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A REVISION OF THE NEOTROPICAL TURTLE GENUS *CALLOPSIS* (TESTUDINES: EMYDIDAE: BATAGURINAE)

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ABSTRACT: The turtle genus *Callopsis* Gray occurs from northern Mexico southward to northern South America, and consists of four monotypic species (*C. annulata*, *C. areolata*, *C. funerea*, and *C. nasuta*, which is elevated from subspecific rank) and three polytypic species (*C. pulcherrima*, *C. punctularia*, and *C. rubida*). The subspecies of *C. pulcherrima* are *C. p. pulcherrima*, *C. p. incisa*, *C. p. manni*, and a new taxon, *C. p. rogerbarbouri*. The subspecies of *C. punctularia* are *C. p. punctularia*, *C. p. diademata*, and *C. p. melanosterna*. *Callopsis rubida* has two subspecies: *C. r. rubida* and *C. r. perixantha*. A key for identification, a description, and the geographical range are presented for all species and subspecies.

The genus includes three groups based on shell morphology and color, and on figure patterns of the head, carapace, plastron, and bridge: (1) the *pulcherrima-rubida* group of terrestrial turtles; (2) the *punctularia* group of aquatic and terrestrial species (including *C. annulata*, *C. funerea* and *C. nasuta*); and (3) *C. areolata*, of uncertain relationships. The similarities and differences within each group are discussed, and a hypothesis on the radiation within the genus is presented.

The form *Rhinoclemmys lunata* Gray, 1873, is synonymous with *Rhinoclemys bellii* Gray, 1863, and both are only head pattern variants of *Testudo punctularia* Daudin, 1802 [= *Callopsis p. punctularia*].

THE Neotropical *Callopsis* were formerly assigned to the genus *Geoemyda* Gray along with several Asiatic species. In 1964, McDowell separated the New and Old World species on the basis of cranial morphology and other skeletal features and placed the Neotropical species in the genus *Rhinoclemys* Gray. Further, he showed them to be members of the subfamily Batagurinae, a predominantly Old World group. Later Smith et al. (1976) interpreted *Rhinoclemys* Gray and *Geoclemmys* Gray as erroneous spellings of *Rhinoclemmys* Fitzinger and *Geoclemys* Gray, respectively, and therefore unavailable for these American turtles. They reassigned the Neotropical turtles to the only available remaining name, *Callopsis* Gray.

Aside from the confusion at the generic and subfamilial level, McDowell (1964) noted that the precise number of species remained to be determined, and recognized *C. annulata*, *C. areolata*, *C. funerea*, *C. pulcherrima*, *C. punctularia*, and *C. rubida*, but did not list subspecies. Smith et al. (1976) also recognized only these species, and listed the following subspecies: *C. pulcherrima pulcherrima*, *C. p. incisa*, and *C. p. manni*; *C. punctularia punctularia*, *C. p. diademata*, *C. p. lunata*, *C. p. melanosterna*, and *C. p. nasuta*; and *C. rubida rubida* and *C. r. perixantha*.

In 1973, I began a systematic review of *Callopsis* with the hope of determining the status of such questionable forms as *C. punctularia lunata*, *C. p. diademata*, and

C. p. nasuta. The results of these studies are reported here. Karyotyping and serum electrophoretic studies are currently being carried out by other investigators. Shell scute designations are taken from Zangerl (1969).

Methods and Materials

Straight-line measurements of each specimen were taken with either dial calipers (accurate to .01 mm) or metal dividers (accurate to 1 mm) of the greatest carapace length, carapace width and depth at the level of the seam between vertebrals 2 and 3, marginal width (the difference between the carapacial width and the width across the pleurals taken between the points of juncture of the marginals and pleurals at the level of the seam between vertebrals 2 and 33), greatest plastron length, greatest width of both plastral lobes, greatest bridge width, greatest width and length of vertebrals 1 and 2 and pleural 2, and the medial seam length and greatest width of all plastral scutes. Careful notes and drawings were made of head, neck, limb, carapacial, plastral, and bridge patterns. Colors were recorded from living turtles and color transparencies. Shell proportions are expressed as ratios of one measurement to another. Twelve ratios proved useful for differentiating adults of the several species (abbreviations used in the text are given in parentheses): width/length of first vertebral (W/L 1st V), width/length of second vertebral (W/L 2nd V), width/length of second pleural (W/L 2nd Pl), marginal width/carapacial width (MW/CW), carapacial width/carapacial length (CW/CL), carapacial depth/carapacial length (D/CL), plastral length/carapacial length (PL/CL), bridge length/plastral length (B/PL), gular width/gular length (GW/GL), intergular seam length/interhumeral seam length (IGL/IHL), interfemoral seam length/interanal seam length (IFL/IAL), and anal width/anal length (AW/AL). The number of rows of large scales at the lateral edge of the antibrachium between the claw of digit V and the first horizontal skin fold proximal to the elbow (presented in text as foreleg scale rows) was recorded.

Student's *t*-test was used to determine if significant differences existed between the means of ratios and mensural and meristic characters of the different taxa.

