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Hydromedusa tectifera Cope 1870 – South American Snake-necked Turtle, Argentine Snake-necked Turtle, Tortuga Cuello de Vibora, Cágado Pescoço de Cobra

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SUMMARY. – The South American Snake-necked Turtle, Hydromedusa tectifera (Family Chelidae), is a medium-sized freshwater turtle, found in southern Brazil, Uruguay, southern Paraguay, and east and central Argentina. Maximum recorded straight carapace length (CL) is 30.6 cm in females and 28.4 cm in males, although most individuals are usually less than 25.0 cm. Its skull and carapace structure show characters quite distinct from those of the superficially similar chelid snake-necked turtles of Australia (genus Chelodina). Clutch size is 5–15 eggs and eggs are elongate, ranging from ca. 24–40 x 20–24 mm; hatchlings have a CL of ca. 35–37 mm. Preferred habitats for H. tectifera consist primarily of natural lentic and lotic waters, including anthropogenically altered or constructed habitats (e.g., creeks, dams, lakes, lagoons, streams, rivers, and coastal estuaries). The species is specialized for feeding upon a wide spectrum of food items, mainly aquatic arthropods. The international pet trade in this species is modest, and although it seems to be affected by industrial and agricultural pollution in several parts of the range (e.g., Rio de Janeiro State in Brazil, Buenos Aires Province in Argentina), it shows considerably greater tolerance for polluted conditions than does its congener H. maximiliani.

DISTRIBUTION. – Central and northeastern Argentina (Buenos Aires, Córdoba, Entre Ríos, Misiones, Santa Fe, Salta, San Luis, Santiago del Estero), southern Brazil (Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo), southeastern Paraguay (Alto Paraná, Itapuá, Guairá), and most of Uruguay.

SYNONYMY. – Hydromedusa tectifera Cope 1870, Hydromedusa platanensis Gray 1873, Hydromedusa platensis, Platemys antiqua † Ameghino 1882 (nomen nudum), Platemys fossilis † Ameghino 1882 (nomen nudum), Platemys laevis † Ameghino 1882 (nomen nudum), Platemys robusta † Ameghino 1882 (nomen nudum), Hydromedusa wagleri Günther 1884.

SUBSPECIES. – None currently recognized.

STATUS. – IUCN 2021 Red List: Least Concern (LC) [Not Listed] (TFTSG 1996); TFTSG Provisional Red List: Least Concern (LC; assessed 2011); CITES: Not Listed; U.S. ESA: Not Listed.

Taxonomy. – Hydromedusa tectifera was described by Cope (1870) and is a member of the side-necked turtle family Chelidae and the subfamily Hydromedusinae. One other extant congeneric species (H. maximiliani) is recognized. Several fossil species have been synonymized with H. tectifera (Ameghino 1882; see synonymy above). No genetic studies on the phylogeography of H. tectifera have been published, and no subspecies have been described.

There are numerous points of distinction between the two extant Hydromedusa species, including the following features distinguishing H. maximiliani from H. tectifera: smaller adult size (generally less than 180 mm CL); earlier closure of shell fontanelles; narrower nuchal scute (much narrower than the first vertebral); second peripheral bones larger than the first peripherals; interabdominal seam the shortest along plastral midline (interhumeral shortest in tectifera; suture between hypoplastra and xiphiplastra posteriorly angled, usually crossed by abdomino-femoral seam; nuchal bone recessed posteriorly from anterior margin of carapace; anterior and posterior plastral lobes of approximately equal width; suprapygal broader than long; first pair of marginal scutes very small and narrow; entoplastron with relatively large rugose area on visceral surface; and habitat higher altitude in well-oxygenated creeks.

In his original description of H. tectifera, Cope (1870) expressed some confusion as to the source of his specimens: “This turtle occurs in some of the tributaries of the Paraná or Uruguay Rivers, either in the Argentine Confederation or the Banda Oriental, but in which, I do not know.”

The names Hydromedusa platanensis Gray 1873 and Hydromedusa wagleri Günther 1884 are considered
synonyms of *H. tectifera*. In addition, the valid name of the congener *H. maximiliani* has sometimes been misapplied to specimens of *H. tectifera*, e.g., by Wagler (1830); or rendered as *Chelodina maximiliani* by Duméril and Bibron (1835). Some such designations (e.g., by Burmeister 1886) occurred after Cope’s (1870) description of *H. tectifera*. Curiously, the smaller, less common, more localized and more rarely seen species *H. maximiliani* has a much more complex synonymy than the relatively widespread and more familiar *H. tectifera* (Fritz and Havas 2007; TTWG 2017). The vernacular name of this species in Uruguay, Paraguay, and Argentina is *Tortuga Cuello de Vibora*, and in Brazil it is *Cágado Pescoço de Cobra*.

Variation in carapacial morphology was recently reported for *H. tectifera* in association with hydrographic basins (Clavijo-Baquet et al. 2010), but no subspecies have been described. The karyotype of the species is 2n = 58, composed of 22 macro- and 36 microchromosome (Noleto et al. 2006; Alcalde and Sánchez J., unpubl. data).

The fossil history of the genus dates from 5 million years ago (de la Fuente and Bona 2002). Wood and Moody (1976) described a fossil nuchal bone of the shape typical of *H. tectifera* from early Eocene deposits of southern Argentina, and de la Fuente (1992) described a fossil chelid from the Quequén Salado River, Buenos Aires Province, Argentina, that he identified as *H. tectifera* or

*Figure 1*. Adult *Hydromedusa tectifera* from Brazil. Photo by Peter C.H. Pritchard.

