

Population Status. — This species is still very common in many areas across its extensive range. Dean (1980) found a density of 48.2 turtles/ha (ca. 10 kg/ha; Iverson 1982) in

coastal Chiapas, and Moll (1990) reported densities of 13.8 to 21 turtles/ha in Belize. Iverson (1982) reported a density of 272.4 turtles/ha (59.2 kg/ha) in the central valley of Chiapas, Mexico, and in Costa Rica, Guinn and Luger (2011) found as many as 316.5 turtles/ha, whereas Marquez (1995) estimated 361/ha. Forero-Medina et al. (2007) estimated population densities of 77 to 254 turtles/ha on San Andrés Island, Colombia, where it may have been introduced (Dunn and Saxe 1950).

Although Dean (1980) reported 14 males in a sample of 21 turtles from Chiapas, Mexico, all other well-sampled populations of *K. s. cruentatum* are female-biased (review in Iverson 2010). Iverson (2010) noted the same female-biased ratio in *K. s. abaxillare*. The only well-sampled population of *K. s. albogulare*, that on San Andrés Island (Forero-Medina et al. 2007), showed the same pattern, with nearly twice as many females as males. No apparent sex ratio bias is known for *K. s. scorpioides* (review in Iverson 2010), although some populations seem to be dominated by males (Oiviera et al. 2005). Whether this apparent geographic variation is related to the temperature-dependent sex determination found in this species is unknown.

Threats to Survival. — The primary threat to populations of *K. scorpioides* is from habitat destruction and degradation. Throughout its range, anthropogenic activities which result in degradation, loss, or alteration of freshwater habitats such as rivers, lakes, and wetlands have negatively affected natural populations. For example, Berry (1978) reported that *K. s. abaxillare*, which was once common in the Río Sabinal at Tuxtla Gutierrez, Chiapas, Mexico (the type locality of the subspecies), has been completely extirpated (along with most other aquatic life) by anthropogenic pollution and habitat degradation. In Costa Rica, Klemens et al. (2003) found organochlorine residues in the tissues of three turtle species (including *K. scorpioides*). Climatological extremes contribute to environmental stresses placed on *K. scorpioides*. Acuña-Mesén (1990; see also Leender 2001, Vogt 2008, Guinn and Luger 2011) reported that 140 individuals of a marked population of 206 *K. scorpioides* in Costa Rica were killed by fire during a very dry period, with another 24 individuals dying later from drought-related causes. While it is clear that *K. scorpioides* has the advantage of being able to survive in a variety of human-altered aquatic environments throughout its range, even when most other aquatic life is gone (see references under Habitat and Ecology above), it is quite likely that such human activities can only serve to alter the natural life history of the species and ultimately result in its decline.

Pritchard and Trebbau (1984) stated that *K. scorpioides* is of negligible economic importance. While it is undoubtedly true that it does not have the commercial importance of some other freshwater turtle species, and that it has probably been ingested at least occasionally by humans in prehistoric times (Langebartel 1953; Carr 1991; Chávez-Chávez 1999; Schaan 2010), it is equally true that contemporary economic and market pressures play a role in the species' survival. *Kinosternon* is eaten locally in

southern Mexico and Central America (Carr 1952; Pritchard and Trebbau 1984; McCranie et al. 2006; Marineros 2007), and in Central America, it was not uncommon in markets where it was sold for food (Mittermeier 1970). In the 1970s the authors observed dried and stuffed specimens of *K. scorpioides*, as well as trinkets made from shells, for sale in Mexican markets. Leender (2001) reported that in parts of Central America its meat is thought to have medicinal properties and to cure heart conditions.

Populations in South America are similarly exploited. Over three decades ago Smith and Smith (1979) reported that the species had already declined substantially due to overexploitation as a food resource in the Amazon basin. Fiasson (1945; see also Pritchard and Trebbau 1984) found it to be a delicacy in Venezuela, where it was thought to have curative properties. It is also eaten in Peru (Dixon and Soini 1986) and Colombia (Cuesta-Ríos et al. 2007; Gallego-García and Castaño-Mora 2002). In Brazil, Freiberg (1954), Alho (1985), Rocha and Molina (1990), Vogt (2008), and Carvalho et al. (2010) reported that this turtle is sold on beaches, in markets, and in restaurants, despite current legislation restricting that activity, and Nóbrega Alves et al. (2008) reported on its supposed medicinal value. Pezzuti et al. (2010) found that it is rarely found or consumed along the Rio Negro in Brazil; however, no published records are known from that specific drainage.

