Catalogue of American Amphibians and Reptiles.

Ernst, C.H. and T.E.J. Leuteritz. 1999. *Geochelone carbonaria.*

Geochelone carbonaria (Spix)
Red-footed Tortoise

Testudo carbonaria Spix 1824:22. Type locality, "Habitat, sub cognomine 'Capitary' (?) ad flumen Amazonum." Vanzolini (1994) suggested that "the stretch of the Rio Amazonas between the mouth of the Negro, at 03°08'S, 59°55'W, and the mouth of the Furo do Tajapuru, at 01°02'S, 51°2'W" be considered Spix's "flumen Amazonum" until a more specific restriction of the type locality is justified. Holotype, not designated; may have originally been in the collection of the Zoologisches Sammlung des Bayerischen Staates, München, but now lost (Hoogmoed and Gruber 1983). Hoogmoed and Gruber (1983) designated the specimen illustrated in plate XVI in Spix (1824) as a lectotype.

Testudo boiei Wagler 1833:plate XIII. Type locality, unknown. Holotype, not designated; may have originally been in the collection of the Zoologisches Sammlung des Bayerischen Staates, München, but now lost (Hoogmoed and Gruber 1983). Hoogmoed and Gruber (1983) designated the specimen illustrated in plate XIII in Wagler (1830) as a lectotype.

Geochelone (*Chelonoidis*) *boiei*: Fitzinger 1835:122.

Geochelone carbonaria: Williams 1960:10. First use of present combination.

Geochelone (*Chelonoidis*) *carbonaria*: Pritchard 1967a:269.

Geochelone (*Chelonoides*) *carbonaria*: Auffenberg 1971:110.

Testudo (*Chelonoidis*) *carbonaria*: Wermuth and Mertens 1977: 78.

Testudo (*Geochelone*) *carbonaria*: Peaker 1978:421.

Chelonoidis carbonaria: Bour 1980:546.

FIGURE 1. *Geochelone carbonaria*. Photograph by Roger W. Barbour.

FIGURE 2. *Geochelone carbonaria*, plastron. Photograph by Roger W. Barbour.

• **CONTENT.** *Geochelone carbonaria* is a monotypic species. Although no subspecies are recognized, Pritchard (1975) and Pritchard and Trebbau (1984) suggested that pattern and size differences exist among the various populations.

• **DEFINITION.** This tortoise has an elongated carapace (to 55-60 cm, Chebez et al. 1994) with a shallow cervical indentation, the lateral borders distinctly concave when viewed dorsally, and a smooth posterior rim. No cervical scute is present. Vertebral scutes are broader than long, and the 1st and 5th are laterally expanded. Well-defined growth annuli surround the raised vertebral and pleural areolae. Eleven marginal scutes are usually present on each side, and the single supracaudal is undivided and downturned. The carapace is black, with the vertebral and pleural areolae yellow to reddish orange, and a light spot of the same color occurs at the base of each marginal. The plastron is well developed. Its upturned forelobe tapers anteriorly and is about as long and broad as the hindlobe, which bears an anal notch. The formula for plastral scute length is: abdominal > femoral ≥ humeral > gular > anal >< pectoral; the paired gulars are thickened, but do not extend much beyond the carapacial rim, if at all. The dorsal surface of each gular scute is usually not subdivided. The bridge is long with a moderate axillary and a moderate to large inguinal, with the latter in broad contact with the femoral scute. The plastron is yellowish brown with some dark pigment along the mid- and transverse seams. The head is moderate in size with a short snout and a slightly hooked upper jaw. Its prefrontal scale is short, divided longitudinally, and followed by a large undivided frontal scale. Other head scales are small, and are yellow, red, or orange; the jaws are dark. The anterior surface of each forelimb is covered with large, red, and slightly or non-overlapping scales. No enlarged tubercles occur on the thighs, and the tail lacks a large terminal scale.