Specimens from the following collections were examined (abbreviations used in the text are given in parentheses): Anders G. J. Rhodin personal collection (AGJR); American Museum of Natural History (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); British Museum of Natural History (BMNH); Bryce C. Brown collection, Strecker Museum, Baylor University (BCB); California Academy of Sciences (CAS); Carl H. Ernst personal collection (CHE); Carnegie Museum (CM); Cornell University (CU); Field Museum of Natural History (FMNH); Illinois Natural History Survey (INHS); Los Angeles County Museum (LACM); Michigan State University Museum (MSU); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum National D'Histoire Naturelle, Paris (MHNP); Naturhistorisches Museum Wien, Vienna (NMW); Peter C. H. Pritchard personal collection (PCHP); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Russell A. Mittermeier personal collection (RAM); Senckenberg Museum, Frankfurt (SMF); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); Texas Technological University Museum (TTM); Tulane University Museum (TU); University of Florida, Florida State Museum (UF/FSM); University of Illinois Natural History Museum (UINHM); University of Kansas Museum of Natural History (KU); University of Michigan Museum of Zoology (UMMZ); University of Southwestern Louisiana (USL); United States National Museum of Natural History, Smithsonian Institution (USNM).

A statement of geographical range is

given for each taxon, but maps are not presented since these will be included in accounts being prepared for the *Catalogue of American Amphibians and Reptiles*. Also given is a list of specimens examined of each taxon; exact locality data for these are available[1].

Systematic Account

Callopsis Gray

Callopsis Gray, Ann. Mag. Nat. Hist. (London), Ser. 3, 12: 183 (1863). Type species, *Rhinoclemys annulata* [= *Geoclemmys annulata* Gray, 1860].

Rhinoclemys Gray, Ann. Mag. Nat. Hist. (London), Ser. 3, 12: 183 (1863).

Chelopus, Cope, J. Acad. Nat. Sci. Philadelphia 2: 186 (1865).

Rhinoclemmys Gray, Ann. Mag. Nat. Hist. (London), Ser. 4, 11: 144 (1873).

Nicoria Boulenger, Cat. Chel., Rhynch., Croc. British Mus., London, p. 119 (1889).

Geoemyda Siebenrock, Zool. Jahrb. Jena, Suppl. 10, p. 494 (1909).

(See Smith et al. 1976, for a discussion of the validity of *Callopsis*, *Rhinoclemys*, and *Rhinoclemmys*.)

Diagnosis.—Aquatic and terrestrial Neotropical batagurine turtles with squamosal loosely attached and barely in contact with jugal, but touching postorbital; ethmoid fissures broadly triangular or oval; anterior edge of inferior process of parietal not flexed outward, separated from jugal but touching palatine; ventral end of jugal broad; plastron large, hingeless, and attached to carapace by well-ossified buttresses; hexagonal neurals short-sided posteriorly; well-developed carapace with vertebral keel; cloacal bursae present; head and limb patterns vividly colored.

Geographic distribution.—Southern Sonora (and possibly southern Chihuahua) in western Mexico, and southern Veracruz, Tabasco, eastern Chiapas, and the Yucatan Penninsula in eastern Mexico, southward through Mexico and Central America to northern Ecuador in the west and to Trinidad, the Guianas, and northeastern Brazil in the east.

Key to Adults of the Species and Subspecies of *Callopsis*

1a Interdigital webbing heavy 2
b Little or no interdigital webbing 6
2a Dorsal head stripes extend from nape to level of orbits or less; no light spots present at occipital region 3
b Dorsal head stripes from nape to beyond orbits or broken at orbits with a spot anteriorly; light spots present at occipital region 4
3a Snout strongly pointed; shell distinctly depressed; chin and lower jaw with dark bars ..... *Callopsis nasuta*
b Snout only moderately protruding; shell domed; chin and lower jaw with numerous large black spots ..... *Callopsis funerea*
4a Dorsal head stripes broken; a large light spot anterior to orbit, or the stripes unite behind the orbits forming a horseshoe-like pattern 5
b Dorsal head stripes unbroken and extending anterior to orbits, never united ..... *Callopsis punctularia melanosterna* (Fig. 1)
5a Dorsal head stripes united behind orbits by a transverse bar; posterior horns flared and enclosing a large dark spot ..... *Callopsis punctularia diademata* (Fig. 1)
b Dorsal head stripes may bend to unite behind the orbit, but never flared posteriorly to enclose the dark pigment of the back of head ..... *Callopsis punctularia punctularia* (Fig. 1)
6a Tip of the upper jaw hooked and unnotched 7

[1] See NAPS document #03252 for 18 pages of supplementary material. Order from NAPS, c/o Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, New York 10017. Remit in advance for each NAPS accession number. Institutions and organizations may use purchase orders when ordering; however, there is a billing charge of $5.00 for this service. Make checks payable to Microfiche Publications. Photocopies are $5.00. Microfiche are $3.00 each. Outside the United States and Canada, postage is $3.00 for a photocopy and $1.00 for a fiche.

