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Iverson, J. B., L. Schneider, and R. C. Vogt.
2017. *Podocnemis sextuberculata*.

***Podocnemis sextuberculata* Cornalia
Six-tubercled River Turtle, Iaçá, Pitiú, or Cupiso**

Podocnemis sextuberculata Cornalia 1849:13.

Type locality: “Fl. Amazonum” [=Amazon River], South America. Holotype (a hatchling): Not located; originally in the Milano Museum (Roger Bour, personal communication). Collected by G. Osculati (Vanzolini 1977b), date unknown (see Remarks). Not examined by authors.

Podocnemis expansa: Gray 1856:61 (in part).

Podocnemis pitiu Silva Coutinho 1868:150.

Type locality: “l’Amazone” [Amazonas, Brazil]. Holotype specimen, collector, and collection date unknown. Not examined by authors.

Bartlettia pitipii Gray 1870:720. Type locality: “Lakes of the Upper Amazons.” Syntypes (Four mentioned by Gray, but only three listed by Boulenger [1889] and in the catalog of the British Museum of Natural History of London [BMNH]): BMNH 1946.1.22.90 (adult in alcohol), 1947.3.5.82 (adult, stuffed), and 1947.3.5.83 (adult, skeleton), collected by Edward Bartlett (date unknown). Not examined by authors.

Emys amazonica: Baur 1893:213 (in part). Result of inappropriate synonymy of *E. amazonica* Spix 1824 (= *Podocnemis expansa*) with *P. sextuberculata* Cornalia and *Bartlettia pitipii* Gray.

Bartlettia pitipiti: Williams 1954:281. *Lapsus*.

Podecnemis sextuberculata: Medem 1960:347. *Lapsus*.

Podocnemys sextuberculosa: Voženílek 1981:85. *Lapsus*.

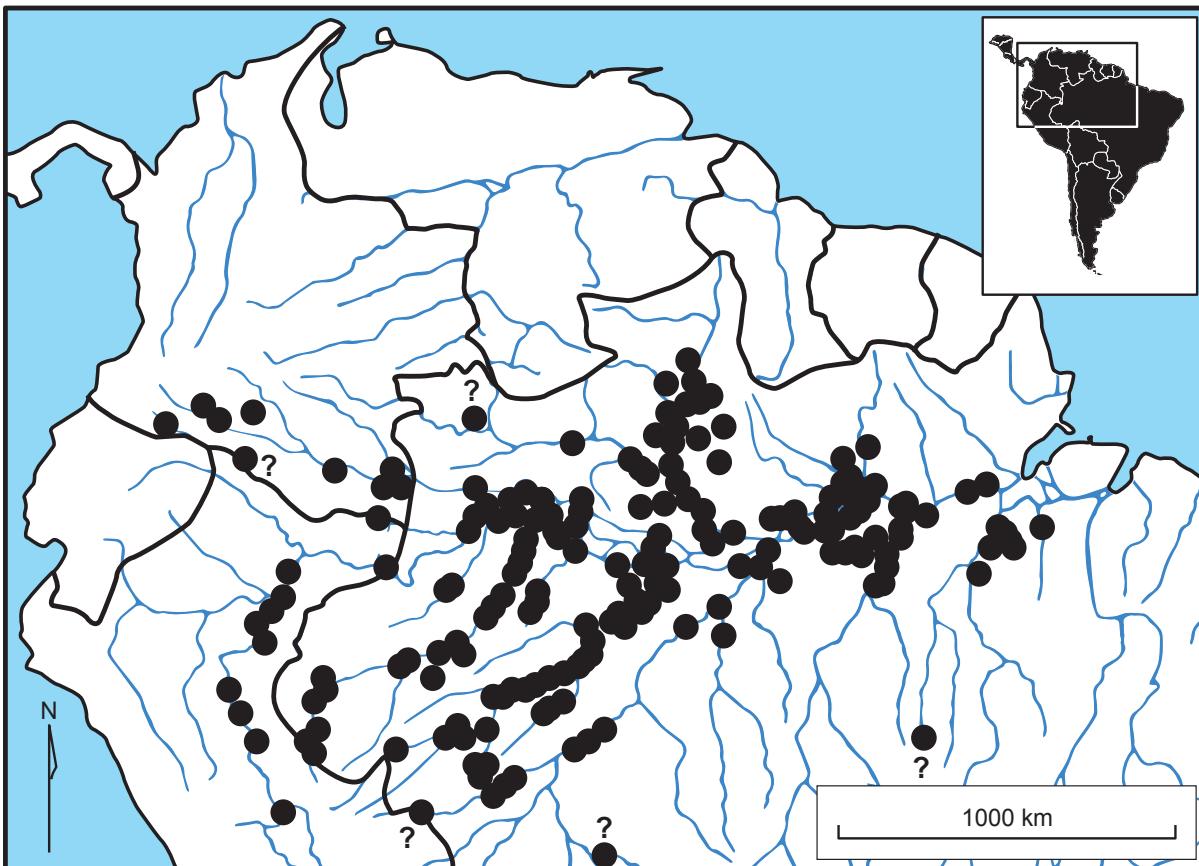
Podocnemis sextuber culata: Chegodayev 2002:82. *Lapsus*.