*Figure 2*. Adult male *Hydromedusa tectifera* from Rio Grande do Sul, Brazil. Photos by Raissa Bressan.
a very similar species. Later, de la Fuente et al. (2001) described *Yanimechelys* from the Upper Cretaceous of Patagonia as the sister taxon of *Hydromedusa*. The single extinct species of *Hydromedusa*, *H. casamayorensis* de la Fuente and Bona 2002 is known from the Paleocene of Patagonia, in Chubut province, Argentina (Maniel et al. 2018). The several fossil species of *Hydromedusa* described by Ameghino (1882) are all considered *nomina nuda* and are synonymized under *H. tectifera* (TTWG 2017). Maciel et al. (1996) and Oliveira and Romano (2007) reported fossils of *H. tectifera* from the Touro Passo formation (Upper Pleistocene – Lower Holocene; Paraná, Brazil). Similarly, Deschamps and Tomassini (2016) reported fossils of *H. tectifera* from the Middle Pleistocene (Bonaerian Age) of the Bajo San Jose formation (Buenos Aires Province, Argentina). Perea and Martínez (1984) reported a fossil of *Hydromedusa* from the Upper Pleistocene of the Gutiérrez Chico and Grande streams, Uruguay.

**Description.** — For previous morphological descriptions of this species, see Müller (1968), Freiberg (1971), Gaffney (1977), Pritchard (1979, 1984), and Cabrera (1998).

The carapace is typically oval in juveniles and subadults, with a shallow gutter along each side. With growth, the shell becomes more elongate and parallel-sided or even slightly incurved at the sides, and the gutters disappear. A vertebral keel is persistent until old age, but the largest individuals may have a bilobed carapace, with a median trough, and with distinct prominence of the shell in the area under the first costal on each side. The nuchal scute is extremely wide—as wide as, or wider than, the broad anterior end of the first vertebral. Moreover, it is uniquely recessed posteriorly from the anterior margin of the carapace, and thus takes the form of a short, wide, additional first element in the vertebral series. Vertebral 2 is large, and vertebrae 3 and 4 are progressively smaller and narrower, whereas vertebral 5 is very large and heptagonal. The vertebral scutes become relatively narrower with age. There are four pairs of costal scutes and eleven pairs of marginal scutes, marginals 5, 7, 9, and 11 being distinctly elevated where they make contact with the intercostal seams. A single pair of supracaudals is present.

The texture of the carapace is exceedingly rough and highly sculptured in hatchlings, and the rough surface is still evident in juveniles of 10–15 cm CL. The species name *tectifera* (or “roof-bearing”) refers to the ridged, roof-like form of the carapacial scutes. Ultimately, however, most of the roughness disappears (partly by shedding of the outer layers of the scutes, partly by a smoothing on the underlying bone with growth), apart from a knobby tubercle near the posterior margin of costal 4 on each side, and a widened tubercle near the posterior margin of vertebral 5. In very large specimens, the carapacial scutes assume...
a taught, wrinkled appearance, and by then are very thin. The peeling of the outer layer of the scutes with growth effectively expunges growth annuli in larger specimens.

The plastron is large and flat, with an expanded anterior lobe (longer and wider than the posterior lobe) and a short bridge. A deep anal notch is present. The plastral formula is very variable, but in general the huge intergular is the longest scute along the midline, the abdominals, femorals, and anals shorter than the intergular and subequal, and the humerals and pectorals the shortest. The intergular is larger than the combined gular scutes, and nearly as large as each of the humerals. It has an extensive, wavy anterior border along the anterior margin of the plastron that completely separates the gulars and offers a variable degree (50–90%) of separation of the humerals. The hyo-hypoplastral suture usually approximately bisects the abdominals.

The neck is extremely long, and the head is elongate, depressed, and anteriorly tapered in lateral aspect. The neck is coarsely wrinkled below and papillose above. The eyes are antero-dorsally located. The dorsum of the head is covered with granular scales, which grade into divided or wrinkled skin anteriorly.

Some specimens have a differently pigmented area where other chelids often have submental barbels. One adult male (20.0 cm CL) from Magdalena, Buenos Aires, Argentina, had a very short, but clearly distinguishable pair of mental barbels (Alcalde, pers. obs.). The limbs are small and the digits are elongate and webbed. The limbs bear transverse lamellae along the anterior face, with squarish scales on the digits. Each of the four limbs bears four claws, each posterior limb also bearing a flattened “swimming flap” covered with relatively stiff scales. The tail is short and pointed, and thick-based in both sexes. The skin of the tail is moderately papillose or covered with soft scales.

The bony carapace includes a large, elongate, posteriorly broadened nuchal bone, with a relatively narrow anterior border (but never recessed behind the anterior pleurals). The first peripheral on each side is large and triangular, presence of paredo-squamosal arches (absent in Chelodina), and virtually absent supraocipital process. The median prefrontal contact, doubtless associated with the anteradorsal migration of the expanded orbits and actually causing separation of the frontals into (small) anterior and (large) posterior sections, and the enormous internal nares, are unique among Chelidae to Hydromedusa.

Intercostal fontanelles are very persistent. They close progressively from both anteriorly and posteriorly with age, but even in large adults, as many as five fontanelles (corresponding to the location of the axillary and inguinal buttresses and three in between) may persist on each side. In adult females, even when some of these fontanelles close, sutural bonding between the juxtaposed pleural and peripheral bones does not occur. In one examined specimen, a 26.2 cm CL male (PCHP 4060), fontanelle closure was complete except for a pair of persistent inguinal fontanelles, a parallel to the condition found in adult Notochelys (Geemydidae). In that the plastron does not fuse with the carapace even in large specimens, the fibrous bridges and persistent fontanelles may allow for some compression or expansion between carapace and plastron.

The plastral bones include a very large, roughly triangular (but posterior convex) entoplastron, comparable in size to each of the expanded epiplastra. The posterior margin of the entoplastron reaches close to the humeropectoral suture. The bridge is short, approximately 20–25% of the maximum plastral length, and has approximately equal contributions by the hyo- and hypoplastral bones. The plastral buttresses are feeble, the axillary buttresses being larger than the inguinal ones. A single musk duct perforates each of the plastral buttresses, detectable in prepared bony elements as a slit rather than a circular perforation. The longest midline suture is that between the xiphiplastra. A mid-plastral fontanelle is almost always present, but is very variable in extent even within a series of specimens of comparable size. Only rarely (e.g., in PCHP 3923, a 23.8 cm CL female, or PCHP 4060, a 26.2 cm CL male) is the mid-plastral fontanelle almost closed.