b Tip of upper jaw straight and notched (sometimes with cusps) 9

7a Dorsal head pattern consists of a large, irregular horseshoe-shaped blotch; carapace depressed 8

b Dorsal head pattern consists of a pair of supratemporal stripes or no stripes present; carapace rather high, but flat on top ..... *Callopsis annulata*

8a Carapacial scutes uniformly light brown; gular scute approximately twice as long as the humeral; marginal scutes little flared; an elongated temporal spot ..... *Callopsis rubida rubida*

b Pleural scutes darker colored than vertebrals or marginals; gular scute only slightly longer than humeral; marginal scutes strongly outward projecting; an oval temporal spot ..... *Callopsis rubida perixantha*

9a Head pattern with red stripes (usually 2 or 3) crossing the tip of the snout and also a prefrontal arrow formed when a middorsal stripe meets two supratemporal stripes on the dorsal tip of the snout; bridge with extensive dark pigment 10

b Head pattern with only a pair of broad supratemporal stripes posterior of orbit; bridge usually plain yellow without extensive dark pigmentation ..... *Callopsis areolata*

10a Bridge completely dark; plastron with an unbroken dark central figure 11

b Dark bridge divided by a yellow bar; plastron with the dark central figure usually divided on gulars and humerals 12

11a Carapace high (somewhat domed); pleurals with bright ocelli or stripes; plastron with a narrow dark central figure ..... *Callopsis pulcherrima incisa*

b Carapace low; pleurals essentially unpatterned; plastron with a wide dark central figure ..... *Callopsis pulcherrima rogerbarbouri*

12a Carapace high (somewhat domed); pleural pattern extensive and consisting of a series of bright ocelli ..... *Callopsis pulcherrima manni*

b Carapace low; pleural pattern consists only of a central dark bordered light spot ..... *Callopsis pulcherrima pulcherrima*

Callopsis annulata (Gray)

Geoclemmys annulata Gray, Proc. Zool. Soc. London, p. 231 (1860).

Chelopus gabbii Cope, J. Acad. Nat. Sci. Philadelphia 2: 153 (1876).

Cotypes.—BMNH 1946.1.22.56 (alcoholic juvenile) and BMNH 1947.3.5.58 (dry adult male), collected by M. Frezer; BMNH 1947.3.5.59 (dry adult female), collected by J. Rosenberg. All from Esmeraldas, Ecuador.

Range.—Southern Honduras (Los Andes, Colón) southward through eastern Nicaragua. Costa Rica, and Panama to western Colombia and northern Ecuador.

Diagnosis.—A forest species of *Callopsis* with little or no digital webbing, a hooked (unnotched) upper jaw, a rather high but flat-topped carapace, and a dorsolateral head pattern of a pair of supratemporal stripes running from the nape to the orbits.

Description.—Carapacial length to 204 mm (males 202, females 204), oval, high (D/CL, 0.34–0.51, $\bar{x} = 0.42$; CW/CL, 0.61–0.79, $\bar{x} = 0.72$), often depressed across the vertebrals; widest at level of marginals 6–8, highest at posterior of vertebral 2 or seam between vertebrals 2–3. Sides of carapace straight to slightly bowed, but some with a concavity at the bridge. Posterior marginals slightly serrated, and in some, flared (MW, 6.0–30.0 mm, $\bar{x} = 14.8$; MW/CW, 0.04–0.25, $\bar{x} = 0.12$). General texture of scutes somewhat rough due to growth rings or granulations. Cervical scute bifurcated posteriorly to form a broad to elongated badge-shape, and each vertebral wider than long with a blunt median keel which may be prominent. Carapacial coloration extremely variable, ranging from totally black or dark brown with orange pleural and vertebral blotches to tan with yellow blotches on the pleurals and vertebrals. The pleural blotch often consists of radiations from the dorsoposterior corner; the vertebral keel is usually yellow. The upper surface of each marginal has a rectangular-

to-square yellow or orange blotch; the underside has a yellow blotch which may be triangular. In preservative most carapacial light colors are subdued.

Plastral length to 190 mm (males 190, females 189); PL/CL, 0.82–1.02, $\bar{x} = 0.91$. Concave in males; upturned anteriorly in both sexes but greatest in females. The posterior plastral lobe is longer and wider than the anterior. Femoral and anal scutes are curved gradually toward midline (IFL/IAL, 0.66–1.95, $\bar{x} = 1.01$; AW/AL, 0.93–1.62, $\bar{x} = 1.21$), and the anals are widely notched posteriorly. B/PL, 0.38–0.52; $\bar{x} = 0.45$. Plastral formula: Abd. > Pect. > Fem. > An. > Hum. > Gul. GW/GL, 0.71–2.07; $\bar{x} = 1.33$; IGL/IHL, 0.34–2.10; $\bar{x} = 0.81$. In juveniles, each gular scute has three anterior projections. Small axillary and inguinal scutes are present. Plastron is black or dark brown with a yellow border. The midseam may also be yellow. The bridge is black or dark brown.