FIGURE 1 Mature female *Podocnemis sextuberculata* in Parana da Floresta (a tributary of the Rio Branco which is a tributary of the Rio Negro), Roraima, Brazil. Photograph by Richard C. Vogt.

CONTENT. No subspecies are recognized.

DEFINITION. *Podocnemis sextuberculata* is one of the smaller species of *Podocnemis*, reaching a carapace length of only 34 cm (Vogt 2008a, 2008b, 2008c). The domed carapace is elliptical and broader behind the center. The posterior carapacial rim is serrated in juveniles, but only slightly so or smooth in adults; a cervical indentation may be present. A blunt medial keel is present on vertebrals V2 and V3. All vertebrals are broader than long with V1 and V5 the smallest, and V5 posteriorly expanded. Surfaces of the carapacial scutes are usually smooth in adults and show few, if any growth annuli. The carapace is gray to olive brown. The plastron is large, but does not completely cover the carapacial opening; the anterior lobe is rounded in front and the posterior lobe is broader posteriorly. The anal scutes are decidedly tapered and much narrower than the femorals; a shallow medial posterior notch is present. A unique character (which gives this turtle both its scientific and English common names) is the presence of six pairs of prominent tubercles on the plastron of juveniles. These tubercles occur at the base of the bridge on the pectoral and abdominal scutes and at the outer posterior point of the femorals. These protuberances disappear with age, although those on the pectoral scutes may persist into adult-



MAP 1. Distribution of *Podocnemis sextuberculata* derived from Ferrara et al. 2017. A single dot may represent multiple adjacent localities; question marks adjacent to dots indicate unverified localities.



FIGURE 2. Mature adult female *Podocnemis sextuberculata* with spotted head pattern. This unusual pattern only occurs in tributaries of the Rio Branco, Roraima, Brazil. Photograph by Richard C. Vogt.



FIGURE 3. Mature adult female *Podocnemis sextuberculata*. Photograph taken in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil by Rafael Bernhard.



FIGURE 4. Plastron of adult female *Podocnemis sextuberculata* demonstrating persistent protuberances on pectoral scutes. Photograph taken in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil by Rafael Bernhard.

hood. A long intergular separates the gulars. The bridge is not as broad as the width of the plastral posterior lobe. Both plastron and bridge are yellow to gray or brown. The broad head has a protruding snout and notched upper jaw. There is only a single weak ridge on the triturating surface of the maxilla. The premaxillae separate the maxillae and extend to the choanal rim. The incisive foramina lie completely within the premaxillae. There is no vomer. The interparietal scale is elongated and widely separates the parietals, which, although also elongated, do not touch behind the interparietal. Large subocular scales are usually present. A deep groove lies between the orbits, and the tympanum is about as broad as the orbit. One or two chin barbels are present. The head is olive to reddish brown with cream-colored jaws. The neck is dark gray to olive dorsally but lighter colored ventrally; limbs are gray to olive. However, the head coloration in the Rio Branco drainage is different: most females retain the juvenile color pattern of light yellow or light green markings on the head (see **Remarks**). Three large scales occur on the posterior margin of the hind foot. Males have longer, thicker tails than do females.