The skull was illustrated and described by Gaffney (1977), and its adaptations and comparisons with Chelus and Chelodina were discussed by Pritchard (1984). It is noteworthy for its enlarged, narrowly-separated orbits, elongate form, presence of parieto-squamosal arches (absent in Chelodina), and virtually absent supraoccipital process. Small, paired nasals and prefrontals, and large, paired frontals (note the fused frontals in Chelodina) are present. The median prefrontal contact, doubtless associated with the anterodorsal migration of the expanded orbits and actually causing separation of the frontals into (small) anterior and (large) posterior sections, and the enormous internal nares, are unique among Chelidae to Hydromedusa.

The carapace is brown to dark brown in subadults. In adults, the carapace is typically brown, with dark brown to black spotting. The plastron is yellow-buff, with dark gray-brown bridges. In large adult males the plastral concavity is gray. Some dark spots may be present on the ventral aspect of the marginals. Specimens from the Upper Parana River tributaries in Misiones, Argentina, and probably from adjacent Brazilian and Paraguay populations, usually have
red-stained plastrons because soils are red with iron-rich laterite sediments. The head, neck, and limbs are basically dark gray, the limbs having light to white ventral surfaces. A light whitish band extends posteriorly from the angle of the jaw on each side, and there are light, irregular, elongate markings on the underside of the neck.

Maximum recorded straight CL sizes for *H. tectifera* are males at 28.4 cm and females at 30.6 cm (Bager et al. 2003; Chinen et al. 2004; Regis and Meik 2017). Isolated reports made by other authors show smaller CL values. For example, the largest specimen examined by Wood and Moody (1976) measured 25.5 cm CL. Freiberg (1971) gave a figure of a turtle measuring 27.0 cm CL, and Luederwaldt (1926) provided details of several specimens of both sexes in the range of 25–30 cm CL. Similarly, Costa et al. (2010) reported the CL (18.1–24.4 cm) and weight (540–1270 g) ranges of five adults of both sexes trapped near Lavras, Minas Gerais, Brazil. The five largest specimens in the Chelonian Research Institute (CRI, PCHP collection) were caught in the sewage-enriched waters of Río Santa Lucía, Melilla, Montevideo, Uruguay: two males measured 26.0 and 26.5 cm CL and the three females measured 27.4, 29.1, and 29.8 cm CL. Bujes (2010) also reported CL measurements and weights from a Rio Grande do Sul, Brazil, population of the species: in a sample of 11 turtles (six females and five males) the largest female was 26.3 cm CL and 1200 g, while the largest male was 22.4 cm CL and 1180 g.

At population levels, Lescano et al. (2008) studied 26 males, 20 females, and 48 juvenile *H. tectifera* from Toro Muerto stream, Córdoba, Argentina, and categorized their straight CLs into five size classes. They found that the most abundant sizes were those of size classes 1 and 2 (turtles < 15 cm CL: 62% of captures), and that they decreased in abundance through size class 5 (turtles > 25 cm CL: 9.5% of captures). Conversely, Šemčiúk et al. (2019) studied 56 males, 46 females, and 7 juveniles from the population from Rodriguez stream, Buenos Aires, Argentina, and found that most captures corresponded to size classes 3 and 4 (turtles between 15.1–25.0 cm CL). The Alcalde team (unpubl. data) has recorded nearly 600 CLs of individuals from Buenos Aires (Buñirigo, Tubichamini, Cajaravilla, Carnaval, El...
Gato, Martin, Rodríguez, Zapata streams and Río Sauce Grande), Córdoba (Tanti and Toro Muerto streams), and San Luis (Río Quinto), and recorded the largest female at 26.5 cm CL (1682 g) and largest male at 28.6 cm CL (2000 g), both from Buñirigo stream. More recently, da Silva et al. (2020) compared measurements between two Brazilian populations: Lavras (n = 11 turtles; Minas Gerais) and a mix from Arroio Grande, Taim, and Pelotas (n = 62 turtles; Rio Grande do Sul). They found that turtles from the southernmost populations reached larger sizes (males: 28.0 cm CL vs. females: 29.8 cm CL) than those from Lavras (males: 24.4 cm CL vs. females: 26.9 cm CL), concluding that such size differences may be attributable to phenotypic plasticity related to latitude (higher in Río Grande do Sul), altitude (higher in Minas Gerais), and climate (warmer in Minas Gerais). In a recent osteohistological study, Pereyra et al. (2020) documented similar growth differences between the large extinct Yaminuechelys maior and its sister extant species, *H. tectifera*, and suggested that the larger body size in the former may be explained by hypermorphosis rather than by hypomorphosis in the latter.

Sexual dimorphism in adults is most evident in the relatively deep, narrow plastral concavity of the male—an unusual feature in a flat-shelled, aquatic turtle, but one that is also present in the related chelid genus *Chelus*. It is already evident in a juvenile specimen of 11.2 cm CL. The vent is markedly larger and wider in males than females, with the vent slightly more posterior in the male (Bujes 2010). The hind plastral lobe shows some slight differences between the sexes, being somewhat narrower in the male, but variation within each sex is considerable. There is only minor sexual size dimorphism (see above), with females slightly larger than males.

**Distribution.** — *Hydromedusa tectifera* has a much more extensive distribution than its congener *H. maximiliani*. The species is present in several localities from central and northeastern Argentina, almost all of Uruguay, southeastern Paraguay, and southern Brazil (Iverson 1992; TTWG 2017, 2021; Sánchez et al. 2019). Freiberg (1967) reported the species as occurring in Bolivia based on an ancient reference (Koslowsky 1898), but this was considered as undocumented and erroneous by Cabrera (1995). Sánchez et al. (2019) published a recent review of the distribution of the species that lists several new localities. Several well-documented localities taken from Citizen Science sites (www.ecoregistros.org; www.inaturalist.org) plus some that were erroneously omitted by Sánchez et al. (2019) or published or discovered more recently are now included here on our distribution map for the species.