Head small with snout only slightly projecting. Upper jaw serrated laterally and slightly hooked at tip (unnotched). Width of lower jaw symphysis less than diameter of the orbit. Ground color gray to yellow-brown or dark brown, occasionally reddish; rarely unicolor, but most with cream (or yellow) to red stripes which bleach to white or gray in preservative. There is a supratemporal stripe running from behind the orbit at a slight downward angle to the nape where it continues as a neck stripe. Another runs from the lower posterior orbit to the tympanum where it meets a similar stripe from the upper jaw; these may fuse and continue posteriorly onto the side of the neck as one stripe. There is a line from the upper anterior orbit to the tip of the snout. The iris is brown. The lower jaw is cream (or yellow) to horn; the upper jaw is usually yellow. The chin is yellowish and often mottled with very small brown spots. The neck is gray-brown with light dorsal and lateral stripes; ventrally it may have small brown spots.

The digits are only slightly webbed. The forelegs are covered with large scales (7–13 rows; $\bar{x} = 10.6$). The coloration is yellow with a pattern of dark stripes formed of wide black spots. Hind limbs also have large scales which are gray on the outside and yellow on the inside of the limb. The tail is gray to brown, with dorsal yellow stripes. Other skin is gray-brown, or, in some, reddish.

Males have concave plastra only slightly upturned anteriorly and longer tails with the vent beyond the carapacial margin; females have flat plastra which turn sharply upward anteriorly, and shorter tails with the vent beneath the carapace.

Variation.—*Callopsis annulata* is highly variable, but is not composed of separate recognizable populations. Much variation occurs in all populations with regard to carapacial coloration and pattern, and this has led to confusion regarding the status of individuals within populations. The situation is similar to that which occurs within populations of the North American box turtle, *Terrapene carolina carolina* (Milstead, 1969). The entire population must be examined in these cases. Confusing variation also occurs in some measurable characters such as W/L 2nd V, MW, MW/CW, GW/GL, and IFL/IAL. Only one character, IGL/IHL, showed significant differences among populations. In this character, Colombian *C. annulata* averaged 0.59 (SD = 0.11, n = 8) and were different at the $P \leqslant 0.01$ level from *C. annulata* from Ecuador ($\bar{x} = 0.95$, SD = 0.22, n = 12), Costa Rica ($\bar{x} = 0.89$, SD = 0.25, n = 8), and Nicaragua ($\bar{x} = 0.82$, SD = 0.16, n = 6).

Comparisons.—The only other terrestrial *Callopsis* occurring near its range are *C. pulcherrima incisa* and *C. p. manni*, which have notched (unhooked) upper jaws, high domed carapaces, bright ocelli or stripes on the pleurals, a yellow plastron with a narrow, dark central figure, and numerous red lines crossing the snout and upper jaw.

Specimens examined (108).—Ecuador (20): AMNH 22088; BMNH 1874.3.5.7, 1898.4.28.2, 1901.3.29.4–5, 1902.5.27.9, 1946.1.22.56, 1947.3.5.58–59; CAS 13297; MVZ 77497; MHNP 1903-206, 1906-219; PCHP 48; SMF 66774; USNM 96020, 201594–97. Colombia (9): BMNH 1894.11.16.1; FMNH 42802, 55899–900; LACM 36784, 75040, 75042; USNM 129832. Panama (60): AMNH 67091, 75993, 77580, 79932, 107401; ANSP 22305–09; CAS 7425; CM 6879; FMNH 6124, 13428, 42699, 57621–22, 130734, 171923; KU 77701, 80606, 96976, 96999–7000, 107885–89; MCZ 22297, 29196, 29257; MVZ 57593; PCHP 49, 1132; RAM(5); UF/FSM 3376, 7526; USNM 7571a,b, 29316, 50250, 54114–15, 107638, 142310, 148265–67, 150029–32, 150145–46, 203683. Costa Rica (8): KU 67458; MCZ 29111, 29113–14, 29258; UF/FSM 10736; USNM 8217, 45905. Nicaragua (6): AMNH 12425, 12427–30; ANSP 20872. Honduras (1): ANSP 26657. Locality unknown (4): BMNH 1876.1.13.16; PCHP 139; MHNP 6621; SMF 7660.

Callopsis areolata (Duméril and Bibron)

Emys areolata Duméril and Bibron, Cat. Méth. Coll. Reptiles, p. 10 (1851).

Nicoria punctularia var. *areolata* Boulenger, Cat. Chel., Rhynch., Croc. British Mus., p. 119 (1889).

Holotype.—MHNP 9424 (dry adult female), collected by M. Morelet. Type locality restricted to La Libertad, El Petén, Guatemala, by Smith and Taylor (1950).

Range.—Southern Veracruz, Tabasco,

and eastern Chiapas to Yucatan in Mexico southward through Belize and eastern Guatemala. There is also a questionable record from the Rio Segovia in eastern Honduras (USNM 24539).

Diagnosis.—A savanna species of *Callopsis* with little or no digital webbing, a notched (unhooked) upper jaw, a rather high olive-colored carapace with dark seams, yellow and dark mottling, and a small dark-bordered yellow spot on each pleural.