FIGURE 5. Plastron views of adult females (top row) and adult males (middle and bottom rows). Females have V-shaped notches in their anal scutes, and adult males have larger U-shaped indentations in their anal scutes. The plastral coloration in males and females can range from solid light yellow to cream or mottled brown; the darker colorations often are stains absorbed from the water they live in. Photograph taken in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil by Rafael Bernhard.

DIAGNOSIS. The body size is small relative to other *Podocnemis* (to only 34 cm carapace length; Vogt 2008a, 2008b, 2008c). The species name derives from the presence of three pairs of prominent protuberances on the sides of the plastron, and the axillary pair is often still obvious in adults (Williams 1954). Several characters can be used to distinguish *Podocnemis sextuberculata* from its five congeners: the forehead is grooved, the masseteric scale does not reach the orbit, the interparietal scale usually widely separates the parietal scales, large subocular scales are present, the jugal bone contacts the parietal bone, the vomer is absent, the shell is always smooth, the dorsal surface of marginal six is more than half as wide as long, there are three large scales on each hind foot and two chin barbels are present (Williams 1954).



FIGURE 6. Normal patterned adult female (left) and male *Podocnemis sextuberculata* from Rio Trombetas, Pará, Brazil. Adult males are smaller than adult females. Photograph by Richard C. Vogt.

PHYLOGENETIC RELATIONSHIPS. The relationships among the six species of *Podocnemis* are still uncertain. A tree based on unpublished mitochondrial DNA data was presented by Iverson et al. (2007: *erythrocephala* (*sextuberculata* (*lewyana* (*unifilis* (*expansa*, *vogli*))))), one based on mitochondrial and nuclear DNA sequences was published by Vargas-Ramírez et al. (2008: *expansa* (*vogli* (*sextuberculata* (*unifilis* (*lewyana*, *erythrocephala*))))), and one based on combined morphological and molecular data was published by Cadena et al. (2012a: *expansa* (*vogli* (*sextuberculata* (*erythrocephala* (*lewyana*, *unifilis*

PUBLISHED DESCRIPTIONS. General descriptions were provided by Bonin et al. (1996, 1998, 2006a, 2006b), Carvalho et al. (2002), Castaño Mora (2002), Ceballos et al. (2012), Ernst and Barbour (1989), Hoge (1952), Honegger et al. (1985), King and Burke (1989), Mittermeier (1975, 1978), Neill (1965), Pritchard (1967, 1979), Siebenrock (1902, 1904), Vogt (2008a, 2008b, 2008c), and

Williams (1954). Cervical vertebrae were described by Williams (1950), hatchling anatomy by Malvasio et al. (2002), jaw musculature by Schumacher (1954), neural bone variation by Pritchard (1988), plastral anatomy by Cadena et al. (2012b) and Gaffney et al. (2006), throat morphology by Magalhães et al. (2014) and Vogt et al. (1998), and comparisons with other species by Müller (1935), Siebenrock (1902), and Williams (1954). The karyotype was described by Ayres et al. (1969), Barros et al. (1976), Bull and Legler (1980), Fantin and dos Santos Monjeló (2011), Gunski et al. (2013), Killebrew (1975), Ortiz et al. (2005), Rhodin et al. (1978), and Ventura et al. (2014).

ILLUSTRATIONS. Color photographs were published by Alves et al. (2012), Balensiefer et al. (2007), Bartlett and Bartlett (2003), Bonin et al. (1996, 1998, 2006a, 2006b), Castaño-Mora (2002), Ceballos et al. (2012), Ferrara et al. (2017), Ferri (1999, 2002), Ferronato and Morales (2012), Franklin (2007), Kato (1992), Koshikawa (1996), Lehr (2002), Nascimento et al. (2012), Obst (1986a, 1986b), Obst et al. (1984, 1988), Páez (2013), Pritchard (1979), Rogner (1996), Rueda-Almonacid et al. (2007), Soini and Cóppula (1995), Vetter (2005), Vogt (2008a, 2008b, 2008c), and Zhou (2004). Color illustrations were presented by Bonin et al. (1996, 1998, 2006a, 2006b) and Freiberg (1981). Black-and-white photographs were published by Carillo de Espinoza (1970), Ernst and Barbour (1989), Ferreira (1923), Gaffney et al. (2011), Mittermeier (1975), Neill (1965), Pritchard (1979), and Smith (1979a, 1979b). Black-and-white illustrations were presented by Bonin et al. (1996, 1998, 2006a, 2006b), Boulenger (1889), Cadena (2011), Castaño Mora (2002), Gaffney et al. (2011), Gray (1870), Honegger et al. (1985), King and Burke (1989), Mueller (1998), Siebenrock (1902), Wermuth and Mertens (1961), and Williams (1954).