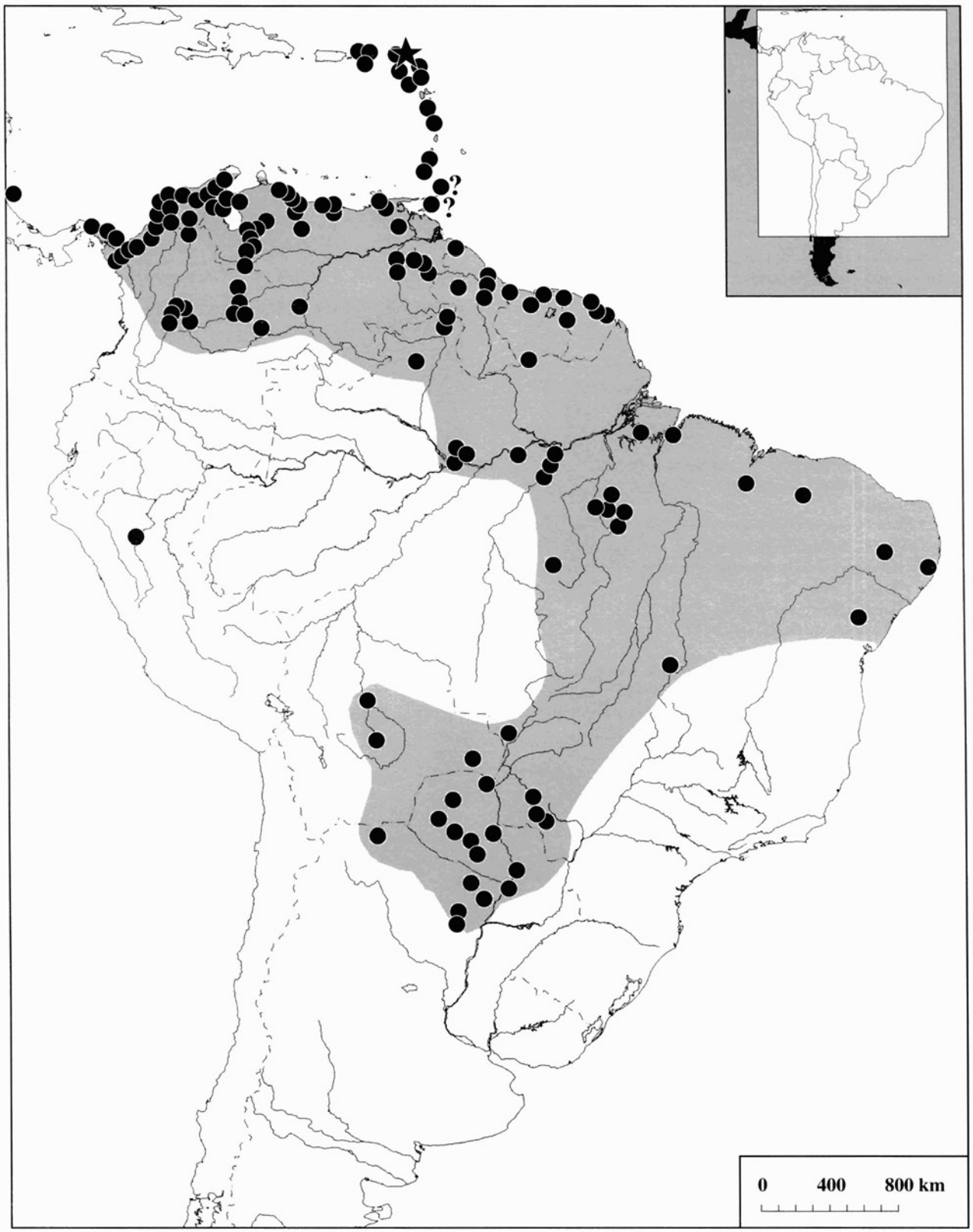
Males are larger (to 60 cm) than females (to approximately 40 cm), but females usually are of a greater mass. Males have concave plastra, lower flattened carapaces with deep lateral concavities, and longer, thicker tails. Females have more domed, shallow, laterally concave carapaces, flat plastra, and shorter tails.

Geochelone carbonaria has 52 chromosomes; 28 are macrochromosomes (18 metacentric or submetacentric, 10 telocentric or subtelocentric) and 24 are microchromosomes (Bickham and Baker 1976a, 1976b; Stock 1972).