*Hydromedusa tectifera* has thus far been recorded from 18 of the 19 departments of Uruguay; from 7 (or 8 pending confirmation of an ancient, doubtful record from Rosario, Santa Fe, by Siebenrock 1909) of the 24 provinces of Argentina, from 3 of the 18 departments of Paraguay; and from 6 of the 27 states of Brazil. The most peripheral populations (in the west, south, north, and east, respectively) have been recorded from: Río Popopis, Justo Daract, San Luis, Argentina; Río Sauce Grande, Sierra de la Ventana, Buenos Aires, Argentina; São Francisco River, São Roque de Minas, Minas Gerais, Brazil; and Serra dos Órgãos National Park, Teresopolis, Rio de Janeiro, Brazil. This last locality also constitutes the maximum altitude recorded for the species, at nearly 1500 m a.s.l. (Pontes et al. 2006). The lowest recorded altitudes are near sea level (e.g., populations near the Río de La Plata River and Atlantic Ocean shorelines in Argentina, Uruguay, and Brazil). The species is present in hydrobasins associated with the following biomes: Pampa (Argentina, Uruguay, and Brazil), Espinal (Argentina, Uruguay), Cerrado (Brazil), Dry Chaco (Argentina), and Atlantic Rainforest (Argentina, Brazil, and Paraguay).

Alvarez de Miguel (2017) analyzed the origin of the disjunct populations of *H. tectifera* in the mountainous Córdoba province of Argentina. Considering the current and past (Holocene and Last Glacial Age) optimal and suboptimal temperature values for the species, she found no evidence to reject the natural origin of these populations.

**Habitat and Ecology.** — Cabrera (1998) and Souza (2004) provided useful reviews of the natural history and other ecological aspects of *H. tectifera* based mostly on miscellaneous field observations and data obtained from captive turtles.

**Habitat.** — Preferred habitats for *H. tectifera* consist primarily of natural lentic and lotic waters, including anthropogenically altered or constructed habitats (e.g., creeks, dams, lakes, lagoons, streams, rivers, and coastal estuaries) (see Vaz-Ferreira and de Soriano 1960; Freiberg 1981; Gallardo 1987; Gudynas 1989; Lema and Sarmento Ferreira 1990; Ribas and Monteiro Filho 2002; Bujes 2008; Estrades et al. 2008; and Sánchez et al. 2019). Cei (1993) described specimens from the coast of Buenos Aires that had colonies of small barnacles of the genus *Balanus* on the carapace, indicative of prolonged exposure to saline conditions. The species is rarely seen outside of water (it presumably practices subaquatic basking, see Astort 1983); it commonly has its carapace as well as its plastron and soft parts completely or partially covered by filamentous algae and colonized by different species of *Temnocephala* (Platyhelminthes) among other commensal epibionts and ectoparasites (see below).

Cei (1993) reported that the species appears to hibernate completely submerged in rivers; a similar observation by Carreira et al. (2015) may have been based on Cei (1993). Both these reports, together with the statement made by Lema and Sarmento Ferreira (1990)
that the species spends winters buried under dried mud, need strong further evidence since they are contrary to the observations based on long-term population studies (see below). In the aquatic environments of the Rio de La Plata shoreline, the species undergoes partial hibernation (torpor) since it never ceases food ingestion and can be trapped on the warmest days of winter (e.g., July, see Alcalde et al. 2010).

Semeniuk et al. (2020) studied habitat use and preferences for a population of *H. tectifera* inhabiting a polluted urban stream in Buenos Aires. Turtles used four types of underwater refuges during the year: dams of garbage and floating vegetation, denuded bottom surfaces, burrows along the stream margins, and raised marginal aquatic vegetation, with the last two being the most used by turtles of both sexes and of all size classes. The authors also detected

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both aggregative patterns and individual recurrences in the use of marginal burrows. Our observations (Alcalde and Sánchez, pers. obs.) have revealed that the species can be active at any time and not only at night or in the daytime as suggested in previous works (Cabrera 1998; Balestra et al. 2016; Molina and Leynaud 2017). We have observed the species basking underwater, bottom walking, feeding, and mating in shallow stream zones during the daytime and also at night. Molina and Leynaud (2017) found that H. tectifera is a thermoconformer and eurythermal species whose body temperature seems to be strongly associated with water temperature without influence from factors such as air temperature, sex, age, body size, and mass.

With respect to sympatry and syntopy with other freshwater turtle species, H. tectifera is known to be sympatric with Acanthochelys spixii (e.g., northeastern Uruguay and southern Brazil: Bujes 2008), Phrynops hilarii (e.g., in the Pampa and Espinal regions of Argentina and Uruguay and in southern Brazil: Bujes 2008; Alcalde et al. 2010; Sánchez et al. 2019), Phrynops williamsi (e.g., Atlantic Rainforest areas of Misiones, Argentina: Sánchez et al. 2019), Trachemys dorbigni (in the Pampa and Espinal regions of Argentina and Uruguay and in southern Brazil: Bujes 2008; Alcalde et al. 2012; Sánchez et al. 2019), and with the congener H. maximiliani (e.g., in the Cerrado and Atlantic Rainforest areas of Brazil: Souza 2005; Molina et al. 2016). With most of these species, H. tectifera is capable of sharing the same microhabitat, but according to Souza (2005), H. tectifera and H. maximiliani are often mutually excluded by altitude from areas where they are in apparent sympatry. This author reported that in cases where these turtles are found in broad sympathy, H. maximiliani occurs at altitudes higher than 600 m while H. tectifera occupies lowland waters nearer sea level. In areas where these species do not occur in sympathy, H. maximiliani can be found in lowland waters and, conversely, H. tectifera may inhabit waters up to 900 m (Souza 2005).