DISTRIBUTION. *Podocnemis sextuberculata* is known in the Amazon River drain-

age of northern Brazil, southern Colombia and northeastern Peru (Castro 2007; Iverson 1986, 1992; Lehr, 2000; Ramo 1982; The IUCN Conservation Monitoring Centre 1988). Distributional information was published for Colombia by Ceballos-Fonseca (2000), Ceballos et al. (2012), and Medem (1958, 1960, 1969); for Brazil by Da Silva et al. (2016) and Hoogmoed and de Avila-Pires (1990); and for Perú by Carrillo de Espinoza (1970), Carrillo de Espinoza and Icochea (1995), Dixon and Soini (1977, 1986), Ferronato and Morales (2012), Lehr (2002), and Rodriguez and Knell (2004a, 2004b). Extralimital introductions were listed by Iverson and Etchberger (1989), King and Krakauer (1966), and Kraus (2009).

FOSSIL RECORD. No fossils are known; however, the Eocene *Podocnemis olssoni* is similar to living *Podocnemis sextuberculata* (Schmidt 1931).

PERTINENT LITERATURE. General reviews were published by Bartlett (1996), Cantarelli and Herde (1989), Ceballos et al. (2012), David (1994), Ferrara et al. (2017), Freiberg (1981), Köhler (2004); Moll and Moll (2004), Monzel (2016), Rueda-Almonacid et al. (2007), Schmidt (1931) and Vogt (2008a, 2008b, 2008c). Other information is listed by topic: **behavior** (Emmons 1989; Malvasio et al. 2003; Nascimento 2002; Venegas and Gagliardi 2013); **captive longevity records** (Bowler 1977; Obst 1986a, 1986b; Slavens and Slavens 1991, 2000); **captive maintenance** (Fachín-Terán et al. 1992; Lima 2000); **capture methods and tracking technologies** (Barboza et al. 2013a; Guilhon et al. 2011); **checklists and nomenclature** (Artner 2003, 2008; Frank and Ramus 1995; Fritz and Havaš 2007; Fróes 1957; Goeldi 1906; Hutchins et al. 2003; Iverson 1985, 1986, 1992; Lamar 1997; Luederwaldt 1926; Medem 1968; Mertens and Wermuth 1955; Mittermeier and Wilson 1974; Mlynarski and Wermuth 1971; Morales-Betancourt et al. 2015; Nascimento et al. 2012; Rhodin et al. 2008; Siebenrock 1909;