Description.—Carapacial length to 206 mm (males 188, females 206), slightly ovoid (wider posteriorly than anteriorly), high (D/CL, 0.36–0.49, $\bar{x} = 0.42$; CW/CL, 0.65–0.83, $\bar{x} = 0.72$) widest at level of marginals 6–8, highest at seam between vertebrals 2–3 or anterior vertebral 3. Carapacial sides usually straight, but some concave at bridge. Posterior marginals serrated and in some flared; lateral marginals may be flared or upturned (MW, 7.0–25.0, $\bar{x} = 12.8$; MW/CW, 0.08–0.24, $\bar{x} = 0.13$). General texture of scutes smooth in older animals, granulated or with growth rings in the young. Cervical scute often bifurcated posteriorly to form a broad badge-shape. Each vertebral is usually wider than long (the first may be slightly longer than wide) and bears a low blunt median keel. Carapace usually olive with dark seams and much yellow mottling forming a lichen-like pattern, but tan to black in some. Each pleural has a small, yellow, often dark-bordered spot (this may disappear with age). Some with much yellow along the interpleural-marginal seams. Undersides of marginals yellow with olive outer edges and dark seams.

Plastral length to 202 mm (males 178, females 202); PL/CL, 0.88–1.04, $\bar{x} = 0.95$; concave in males and slightly upturned anteriorly in both sexes. The posterior plastral lobe is longer and wider than anterior. Femoral and anal scutes curved gradually toward midline (IFL/IAL, 0.66–1.79, $\bar{x} = 1.07$; AW/AL, 0.84–1.61, $\bar{x} = 1.16$); and the anals are notched posteriorly. B/PL, 0.35–0.48; $\bar{x} = 0.42$. Plastral formula: Abd. > Pect. > Fem. > An. > Gul. > Hum. GW/GL, 0.60–2.50; $\bar{x} = 0.89$. IGL/IHL, 0.67–3.52; $\bar{x} = 1.70$. Gulars with three anterior projections in juveniles. Small axillary and inguinal scutes are present. Plastron is yellow with a dark central figure and often dark seams. The bridge is yellow with dark seams and olive flecks.

Head small with snout only slightly projecting. Upper jaw weakly serrated laterally and notched (straight) at tip. Width of lower jaw symphysis much smaller than diameter of the orbit. Coloration reddish-brown with some dark mottling dorsally. There is a yellow or red supratemporal stripe running posteriorly from the orbit downward to the side of the neck where it continues as a neck stripe. This line may be discontinuous. There are also two elongated red or yellow spots on the nape, another between the orbit and tympanum, and a light bar on each eyelid. The tympanum may be spotted. There may be a light maxillary stripe running from the snout posteriorly along the upper jaw under the orbit to the tympanum. The iris is yellow. Jaws and chin yellow; lower jaw and chin with small black spots or ocelli. The red and yellow lines bleach to cream or gray in preservative. The neck is olive to brown with stripes dorsally, and plain yellow or with small black spots ventrally.

The digits are only slightly webbed. The forelegs are yellow with black spots and covered with large scales (7–15 rows; $\bar{x} = 9.6$). The hind limbs are brown to olive outside, and yellow inside, with some small black spots. The tail is yellow with black dorsal lines.

Males have concave plastra and slightly longer tails with the vent beyond the carapacial margin; females have flat plastra and shorter tails with the vent beneath the carapace.

Variation.—Little variation was found regarding carapacial, plastral, or head patterns. However, certain ratios were found to be significantly different between populations ($P < .05$). Comparisons of Guatemalan (considered the type population) turtles to specimens from Tabasco and Cozumel Island, Quintana Roo, show significantly different MW/CW ratios. Marginals of turtles from Cozumel Island ($\bar{x} = 0.11$, SD = 0.02, n = 18) were shorter, whereas those of the Tabasco turtles ($\bar{x} = 0.16$, SD = 0.02, n = 5) were longer, than in Guatemalan turtles ($\bar{x} = 0.13$, SD = 0.03, n = 49). The Cozumel Island *C. areolata* also had lower D/CL ($\bar{x} = 0.39$, SD = 0.02), IFL/IAL ($\bar{x} = 0.94$, SD = 0.16), and AW/AL ($\bar{x} = 1.05$, SD = 0.09) ratios than the Guatemalan series ($\bar{x} = 0.42$, SD = 0.02; $\bar{x} = 1.10$, SD = 0.22; $\bar{x} = 1.20$, SD = 0.15, respectively). Despite these differences, I am reluctant to rank the Cozumel Island population as a new subspecies, but feel the population is undergoing differentiation. Its isolation from the mainland population makes this an ideal situation for subspeciation.

Comparisons.—Near its range, the only other terrestrial *Callopsis* are *C. pulcherrima*, which has more elaborate head, carapacial, and plastral patterns, and a dark bridge, and *C. rubida*, which has a hooked (unnotched) upper jaw and an elaborate head pattern. The carapace of *C. areolata* somewhat resembles that of kinosternid turtles, but these have hinged plastra and heavily webbed toes.