Behavior. — Freiberg (1971) described H. tectifera in colorful terms, remarking that it seemed to have serpentine aspirations, contrasting sharply with the pleasant, decorative, and docile T. dorbigni; he complained that it remained wild and indomitable, maintaining its skittish behavior even after years in captivity, and never became friendly, although when sufficiently hungry it would seize a piece of meat from the hand. Our field observations on the species confirm this elusive and apprehensive character that Freiberg described so well; but little is known of its behavioral habits in the wild and we consider it a very secretive species.

Feeding and Diet. — All authors who have commented on the diet of H. tectifera have described it as carnivorous. Earlier feeding observations were made either on captive specimens or miscellaneous field observations (Luederwaldt 1926; Gallardo 1956; Ditmars 1957; Benefield 1979; Freiberg 1977; Gallardo 1987). These studies noted a wide variety of animal food items in the diet. Estrades et al. (2008) reported that the diet in the wild includes fish, insects, mollusks, and carrion. The morphological specialization of the head and neck suggest that small, live prey would, at the very least, be an important part of the diet. The “harpoon-strike” mode of feeding, and its anatomical and skeletal adaptations, were described by Pritchard (1984).

Recent long-term field studies have assessed the diet of the species in several Argentinian populations, two from unpolluted mountain streams of Córdoba (Bonino et al. 2009), three from polluted (tannery, meat processing industry, urban waste) lowland streams of Buenos Aires (Alcalde et al. 2010, Palumbo et al. 2021, Sánchez et al. 2021), and two from Rio Grande do Sul, Brazil (Chaviel et al., in press). If these studies are compared by using the same dietary categories (families and orders in most cases and suborders in the cases of Odonata and Trichoptera), H. tectifera consumed 25 dietary categories in the Toro Muerto, Tanti, and Carnaval streams (Bonino et al. 2009; Sánchez et al. 2021), 26 and 30 in the Rodriguez stream (Sánchez et al. 2021; Palumbo et al. 2021), and 29 in the Bufirigo stream (Alcalde et al. 2010), but only eight in the two Brazilian populations studied by Chaviel et al. (in press).

The data from Alcalde et al. (2010) indicated copepods, ostracods, immature chironomids, and ephemeropteran larvae were the preferred items, whereas immature chironomids, corixids, and belostomatids were the items that contributed most to the diet, with high consumption of aquatic hemipterans in the warmer months despite the abundance of this prey remaining stable throughout the year.

The other study by Bonino et al. (2009) found trichopteran and odonate larvae, together with fish, contributing most to the diet. The diet of turtles from the Carnaval stream was dominated by aquatic snails (mainly Pomacea canaliculata), in correlation with the environmental high abundance of this prey item (Sánchez et al. 2021). Turtles from this stream seem to ingest large snails by suction of soft body parts, as first described by Gallardo (1956). The diet of turtles from the Rodriguez stream was dominated by amphipods (the most abundant item in the environmental samples), aquatic coleopterans and, to a lesser degree, water bugs (genus Belostoma) (Sánchez et al. 2021). Work by Palumbo et al. (2021) for the Rodríguez stream rested upon an entire year of sampling, using a large number of turtles (n > 100), contrary to the study by Sánchez et al. (2021) that used 24 samples taken in late spring and summer. Palumbo et al. (2021) found a global dominance of immature chironomids, amphipods, terrestrial oligochates, and aquatic hemipterans, with a
dominance of amphipods in summer, similar to the findings of Sánchez et al. (2021).

Contrary to other dietary studies that rest upon stomach flushing (Bonino et al. 2009; Alcalde et al. 2010) or stomach flushing and feces (Sánchez et al. 2021; Palumbo et al. 2022), the work by Chaviel et al. (in press) involved dissecting stomach and intestine contents from road-crushed turtles. These authors found aquatic snails and Odonata naiads as dominant prey items in 20 H. tectifera examined. Although Alcalde et al. (2010) found no variation in the mean size of food items in relation to the size of turtles, their data showed that larger turtles tend to consume larger prey. Such a tendency was significant in the populations studied by Bonino et al. (2009). The authors compared the maximum size of prey with the size of turtles and found that larger turtles eat larger items (because fish are not consumed by smaller turtles) and have a narrower trophic niche than smaller ones.

Courtship and Mating. — Observations on courtship and mating in captivity were described by Nicol (1982), who observed the male swim closely behind the female and, at the opportune moment, swim over her carapace and thrust his head under her neck, firmly biting the skin. The female became passive and virtually motionless, with her left forelimb positioned over the male’s neck. While maintaining his hold on the female’s neck, the male used his hind limbs to hold the edges of the female’s carapace, with the claws digging into the muscular area of the female’s thigh and his tail tip probing her vent. At this point, the paired turtles were rolled over by the observer, and mating was confirmed. Similar observations were provided by Estrades et al. (2008), who reported that the male bit the neck of the female and scratched her carapace with his claws during mating.

A different courtship behavior was observed by Alcalde (pers. obs.) in shallow water in Tanti stream, Córdoba, during a warm night in autumn (mid-March). A male and a female turtle walked in circles on the bottom of the stream, the male following the female; for a while they walked clockwise, then changed directions and walked counter-clockwise, in a manner similar but not identical to the courtship behavior described by Novelli and Souza (2007) for H. maximiliani. The observation ended before the courtship ended and copulation was not confirmed.