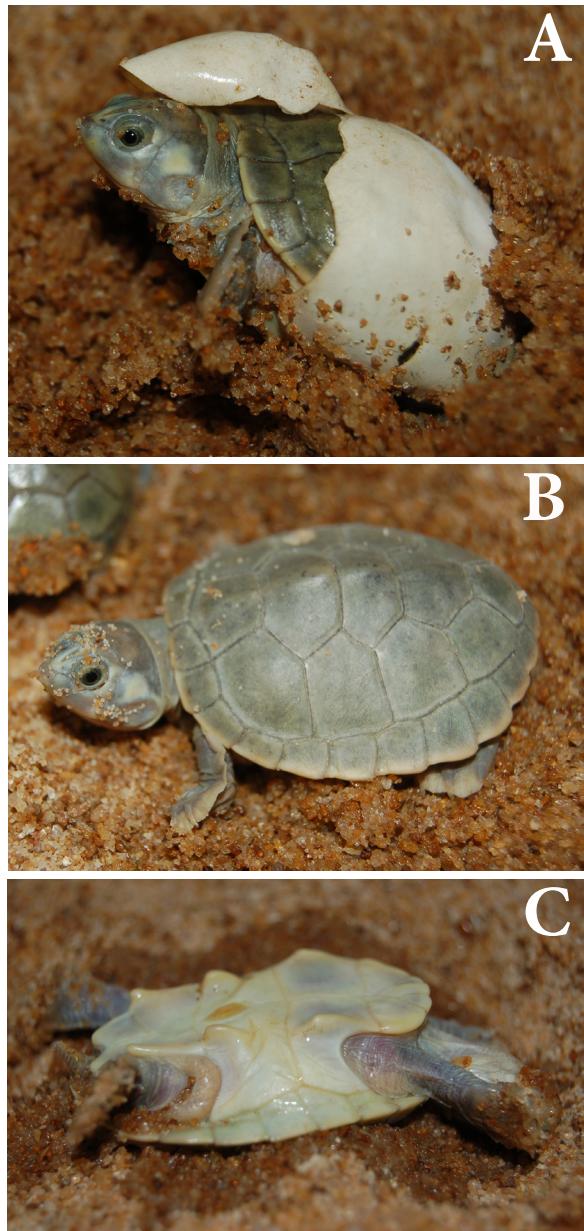


FIGURE 7. Hatchlings of *Podocnemis sextuberculata* from Rio Trombetas, Para, Brazil. A. Emerging hatchling. B. Hatchlings. C. Plastron of hatchling displaying six distinct tubercles, giving this species its name. Photograph by Richard C. Vogt.

Souza and de Barros Molina 2007; Strauch 1890; Turtle Taxonomy Working Group 2014, 2017; Voženílek 1981; Welch 1994; Wermuth and Mertens 1961, 1977); **conservation** (Alfinito 1978; Andrade et al. 2001; Barboza et al. 2013b; Camillo et al. 2012; Cantarelli 1994; Cantarelli and Herde 1989; Cantarelli et al. 2014; Castaño-Mora 1997; Da Silva

and Fachín Terán 2015; Da Silva et al. 2011; Eisemberg et al. 2017b; Fachín-Terán et al. 2003; Fagundes et al. 2016; Forero-Medina et al. 2014; Gomes Lustosa et al. 2016; Groombridge 1982; IUCN/SSC Tortoise and Freshwater Turtle Specialist Group 1989; Johns 1987; May et al. 2011; Medem 1958; Miorando et al. 2013; Nöllert 1992; Petzold 1976; Pezzuti et al. 2010b; Raeder 2003; Schneider et al. 2011b; Soini 1995b, 1995c, 1997, 1999; Soini and Cóppula 1995; Soini and Correa 1995; Vásquez and Tovar 2007; Venegas and Gagliardi-Urrutia 2013a, 2013b; Vinke and Vinke 2009; Vogt 2008a, 2008b, 2008c; Vogt et al. 2017); **density/biomass** (Vogt and Villarreal-Benitez 1997); **developmental anomalies** (Pereira et al. 2014; Perrone et al. 2016); **diet** (Da Cunha 2013; De Almeida et al. 1986; Eisemberg et al. 2017a; Fachín-Terán and Vogt 2014; Fachín-Terán et al. 1995); **effects of dams** (Alho 2011); **genetic and molecular aspects** (Corrêa 1978; Oliveira et al. 2011; Silva et al. 2011; Viana et al. *in press*); **habitat** (Da Cunha et al. 2014); **hematology** (Oliveira et al. 2011); **historical collections** (Monzel 2016); **human attitudes** (Alho et al. 2015; Alves et al. 2012; Pezzuti et al. 2010a); **human use for food** (Alcântara et al. 2013; Fachín-Terán et al. 2004; Fachín Terán et al. 1996, 2000a, 2000b; Hernández and Espín 2003; Kemenes and Pezzuti 2007; Klemens 2000; Klemens and Thorbjarnarson 1995; Lehr 2002; Lemos Lopes et al. 2014; Lopes et al. 2012; Mittermeier 1978; Morales-Betancourt et al. 2015; Pantoja-Lima et al. 2014; Santos 1942, 1955, 1981; Thorbjarnarson et al. 2000); **mercury and other trace element bioaccumulation** (Burger et al. 2010; Schneider 2007; Schneider et al. 2010, 2011a); **morphogenesis** (Fabrezi et al. 2009); **movements** (Perrone et al. 2014); **parasites** (Pineda-Catalan et al. 2013; Soares et al. 2014); **physiology** (Duncan and Marcon 2009; Frair et al. 1978); **predation** (Bernhard and Vogt 2007; Da Silva and Best 1982; Maffei and da Silveira 2013; Soini and Cóppula 1995); **reproduction** (Alfinito 1978; Bermudez-Romero et al. 2015;