• **DESCRIPTIONS.** General descriptions are in Auffenberg (1971), Bertonatti (1997), Castaño-Mora and Lugo-Rugeles (1981), Chebez et al. (1994), da Cunha et al. (1985), Ernst and Barbour (1989), Freiberg (1971), Hagan (1968), Medem (1962a, 1962b), Moreira (1991), Müller (1987), Murphy (1997), Paull (1983, 1997), Pritchard (1964, 1967a, 1975, 1979a), Pritchard and Trebbau (1984), Richard (1990), Schwartz and Henderson (1991), Vokins (1977), Walker (1989), and Williams (1960). Juveniles are described by Legler (1963). Moskovits (1988) described sexual dimorphism, and Zug (1966) the penis.

• **ILLUSTRATIONS. Color illustrations of adults** are in Alderton (1988), Bertonatti (1997), Carrillo de Espinoza and Lamas (1985), Cei (1993), Chebez et al. (1994), Ernst and

Barbour (1989), Houtman and de la Fosse (1989), Métrailler and Le Gratiet (1996), Müller (1987), Murphy (1997), Paull (1997), Powell et al. (1996), Pritchard and Trebbau (1984), and Vinke and Vinke (1998). **Black and white illustrations of adults** are in Anonymous (1969), Borchmann (1979), Chebez et al. (1994), Crumly (1989), Dowling (1961), Freiberg (1967, 1971, 1972, 1981), Gonzalez-Gonzalez (1993), Houtman and de la Fosse (1989), MacLean (1982), Paull (1983, 1997), Pritchard (1980), Pritchard and Trebbau (1984), Schall (1978), Schipperijn (1992), Sowerby and Lear (1872), Spix (1824), Sura



MAP. Distribution of *Geochelone carbonaria*. Dots mark selected localities and the star indicates a fossil locality. The type locality is too imprecise to plot.

(1981), Tonge (1988), and Walker (1989). The **shell** is illustrated in Carrillo de Espinoza and Lamas (1985), Hagan (1968), Legler (1963), Métrailler and Le Gratiet (1996), Pritchard and Trebbau (1984), Sowerby and Lear (1872), Wermuth and Mertens (1961), and Williams (1960). **Head scalation** is presented in color by Cei (1993) and Pritchard and Trebbau (1984), and in black and white by Hagan (1968), Legler (1963), Métrailler and Le Gratiet (1996), and Williams (1960). The **adult skull** is illustrated in Pritchard and Trebbau (1984), and a **juvenile skull** with parietal foramen is pictured in Zangerl (1957). **Hatchlings or juveniles** are illustrated in color by Métrailler and Le Gratiet (1996) and Vinke and Vinke (1998), and in black and white by Freiberg (1971, 1972), Houtman and de la Fosse (1989), Schipperijn (1992), Tonge (1988), and Williams (1960). The **karyotype** is illustrated in Bickham and Baker (1976a, 1976b), and the **electrophoretic pattern of serum proteins** by Newcomer and Crenshaw (1967). Other illustrations are as follows: **habitat** (Métrailler and Le Gratiet 1996, Vinke and Vinke 1998), **eggs** (Frye 1975), **bladder** (Strum and Danon 1975), **erythrocytes** (Coiro et al. 1978, 1979), **growth plots or curves** (Medem et al. 1979, Tonge 1988, Vokins 1977), **male vocalizations** (Campbell and Evans 1967, 1972), **sleep brain waves** (Hartse and Rechtschaffen 1982), **cochlear nuclei** (Miller and Kasahara 1979), **hearing sensitivity curve** (Wever 1978), **tongue** (Winokur 1988), **penis** (Zug 1966), **copulation** (Métrailler and Le Gratiet 1996, Murphy 1997, Vinke and Vinke 1998), and **abnormalities** (Frye 1975, Frye and Carney 1975, Tomson et al. 1976).