Three events of mating in the wild were described by Lescano et al. (2007) in northern Cordóba, Argentina. In all cases, copulation extended for no more than one hour and occurred during the evening or late afternoon in shallow waters (30–90 cm depth) during late winter (August–September) and early spring (October). Similarly, Alcalde (pers. obs.) has observed an attempted mating in late autumn (May) in the evening in a shallow pond (20 cm) near La Plata, Buenos Aires, Argentina, but copulation was not verified. In addition, Sánchez and Alcalde (pers. obs.) have observed one (late August, end winter) and six (September, early spring) successful matings between mid-morning and early afternoon in shallow water areas of Rodríguez stream, Buenos Aires, one of which involved a second male. A male to male copulation, sustained for about ten minutes after sighting, was observed by LA on the Martin stream (La Plata, Buenos Aires) during early spring (mid-September). These episodes may be indicative of bimodal mating for the species, with a peak in late winter (July–August) to early spring (September–October) and fewer mating events in late summer to autumn (March–April).

Reproduction. — Gallardo (1982) reported nesting as occurring in late spring (November and early December) in El Palmar National Park, Argentina, in the sandy banks of creeks and on the fringe between the gallery forest and the water. Bager and Rosado (2010) studied nesting sites for H. tectifera in comparison with syntopic P. hilarii and T. dorborgii; they concluded that H. tectifera nested at 12 m (± 10 m) from the shoreline, closer to the water than the other two species. They proposed that this shorter distance increased the risk of nest loss by flooding, but in turn may be balanced by a lower risk of egg desiccation and hatchling predation. Estrades et al. (2008) reported that eggs are laid in the spring in Uruguay and that emergence occurs between December and January (early summer) (Achaval and Melgarejo 1979). Fagundes and Bager (2007) reported that at the Taim Biological Station, Rio Grande do Sul, Brazil, eggs are laid in the spring, most frequently between 1600 and 2000 hrs.

Reports concerning clutch sizes vary from 5–10 (Estrades et al. 2008, source not clear) to 6–14 (Wolff 2002, captive breeding), and 5–15 (Molina et al. 2016, source not clear), reaching a maximum of 15 eggs (Nöllert 1987, captive breeding; Fagundes and Bager 2007, field clutches). Incubation periods for the species have been reported as follows: 105–110 days incubated at 25–30°C (Benfield 1979, in captivity), 75–200 days depending on temperature (Wolff 2002, in captivity), 70–128 days (Molina et al. 2016, source not stated), and 70 days (Estrades et al. 2008, source not stated).

With respect to the shape and size of eggs, Nöllert (1987) reported that they are elongated (longer than wide). Egg length varies from 23.9 mm (Fagundes and Bager 2007) to 30 mm (Cei 1993) and 36 mm (Nöllert 1987) and reaches a maximum of 40.4 mm (Bujes 2010). Egg width is around 20 mm (Nöllert 1987; Cei 1993) and 24 mm (Bujes 2010). Average egg sizes were provided by Wolff (2002) for captive laid clutches: average length 38 mm, average width 22 mm. The same author provided a weight range for captive bred eggs of 19–25 g, a value clearly higher than the maximum weight of 13.5 g per egg reported by Bujes (2010). The average weight of eggs measured by
Fagundes and Bager (2007) at the Taim Biological Station, Rio Grande do Sul, Brazil, was 11.5 g.

The size and weight of hatchlings born at San Antonio Zoo in Texas was 35–37 mm CL and 7–9 g (Benefield 1979). In northern Buenos Aires, most field sightings of hatchlings <50 mm CL have occurred in early spring (mid-September \( n = 4 \) to early October \( n = 8 \); Alcalde and Sánchez, pers. obs.). Four hatchings in the CRI collection measured 34–40 mm CL; they were described by Gurley (2003) as “truly stunning...with crisp, detailed patterns and beautiful red and black plastral markings.” The smallest size for hatchlings was recorded in two specimens of 32 mm CL from Río Sauce Grande, Sierra de La Ventana, Buenos Aires, Argentina, which are held at the Herpetological collection of the Museo de La Plata. They were examined by Alcalde (pers. obs.) when fresh and lacked such red and black plastral markings. Finally, Volpato et al. (2013) described the eggs and the process of artificial incubation of a clutch recovered by laparoscopy from a road-crushed female of the species.

In comparison with \textit{H. tectifera}, its extant congener \textit{H. maximiliani} has a smaller clutch size (1–3 eggs per female, \( n = 26 \)) but a larger egg size (33.1–45.4 mm in length, 19.9–25.0 mm in width, \( n = 53 \)) (Famelli et al. 2014). Nesting is similar for both species (late spring to early summer; November to January).

\textit{Growth Rates}. — Nöllert (1987) reported that captive-hatched specimens, initially 35–37 mm CL, had grown about 10 mm in length 130 days later, by which time the weight had more than doubled. Unpublished capture-recapture data from three populations of the species from Zapata and Tubichamini streams (La Plata, Buenos Aires, Argentina) and Rodríguez stream (Magdalena, Buenos Aires, Argentina), suggest very slow growth rates for adults (Sánchez and Alcalde, unpubl. data). We used the data of straight carapace length (SCL) and weight gains from six females and seven males to construct a von Bertalanffy growth model, for which we considered hatchling size to be 36 mm SCL and employed a growth equation (GR = -0.1087MNCL + 32.47) that assumed a zero growth rate (GR) when turtles reached an asymptotic size of 298.7 mm SCL. The von Bertalanffy growth model equation for our data is $CL = 298.7 (1 - 0.879*e^{-0.1087t})$, where $t$ = age in years; see Fig. 9). We consider this to be a useful tool for estimating SCL in mm at any age, or vice versa, but age at maturity remains unknown.

\textit{Longevity}. — Slavens and Slavens (1990) reported a specimen that lived for 9 years 6 months in the Fort Worth Zoological Park, Texas, and Bowler (1977) reported longevity of 8 years 10 months for a specimen in the Philadelphia Zoological Garden. Doubtless the potential longevity is considerably longer than these records would suggest. One of us (LA) has a female of unknown origin that is still alive today (2021) at an age of at least 14 years.