Bernhard 2001; Dixon and Soini 1977, 1986; Erickson et al. 2015; Fachín-Terán et al. 2006; Ferrara et al. 2014; Ferronato and Morales 2012; Foote 1978; Freda et al. 2016; Haller 2002; Haller and Rodrigues 2006; Ihering 1904; Malvásio 2001; Malvasio et al. 2002; Medem 1960, 1969, 1976; Mittermeier 1978; Orenstein 2001a, 2001b, 2012; Pezzuti and Vogt 1999; Pezzuti et al. 1999, 2000; Portelinha 2010; Santos 2006; Soini 1995a, 1995b, 1996; Soini and Cóppula 1995; Soini and de Soini 1995a, 1995b; Vanzolini 1977a, 2001; Vanzolini and Gomes 1979); **taxonomy and systematics** (Baur 1893; Cadena et al. 2012a; Honegger et al. 1985; King and Burke 1989; Vargas Ramirez et al. 2008; Viana et al. 2007; Wood 1979, 1983; Wood and Diaz de Gamero 1971); **vocalization** (Ferrara et al. 2014).

REMARKS. This species was first described on page 13 of Cornalia (1849), but the description was reprinted on page 312 in the Appendix of Osculati (1850; see also Osculati 1854). Vanzolini (1977b) commented on the locality of the type specimen. Because the population in the Rio Branco drainage is isolated from all other populations of this species by about 1800 km, the genetics of this population are being currently studied (by Richard C. Vogt) to determine whether specific status is warranted.

ETYMOLOGY. The specific name is from the Latin for six tubercles (*sex* = six; *tuberculum* = a knob or hump), and refers to the three tubercles on each side of the plastron, which are clearly visible in juveniles but disappear with age.

ADDITIONAL VERNACULAR NAMES. The local Brazilian vernacular name Iaçá (Mittermeier et al. 1980) is sometimes spelled Aiaça (Mittermeier and Wilson 1974), Aiaçá (Mittermeier et al. 1980), Aiucá (Mittermeier et al. 1980), Ayacá (Mittermeier et al. 1980), Ayassá (Medem 1968; Mittermeier et al. 1980) or in Colombia, Ayasá (Medem 1960).

In Brazil this species is also known as Pitiú (Baillie and Groombridge 1996; Mittermeier and Wilson 1974; Mittermeier et al. 1980; Sokolov 1988), Jurara-pitiú (Vogt 2008a, 2008b, 2008c), Juara-pitiú, Cambeua, Cambéua (Mittermeier et al. 1980) or Cambéua (Vogt 2008a, 2008b, 2008c). In Colombia and Perú this species is known as Cupiso (Baillie and Groombridge 1996; Carrillo de Espinoza 1990; Medem 1968; Morales-Betancourt et al. 2015) or Teparo (Vogt 2008a, 2008b, 2008c). In French this species is known as Podocnémide tuberculée and Tortue de l'Amazone à six tubercules (Wrobel 2004). In German this species is known as Höcker-Schienenschildkröte (Artner 2003; Sokolov 1988; Wrobel 2004). This species has also been referred to as the six-tuberclied greaved turtle (Breen 1974) and six tuberclied Amazon River Turtle (Sokolov 1988; Wrobel 2004). We consider the use of yellow-headed side-necked turtle (Campbell 1974), (six tuberclied) Amazonian side-neck (Sokolov 1988), and Amazon River Turtle (Lamar 1997) as erroneous.

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