Specimens examined (170).—Honduras (1): USNM 24539. Guatemala (68): AMNH 70018, 70020; BMNH unnumbered (1); FMNH 1750;

KU 59796–97; MNHP 9424; TCWC 17366; UMMZ 75240–52(2), 75253, 75256–84, 79100, 91352–54; USNM 55641, 71416, 71421–27, 71963–65. Belize (20): BCB 13151; BMNH 1973.2499–500; CM 8516; FMNH 49361, 69235; KU 157681–83; LSU 11842–43; MCZ 71632–33, 136040; PCHP 393; UMMZ 70461; USNM 6546, 59934, 102894, 194382. Mexico (77): Quintano Roo (35): BCB 13149–50; CM 27579, 41313, 41319–21, 55817; FMNH 27268–69; INHS 6134; KU 70942–61, 71772; UF/FSM 33120; UINHM 19357. Campeche (9): AMNH 93241; FMNH 36602–03, 116490; KU 75119, 75654, 75665; UF/FSM 33118–19. Yucatan (7): AMNH 38846; FMNH 49362; KU 70962–64; LACM 113912; USNM 19279. Chiapas (16): UMMZ 118297–301; USNM 108646–55, 108658. Tabasco (6): USNM 46289–90, 46298–300, 108645. Vera Cruz (4): AMNH 66483; UMMZ 41686–88. Locality unknown (4): BMNH 1903.9.30.4; FMNH 116511; USNM 51524, 416002.

Callopsis funerea (Cope)

Chelopus funereus Cope, J. Acad. Nat. Nat. Sci. Philadelphia 2: 154 (1876).

Geoemyda costaricensis Kanberg, Zool. Anz. 88: 162 (1930).

Cotypes.—USNM 45000, collected by W. M. Gabb; USNM 45001, 46134–35. Four poorly preserved juveniles, all from Port Limon, Costa Rica.

Range.—From the Rio Coco on the Honduran-Nicaraguan border (Crassa, 60 km W. Waspam) southward in the Caribbean drainages of eastern Nicaragua, Costa Rica, and Panama to the Canal Zone.

Diagnosis.—A large aquatic species of *Callopsis* with strongly webbed toes, large black spots on the lower jaw and chin, and a light stripe on each side of the head running from the neck to above the tympanum.

Description.—Carapacial length to 325 mm (males 325, females 282), oval, high and somewhat domed (D/CL, 0.35–0.53, $\bar{x} = 0.42$; CW/CL, 0.65–0.82, $\bar{x} = 0.76$), widest at level of marginals 5–7, highest at vertebral 3. Sides of carapace straight to slightly bowed; an occasional specimen is concave at the level of the bridge. Posterior marginals slightly serrated, often flared, and with a small median notch (MW, 16.0–37.0 mm, $\bar{x} = 24.6$; MW/CW, 0.08–0.32, $\bar{x} = 0.17$). General texture of scutes smooth to somewhat roughened due to growth rings. Cervical scute broad to rectangular and often bifurcated posteriorly. Each vertebral wider than long (the first the longest, the fifth shortest) and with a blunt median vertebral keel (well developed in young, worn low in older turtles) extending to the posterior carapacial notch. Adult carapacial coloration black to dark brown with few, if any, yellowish radiations or blotches on the pleurals; juveniles usually with more yellow coloration on the pleurals. This species becomes melanistic with age. The undersides of the marginals are yellow with either a dark central blotch or dark seam borders.

Plastral length to 287 mm (males 287, females 267); PL/CL, 0.86–1.04, $\bar{x} = 0.94$; concave in males, notched and upturned anteriorly in both sexes. The posterior lobe is longer and wider than the anterior. Femoral and anal scutes curved slightly toward midline (IFL/IAL, 0.95–1.54, $\bar{x} = 1.27$; AW/AL, 0.93–1.56, $\bar{x} = 1.24$). The anals are notched posteriorly. B/PL, 0.36–0.47; $\bar{x} = 0.43$. Plastral formula: Abd. > Pect. > Fem. > Gul. > An. > Hum. GW/GL, 0.67–1.53; $\bar{x} = 0.86$; IGL/IHL, 0.95–7.58, $\bar{x} = 2.79$. Juveniles have three anterior projections on each gular. Small axillary and inguinal scutes are present. Plastron is black with yellow seam borders and a wide yellow midseam (the yellow may bleach to cream or gray in preservative). The bridge is black to dark brown with yellow seams.

Head moderate with snout only slightly projecting. Upper jaw weakly serrated laterally and notched, often with cusps, at tip (unhooked). Width of lower jaw symphysis smaller than diameter of the orbit. Coloration black to reddish-brown, unmarked in some, but usually with yellow stripe on the side of the head above the tympanum, an elongated yellow bar between the orbit and tympanum, and a yellow line from the corner of the mouth to the tympanum. Often there is a yellow line on the upper jaw running under the orbit to the tympanum and another from the orbit to the tip of the snout. There is much yellow and black mottling on the tympanum and temporal region. The iris is dark brown. The upper jaw is horn-colored to dark brown. The lower jaw and chin are yellow with large black irregular spots. The neck is tan to gray dorsally and laterally with fine black stripes, and yellow ventrally with some black spots and mottling.