• **DISTRIBUTION.** *Geochelone carbonaria* occurs in southeastern Panamá and west of the Andes in the Chocó of Colombia, but its main range is east of the Andes in eastern Colombia, Venezuela, the Guianas, eastern Brazil possibly south to Rio de Janeiro and west to eastern Bolivia, Paraguay, and northwestern Argentina (see Bertonatti 1997, Chebez et al. 1994, and Scott and Lovett 1975). An isolated population occurs at Tarapoto, Province San Martin, Perú (Carrillo de Espinoza and Lamas 1985, Carrillo de Espinoza and Icochea 1995). The second Peruvian locality for *G. carbonaria* mentioned by Carrillo de Espinoza and Lamas (1985), Parque Las Leyendas, is a zoo in Lima City (Javier Icochea, pers. comm.), and not a legitimate distributional record. This tortoise may occur naturally on Trinidad, and has been introduced on several Caribbean Islands, including St. Croix in the Virgin Islands (Censky 1988), and on Reunion Island in the Indian Ocean (Gonzalez-Gonzalez 1993). The recent discovery of a Pleistocene *G. carbonaria* on Anguilla of the northern Lesser Antilles (Lazell 1993) may indicate a greater past distribution. Reports on distribution are in Barbour (1934), Bertonatti (1997), Carrillo de Espinoza and Iocochea (1995), Carrillo de Espinosa and Lamas (1985), Censky (1988), Chebez et al. (1994), Fretey (1977), Gonzalez-Gonzalez (1993), Grant and DeSola (1934), Iverson (1986, 1992), Legler (1963), Medem (1962a, b, 1968), Moreira (1989), Pritchard (1975), Pritchard and Trebbau (1984), Richard et al. (1990), Richard and de la Fuente (1992), Richard and Nakhle (1989), Schwartz and Henderson (1991), Schwartz and Thomas (1975), Scott and Lovett 1975, Strauch (1865), Tamsitt and Valdivieso (1963), Valdivieso and Tamsitt (1965), Vanzolini (1994), Villa, 1994; Walker (1987, 1989), and Williams (1960). Distribution maps are presented in Bertonatti (1997), Cei (1993), Iverson (1986, 1992), Métrailler and Le Gratiet (1996), Pacheco and Aparicio (1996), Paull (1983, 1997), Pritchard (1975), Pritchard and Trebbau (1984), Schwartz and Henderson (1991), Vanzolini (1994), and Walker (1987, 1989).

• **FOSSIL RECORD.** Lazell (1993) reported a Pleistocene fossil from Anguilla.