\textit{Parasites and Ectocomensal Epibionts}. — \textit{Hydromedusa tectifera} is often colonized by Rhynchobdellida leeches, temnocephalans (both dominant), gastropods of the families Planorbidae and Hydrobiidae, immature midges of the family Chironomidae, and amphipods of the family Hyalellidae (Huckembeck and Quintela 2013). Within the neotropics, \textit{H. tectifera} is the host with the highest known species richness of temnocephalans, having recorded.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure9.png}
\caption{Growth rate (change in carapace length over time) of \textit{Hydromedusa tectifera} in relation to the mean carapace length at the first and last capture (MNCL). Solid points are males; open points are females; plus symbol is outlier. Least squares regression equation (excluding outlier) is $GR = -0.1087MNCL + 32.47 \left( r^2 = 0.26; P = 0.09 \right)$. Von Bertalanffy growth model equation from this regression is $CL = 298.7 (1 - 0.879*e^{-0.1087t})$.}
\end{figure}
three species of Platyhelminthes: Tennocephala cucolai, T. brevicornis, and T. pereirai (Brusa and Damborenea 2000; Soares et al. 2007; Novelli et al. 2009; Volonterio 2010; Martinez Aquino et al. 2014). One of these species (Spiroxus contortus), plus another nematode previously unknown for the species (Heduris orestiae), were found in Argentine populations from Buñirigo stream (Palumbo et al. 2016). Chaviel et al. (2020) reported the nematode Camallanus emydidius parasitizing the intestines of *H. tectifera* from Brazil.

A new species of nematode (*Heduris dratinii*) was recently described parasitizing the esophagus of individuals of *H. tectifera* from Rodriguez stream, Buenos Aires (Palumbo et al. 2019). Subsequently, Palumbo et al. (2021) described the ecological relationships of this nematode and its host turtle in the same stream over the course of a year. They found that the life cycle of *H. dratinii* does not stop even in the coldest months, maintaining continuous transmission between both the intermediate host (amphipod Hyalella sp.) and the final host (turtles), since turtles feed and become infected with parasite larvae even in winter.

**Population Status.** — Few data are available on the population status of *H. tectifera*. Two studies have described the abundance, density, activity pattern, and population structure for the species: in Toro Muerto mountain stream, Córdoba (Lescano et al. 2008) and in Rodríguez lowland stream, Buenos Aires (Semeñiuk et al. 2019). Both studies collected turtles all year but differed in identifying peak activity periods. Semeñiuk et al. (2019) caught most turtles during temperate days in autumn and spring (March–April and September–November, respectively). In contrast, Lescano et al. (2008) noted that turtle activity was concentrated in the warmer months (September–March). The differences between the studies are surely an artifact caused by the collection methodology: Lescano et al. (2008) trapped at night and Semeñiuk et al. (2019) collected during daylight hours. Both studies reported similar sex ratios and abundances; Semeñiuk and colleagues caught 109 turtles in three stream sections (1.8 km total) with a sex ratio slightly favoring males of 1.22:1, and Lescano et al. caught 96 turtles in one stream section (2.0 km) with a sex ratio also slightly favoring males of 1.3:1.

*Hydromedusa tectifera* is able to maintain populations even in urban or polluted water systems (e.g., Melilla stream near the city of Montevideo, Uruguay). In Buenos Aires the species is present together with *P. hilarii* and to a lesser degree with *T. dorbigni*, in moderately to highly polluted waterways such as Buñirigo, El Gato, Rodríguez, and Zapata streams, Argentina (Alcalde et al. 2012; Sánchez et al. 2019). Abundance and density of the species appears to be higher in polluted than in unimpacted streams; the reasons may be that polluted streams favor turtles by the absence of fishermen and of several predators of hatching turtles, such as large carnivorous fishes, together with the altered food supply due to sewage and garbage. However, the presence of high population numbers in polluted water bodies suggests a potentially negative effect on the health of turtles. This situation merits monitoring to understand population dynamics and health impacts.

Results of trapping methodologies and associated biases have been analyzed and calibrated for trot lines without hooks (Semeñiuk et al. 2017) and for double mouth funnel traps with bait (Silveira et al. 2019) used to trap the species for population studies.

**Threats to Survival.** — Rocha e Silva and Kischlat (1992) discussed the conservation problems of the five freshwater turtle species, including *H. tectifera*, found in Rio de Janeiro, Brazil. Many of the threats are derived from the extreme urbanization and high human population density of the state, including industrial pollution, riverine siltation, deforestation, illegal infilling of shallow lagoons for human habitation, and the “cleaning” of swamps. They identified *H. tectifera* as a species impacted by pollution from industrial plants, toxic agricultural chemicals, and untreated sewage, as well as by infilling of lagoons.

The international pet trade in this species seems modest. Although few data are available, a recent paper by Kopecký et al. (2013) reported the species enters legally in the Czech Republic (the main producer, importer and exporter of aquatic ornamental animals in the European Union) in low volumes (< 500 individuals for the period 2008–2012). Similarly, Shiau et al. (2006) reported the presence of the species in pet shops in Taiwan. Exportation data for turtles from the region searched on the platform www.veritrade.com have produced positive matches for Uruguay only, with 23 registers of exports to Canada, China (Hong Kong), Taiwan, Czech Republic, Germany, and Japan totaling 2758 turtles in 2016 (most of them to Hong Kong). These export registers fail to discriminate which
species were exported, but *H. tectifera* is surely included since its presence was reported for pet shops from European and Asian countries (see Kopecký et al. 2013 and Shiau et al. 2016). In addition, Estrades et al. (2007) reported that juveniles and hatchlings of *H. tectifera* (together with those of *P. hilarii* and *T. dorbignii*) are commonly sold in street fairs in different parts of Uruguay.