The digits are strongly webbed and the forelegs are covered with large scales (9–12 rows; $\bar{x} = 10.1$). The forelegs are yellow with black vermiculations and a black outer border. The hind limbs are black to dark gray or brown outside and yellowish inside. The tail is yellow-brown with dark stripes.

Males have concave plastra and longer tails with the vent beyond the carapacial margin; females have flat plastra and shorter tails with the vent beneath the carapace.

Variation.—There seems to be little geographi-

cal variation between adults of this species; however, those from Panama had greater ($P < .01$) GW/GL ratios ($\bar{x} = 0.98$, SD = 0.24, n = 9) than turtles from Costa Rica ($\bar{x} = 0.76$, SD = 0.18, n = 32). Data and specimens from the northern part of the range are lacking. Only three Nicaraguan individuals (two juveniles) were examined, and the possibility exists that differences may occur.

Comparisons.—The only other aquatic *Callopsis* near *C. funerea* is *C. punctularia melanosterna*, which has two dorsal head stripes extending from before the orbits to the nape, and its chin seldom contains large black spots. The third aquatic species of *Callopsis*, *C. nasuta*, is not sympatric and is much smaller (maximum about 223 mm), has a strongly projecting snout, dark bars on the chin and lower jaw, and a much depressed carapace. The Neotropical *Chrysemys* have intricate plastral patterns, and a wide reddish-orange bar between the orbit and tympanum.

Remarks.—Kanberg (1930) described *Geoemyda costaricensis* on a basis of a specimen in the Zoological Museum of Berlin. Recent correspondence with Dr. Gunther Peters has revealed that this specimen was never deposited in that museum.

Specimens examined (44).—Panama (9): KU 96977–78, 96996–98; USNM 59877, 142313, 150033, 166827. Costa Rica (32): AMNH 12426, 89157–59, 95076–77; KU 104096; MCZ 28702, 28904–05, 29112, 29116–18; PCHP 348; SMF 57958; UF/FSM 10272, 10500, 15666, 31715, 33123; USNM 8216, 8218, 8269–70, 8272–74, 45900–01, 46134–35. Nicaragua (3): AMNH 12424, 12431; LACM 73824.

Callopsis nasuta (Boulenger)

Nicoria nasuta Boulenger, Ann. Mag. Nat. Hist. (London), Ser. 7, 9: 53 (1902).

Geoemyda punctularia nasuta Mertens, Senckenbergiana Biol. 35: 3 (1954).

Cotypes.—BMNH 1947.3.5.54 (adult male) and BMNH 1947.3.5.55–57 (adult females), collected by G. Flemming, 15–16 April, 2 May 1901, at Belun and Rio Durango, northwestern Ecuador.

Range.—Pacific drainages of western Colombia and northwestern Ecuador where its preferred habitat is large rivers with strong current.

Diagnosis.—A large aquatic species of *Callopsis* with strongly webbed toes, a depressed carapace, strongly projecting upper jaw, dark bars on the lower jaw, and a light stripe running from the snout to the orbit, and another light stripe running from the nape and ending behind the orbit.

Description.—Carapacial length to 223 mm (males 196, females 223), oval, flattened (D/CL, 0.32–0.38, $\bar{x} = 0.35$; CW/CL, 0.67–0.84, $\bar{x} = 0.73$), widest at level of marginals 6–7, highest at seam between vertebrals 2–3. Carapace sides often concave at bridge. Posterior marginals only slightly serrated (MW, 13.0–28.0 mm, $\bar{x} = 20.6$; MW/CW, 0.09–0.22, $\bar{x} = 0.17$). General texture of scutes smooth, but with small rugose granulations in some. Cervical usually broad and badge-shaped. Vertebrals often flattened dorsally and usually wider than long, although the first may be slightly longer than wide. A blunt median keel is present on each vertebral in young individuals, but becomes worn flat with age until it can only be found on the last two, or is lost entirely. Carapacial coloration reddish-brown to black, with the seams between the scutes often black. The undersides of the marginals are yellow with a reddish-brown to black central blotch.

Plastron length to 213 mm (males 179, females 213); PL/CL, 0.85–0.99, $\bar{x} = 0.93$; concave in males; only slightly upturned anteriorly in both sexes. The posterior lobe is longer and wider than the anterior. Femoral and anal scutes are curved slightly toward midline (IFL/IAL, 1.03–1.52, $\bar{x} = 1.25$; AW/AL, 1.14–1.45, $\bar{x} = 1.24$), and the anals are medially notched posteriorly. B/PL, 0.35–0.47, $\bar{x} = 0.39$. Plastral formula: Abd. > Pect. > Fem. > An. > Gul. > Hum. GW/GL, 0.93–1.78, $\bar{x} = 1.28$; IGL/IHL, 0.38–3.77, $\bar{x} = 1.36$. Small axillary and inguinal scutes are present. Plastron is yellow with a large reddish-brown to black blotch on each scute. The bridge is yellow with two dark blotches.