• **PERTINANT LITERATURE.** Following are selected papers concerning *Geochelone carbonaria* (see Comments). **General accounts** are in Alderton (1988), Bertonatti (1997), Borchmann (1979), Cei (1993), Chebez et al. (1994), Ernst and Barbour (1989), Freiberg (1971, 1972, 1981), Fretey (1977), Groombridge (1982), Lazell (1989, 1991), Maclean (1982), Medem (1962a, b), Métrailler and Le Gratiet (1996), Müller (1987), Murphy (1997), Nietzke (1974), Paull (1983, 1997), Pacheco and Aparicio (1996), Pritchard (1967a, 1979a), Pritchard and Trebbau (1984), Schall (1978), Schwartz and Henderson (1991), Underwood (1962), Vokins (1981), and Walker (1989). Selected papers covering other topics are as follows: **evolution and systematics** (Auffenberg 1971; Bour 1980, 1985; Castaño-Mora and Lugo-Rugeles 1981; Coto Rojas and Acuña Mesén 1986; Crumly 1982a, 1989; David 1994; Hoogmoed and Gruber 1983; Marlow and Patton 1981; Newcomer and Crenshaw 1967; Sullivan and Riggs 1967; Wermuth and Mertens 1961, 1977; Williams 1960; Yin et al. 1989; Zug 1966), **karyotype** (Bickham and Baker 1976a, b; Dowler and Bickham 1982; Sampaio et al. 1971; Stock 1972), **zoogeography** (Hedges 1996, Murphy 1996, Pritchard 1979b, Pritchard and Trebbau 1984), **parietal foramen** (Crumly 1982b, Zangerl 1957), **brain activity** (Hartse and Rechtschaffen 1974, 1982), **sleep** (Flanigan 1974, Hartse and Rechtschaffen 1982), **anesthesia** (Hartse and Rechtschaffen 1974), **ear and hearing** (Miller and Kasahara 1979, Wever 1978), **blood** (Barretto et al. 1985; Bordin et al. 1997; Coiro et al. 1978, 1979; Newcomer and Crenshaw 1967; Sullivan and Riggs 1967; Torsoni and Ogo 1995; Yin et al. 1989), **heart rate** (Rummler and Covian 1983), **orbital gland secretions** (Peaker 1978), **buccopharyngeal mucosa** (Winokur 1988), **liver** (de Brito-Gitirana 1989, de Brito-Gitirana and Storch 1988), **rostral pores** (Winokur and Legler 1974), **mental glands** (Winokur and Legler 1975), **excretory system** (Dahon et al. 1974, Peaker 1978, Rummler and Rummler 1994, Strum and Danon 1975), **penis** (Zug 1966), **shell abnormalities** (Vieira de Andrade and Shinya-Abe 1993), **metabolism** (Jackson et al. 1976; Santos-Pinto et al. 1981, 1985), **body temperature** (Bartholmew 1982; de Brito-Gitirana and Storch 1988; Santos-Pinto et al. 1981, 1985; Weathers and White 1971), **locomotion** (Walker 1979), **social behavior** (Auffenberg 1965, 1977; Carpenter and Ferguson 1977; Guix et al. 1989; Pough et al. 1998), **vocalizations** (Auffenberg 1965; Campbell and Evans 1967, 1972), **sexual maturity** (Legler 1963, Moll and Tucker 1975), **courtship and mating** (Carpenter and Ferguson 1977, Davis 1979, Pough et al. 1998, Vinke and Vinke 1998, Vokins 1977), **nesting** (Davis 1979, Medem et al. 1979, Tonge 1988, Vokins 1977), **eggs** (Anonymous 1994; Castano-Mora 1985; Christensen 1991; Davis 1979; Ewert 1979; Frye 1975; Guix et al. 1989; Iverson et al. 1993; Legler 1963; Marcellini and Davis 1982; Medem 1962a, b; Medem et al. 1979; Schipperijn 1992; Tonge 1988; Vokins 1977), **incubation** (Cei 1993, Guix et al. 1989, Houtman and de la Fosse 1989), **development** (Guix et al. 1989), **hatchlings** (Davis 1979, Medem et al. 1979, Vokins 1977), **caesarean delivery** (Frye and Schuchman 1974), **growth and size** (Castano-Moro 1985, Medem et al. 1979, Moll and Tucker 1975, Pritchard 1980, Sura 1981, Tonge 1988, Vaillant 1905, Vokins 1977), **habitat** (Auffenberg and Iverson 1979, Legler 1963, Obst 1986, Vinke and Vinke 1998), **populations** (Gorzula 1989, Moreira 1991, Moskovits 1988), **sex ratio** (Auffenberg and Iverson 1979, Moskovits 1988), **diet and feeding behavior** (Bjorndal 1989, Furrer 1969, Ghilardi and Alho 1990 [1991], Highfield 1992, Moskovits and Bjorndal 1990, Moskovits and Kiester 1987, Rummler and Covian 1982, Schlegel 1968), **predation** (Gorzula 1989), **anomalies** (Frye 1975, Frye and Carney 1975, Tomson et al. 1976), **parasites and disease** (Barten 1982; Ernst and Nichols 1974; Frank and Bosch 1972; Jacobson et al. 1981, 1983; Murphy and Collins

1980, 1983; Oddy 1986; Rideout et al. 1987; Singh et al. 1996; Thorpe-Dixon 1982; Weishaar 1988; Zwart and Truyens 1975), **husbandry** (Davis 1979; Highfield 1992; Houtman and de la Fosse 1989; Marcellini and Davis 1982; Müller 1987; Müller 1971; Murphy and Collins 1983; Netten and Zuurmond 1985; Schlegel 1968; Sims 1991a, b; Vinke and Vinke 1998; Vokins 1977), and **common and vernacular names** (Chebez et al. 1994, Froes 1957, Iverson 1985, Mittermeier et al. 1980, Pritchard 1967b, Richard et al. 1990).

• **ETYMOLOGY.** The species name *carbonaria* derives from the Latin, *carbonis*, meaning charcoal or coal, and refers to the dark ground-color of the carapace.

• **COMMENTS.** *Geochelone carbonaria* (Spix 1824) was generally placed in the synonomy of *G. denticulata* (Linnaeus 1766) until Williams (1960) demonstrated that the two were different species.

The name *denticulata* in literature prior to 1960 often represents a composite of the two taxa making it difficult to determine which species is (are) involved. The same is true of the names *Testudo tabulata* Schoepff 1793 and *T. tessellata* Schneider 1792.

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