Few data have been published on predation upon *H. tectifera*, but Martuscelli (1995) observed an adult being consumed by a giant otter (*Pteronura brasiliensis*) in a small river in southern São Paulo, Brazil; he also found the plastron of a subadult nearby which had been gnawed by an otter, and concluded that otters may be important predators of the species in southeastern Brazil. *Hydromedusa* and other long-necked Chelidae have high vulnerability to such predation in that the long neck remains exposed when the head is retracted. More recently, Resende et al. (2012) reported a predation event on adult females in Rio Grande do Sul populations associated with leaving the water to nest. Adult females of the species (and also of *P. hilarii* and *T. dorbignii*) were depredated by *Caracara plancus* hawks targeting and opening soft body parts and eating eggs from within the body cavity.

In many streams in and near La Plata City, Argentina, individuals of the species, and also *P. hilarii*, are frequently caught on fish hooks. These accidental captures impart different grades of impact upon the turtles, from facial lacerations to death. Vehicular road mortality is also common at these sites, particularly during nights with heavy rain during spring and summer months.

**Conservation Measures Taken.** — The global conservation status of *H. tectifera* has not recently been formally assessed and published on the IUCN Red List. However, the species was assessed as Least Concern (LC) by the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (TFTSG) in 1996, and therefore not included on the IUCN Red List at that time. A provisional assessment conducted by the TFTSG in 2011 again re-evaluated *H. tectifera* as Least Concern (TTWG 2017; Rhodin et al. 2018). It is not listed on the CITES appendices or the U.S. Endangered Species Act.

The species is included on several national lists. In Argentina the species is listed as Not Endangered (Prado et al. 2012), in Paraguay it is Least Concern (Motte et al. 2009), and in Uruguay it has been listed as Insufficiently Known (Canaverio et al. 2010) and Not Endangered (Carreira and Maneyro 2015). The Brazilian population of the species has not been assessed.


In Paraguay, the species is found in two national parks (Cacciali et al. 2016): Ybituruzú National Park (Guairá) and San Rafael National Park (Itapúa).

In Uruguay, the species is found in Quebrada de los Cuervos and Arroyo Yerbal Protected Area (Treinta y Tres: Prigioni et al. 2011), in San Miguel National Park (Rocha: iNaturalist), and it seems likely to occur in Esteros de Farrapos e Islas del Río Uruguay National Park (Río Negro) and in other private and municipal protected areas.

**Conservation Measures Proposed.** — Although *H. tectifera* is widespread in four countries of the eastern parts of southern South America, the species is currently poorly known and little studied. We therefore propose certain measures, most of them related to field research, that may inform our understanding of its conservation status and any potential threats to its survival: 1) surveys to better define its geographic distribution, in particular the apparent gap between certain areas (e.g., the Sierra de La Ventana and Córdoba mountains) and the nucleus of its distribution (Rio de La Plata and Uruguay river basins); 2) assess the presence or absence of the species in other protected areas from which it remains unknown; and 3) develop a detailed
study concerning the impact of industrial pollution and urbanization on the development of ulcerative shell disease in this species. In addition, studies of such conservation-relevant life history traits as fecundity, generation time, and survivorship of eggs, hatchlings, and adults should be pursued. Some of these targeted research topics are under current development (see below).

**Captive Hushandry.** — Many articles have been published in the hobbyist literature dealing with the habits, husbandry requirements, and breeding of the species in captivity (e.g., Lüling 1984; Wolff 2002, 2008; Philippen 2007; Fabius 2010, 2016). In general, captive husbandry of this species is not difficult, the range of temperature tolerance is wide, and, unlike its congener *H. maximiliani*, the tolerance for low-quality or even polluted water, in nature, appears to be well-developed. Nevertheless, Nicol (1991) reported that, in captivity, *H. tectifera* is notorious for developing shell infections. This condition commences in the bone beneath a superficially intact scute, and is externally evident only as a slightly discolored or softened area. Opening and debridement of the infected area may reveal encapsulation of diseased tissues, or they may extend into the viscera. Nicol suggested that maintenance of the turtles in very clean water at a pH of 7.0 or lower may control or at least stabilize the condition.

The apparent ability to survive fairly well in polluted waters in nature, but to be highly sensitive to impure water in captivity is paralleled by soft-shelled turtles (Trionychidae). Gurley (2003) discussed the captive maintenance of *H. tectifera* in some detail; he recommended using acidic water (pH 5.0–5.5), utilizing extensive driftwood and numerous aquatic plants. Such decoration would not only provide desirable tannins in the water, but also provide these shy turtles with extensive hiding places.

The preferred diet of newly imported animals leans towards live fish and earthworms, but individual turtles will eventually adjust to pelleted turtle food (chow). Internal parasites are often found, but can be treated with repeated doses of Panacur. The carapace and plastron are very susceptible to shell rot, which can spread fast, but can be cured by the use of warm, clean, filtered, low pH water, or with application of Baytril or Floxin in severe cases. A short hibernation period (45–60 days) is recommended. Rain or sprinkled water is a strong stimulus for courtship and mating.

Nicol (1989) reported a case of twinning in individuals born in captivity and Schmidt et al. (2011) provided plasma values for key ions (sodium, calcium, potassium) useful for monitoring the health of the species in captivity.

**Current Research.** — Several aspects of the biology and ecology of populations of the species in Argentina are under study by a team led by Alcalde: 1) abundance and prevalence of different groups of parasites is being studied by E. Palumbo; 2) the thermal aspects of the species are being studied by Sánchez; 3) the health of the species (body condition index, ulcers and other carapace injuries, blood parameters, sex ratio) in relation to the degree of human impact on its aquatic habitat and the possible use of the species as a bioindicator of water quality is being studied by Sánchez; 4) basking in the field (mode, aggregative behavior, daily and seasonal frequencies, etc.) is under current study by Sánchez and Alcalde; 5) several aspects of the ectoparasites (leeches) and epibionts that live on the carapace of the species (dominant species, seasonal variations and sex-related aspects of dominance) from a set of polluted and unpolluted streams are being studied by Sánchez and Alcalde; and 6) Alcalde is part of a team with Evangelina Viotto, Gerardo Leynaud, and Julieta Sánchez studying the genetics of the species in Argentina.

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