Kinosternon scorpioides is also common in the pet trade (e.g., Shiau et al. 2006), although it does not command the high prices and intense demand of some other species (e.g., see May 2009). Pritchard and Trebbau (1984) noted an increasing number of Bolivian specimens reaching Miami, Florida, and “Honduran” specimens have regularly been available in the pet trade for at least 20 years (Iverson 2010; Iverson unpubl. data). The authors have also observed pet trade specimens in the past decade which were determined to have originated in southern Mexico, Nicaragua, and Isla de Coiba, Panama.

On San Andrés Island, the species is also threatened by the introduced egg-specializing tegu lizard (*Tupinambis teguixen*) (Castaño-Mora 2002; Forero-Medina et al. 2007; Forero-Medina and Castaño-Mora 2011).

Conservation Measures Taken. — The Turtle Taxonomy Working Group (2010) reported that under IUCN criteria, *K. scorpioides* was considered to be a species of Least Concern when evaluated in 1996. Likewise, under TFTSG Draft 2010 it has the provisional status of Least Concern, South America regional (Turtle Taxonomy Working Group 2010). To date, no conservation measures specific to *K. scorpioides* have been taken; however, preserving the character and quality of freshwater habitats will nearly always protect *K. scorpioides* (and other species). In the Colombia Red Book of Endangered Reptiles the species is listed as Vulnerable (D2).

The species is known to occur in several protected areas: Réserve Naturelle Nouragues in French Guiana (Böhm 2010), Seaflower Biosphere Reserve in Colombia (Forero-Medina and Castaño Mora 2011), Tiputini Bio-

diversity Station in Ecuador (Cisneros-Heredia 2006), Bosawas Biosphere Reserve in Nicaragua (Kohler 1999), Parque Nacional Carara (Laurencio and Malone 2009) and Parque Nacional Palo Verde (Guinn and Luger 2011) in Costa Rica, Monkey Bay National Park in Belize (Turvey and Cooper 1999), and Reserva El Ocote in Chiapas, Mexico (Castellanos and Alonso 1998). It almost certainly occurs in many other reserves: Sian Kaan Biosphere Reserve on the Yucatan peninsula; and Shipstern Nature Reserve, Crooked Tree Wildlife Sanctuary, Rio Bravo Conservation Area, Community Baboon Sanctuary, Lamamai Archaeological Reserve, and Sibun Forest Reserve in northern Belize (S. Platt, pers. comm.).

The only local education program for the conservation of this species is that of Forero-Medina and Mahecha (2006) on San Andrés Island, Colombia.

Conservation Measures Proposed. — As noted above, the greatest threats to the survival of the Scorpion Mud Turtle result from freshwater habitat degradation. Therefore, conservation measures which generally result in the preservation of water quality, and which preserve wetlands, other aquatic habitats, and adjacent terrestrial buffer zones from anthropogenic alterations will assist the survival of the species anywhere in its range.

An important limitation on measures to conserve *K. scorpioides* is the general lack of life history information for the species throughout its range. As noted by Duellman (1979) regarding the South American herpetofauna in general, it is critically important for biologists to collect distributional, taxonomic, and life history data in a systematic fashion so that more effective conservation measures can be proposed or taken.

Various recommendations to preserve biodiversity of New World tropical ecosystems such as the establishment of wildlife preserves and careful land use planning will inevitably benefit all species, including *K. scorpioides* (see, for example, Duellman 1979 and Wilson 1989).

Captive Husbandry. — *Kinosternon scorpioides* generally survives well in captivity (e.g., Rocha and Molina 1990; Goode 1991, 1994; Métrailler and Le Gratiet 1996; Merchán and Fournier 2004; May 2009; Nickl 2011, among others), and has been reported to have been bred at least to F3 progeny (Goode 1994). The species requires a minimum of care, although individuals have a tendency to develop skin and bone infections if neglected (Berry, unpubl. data). It should be maintained in clear water deep enough to cover the shell completely, and there should be access to dry sites for terrestrial activity (including egg-laying). Berry has maintained juvenile and adult *K. scorpioides* in excellent health for over ten years on a diet of commercially prepared catfish chow supplemented monthly with fish. However, the diet must be well-varied, including crustaceans, in order to maintain the vivid red and orange colors characteristic of many populations (May 2009). Dale Jackson (pers. comm.) has maintained his kyphotic adult outside in north Florida for over 24 years in a plastic children's pool filled with shallow water and numerous retreats. It has been fed commercial turtle food sticks supplemented on occasion

with bits of raw tilapia, chicken, pork, or beef (all lean). It is usually brought indoors for cold winters in a similar set-up.

Current Research. — This species is not currently the subject of any known field study; however, a phylogeographic study is in progress (Le and Iverson, unpubl. data). The latter is necessary to test the hypothesis that *K. scorpioides*, the most widely distributed turtle species in the New World, may actually represent a species complex.

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