Head moderate with a strongly projecting snout. Upper jaw weakly serrated laterally and notched at tip (straight). Width of lower jaw symphysis slightly less than the diameter of the orbit. Coloration reddish-brown to black with a yellow to cream narrow stripe running from the tip of the snout to the orbit. Another stripe runs along the side of the head from the posterior margin of the orbit to the nape where it continues as a neck stripe. A third stripe passes posteriorly from the lower orbit to the tympanum where it meets a similar stripe from the corner of the mouth and may form a posterior loop around the tympanum. Each of these stripes may be discontinuous, and they fade to white or gray in preservative. The iris is yellow to brown. The jaws are yellow to horn-colored, and the chin is yellow. Dark barring occurs on the lower jaw. The chin of one specimen (CAS 80969) had seven tubercle-like projections, while that of seven others (SMF 57552–53, USNM 198634–36, USNM 204055–56) had what appeared to be glandular openings.

The legs are black to red-brown on the outer surface and yellowish on the inner. The forelegs are covered with large scales (10–14 rows; $\bar{x} = 11.3$). The hind legs also have large scales on the outer surface. The digits are heavily webbed. The tail is dark dorsally with two yellow lines and lighter ventrally.

Males are smaller and have narrower carapaces, concave plastra with a deep anal notch, and long tails with the vent beyond the carapacial margin. Females are larger and wider with flat to slightly convex plastra having a wide, shallow anal notch; they also have short tails with the vent located beneath the carapace.

Variation.—Although only 17 specimens were examined, two characters showed significant ($P < .05$) differences between turtles from Colombia and those from Ecuador. Ecuadorian *C. nasuta* had much wider marginals ($\bar{x} = 24.7$ mm, SD = 2.2, n = 6) than those from Colombia ($\bar{x} = 19.1$ mm, SD = 2.7, n = 11). Ecuadorian specimens also had wider carapaces than those from Colombia. The mean CW/CL ratio for those from Ecuador was 0.77 (SD = 0.05) and that for Colombian *C. nasuta* was 0.72 (SD = 0.02).

Comparisons.—*Callopsis p. melanosterna*, which also occurs in Ecuador and Colombia, has a much higher (D/PL, 0.32–0.45, $\bar{x} = 0.39$, $P < .05$) and wider (CW/CL, 0.64–0.72, $\bar{x} = 0.68$, $P < .05$) carapace, a wider bridge (B/PL, 0.40–0.51, $\bar{x} = 0.43$, $P < .05$), a less projecting snout, and a bright white to yellow iris. The *Chrysemys* from this area have high domed carapaces and a red-orange temporal bar.

Remarks.—Boulenger (1902) originally described this turtle as a full species, but Mertens (1954) listed it as a subspecies of *C. punctularia* without presenting reasons for this designation. Recent writers have followed Mertens. *Callopsis nasuta* is a unique turtle highly adapted to life in strong river currents and is not conspecific with *C. punctularia*. Besides having a much different head pattern and differing in those characters listed above under *Comparisons*, it differs ($P < .05$) further from *C. p. melanosterna*, which due to its near sympatry should be most closely related, in the following characters: W/L 1st V: *C. nasuta*, $\bar{x} = 1.27$ (SD = 0.10, n = 17), *C. p. melanosterna*, $\bar{x} = 1.03$ (SD = 0.12, n = 22); W/L 2nd V: *C. nasuta*, $\bar{x} = 1.35$ (SD = 0.19, n = 12), *C. p. melanosterna*, $\bar{x} = 0.94$ (SD = 0.08, n = 18); W/L 2nd Pl: *C. nasuta*, $\bar{x} = 1.20$ (SD = 0.13, n = 17), *C. p. melanosterna*, $\bar{x} = 1.28$ (SD = 0.09, n = 22); GW/GL: *C. nasuta*, $\bar{x} = 1.28$ (SD = 0.23, n = 17), *C. p. melanosterna*, $\bar{x} = 0.91$ (SD = 0.17, n = 23); IGL/IHL: *C. nasuta*, $\bar{x} = 1.36$ (SD = 0.81, n = 17), *C. p. melanosterna*, $\bar{x} = 2.28$ (SD = 0.82, n = 23); AW/AL: *C. nasuta*, $\bar{x} = 1.24$ (SD = 0.09, n = 17), *C. p. melanosterna*, $\bar{x} = 1.15$ (SD = 0.14, n = 23); Foreleg scale rows: *C. nasuta*, $\bar{x} = 11.3$ (SD = 1.2, n = 12), *C. p. melanosterna*, $\bar{x} = 9.7$ (SD = 0.9, n = 19).

Specimens examined (17).—Ecuador (6): BMNH 1947.3.5.54–57; USNM 204055–56. Colombia (11): BMNH 1913.11.12.2, 1914.5.21.2; CAS 80969, FMNH 42801; SMF 57552–53; USNM 198634–38.

Callopsis punctularia (Daudin)

Testudo punctularia Daudin, Hist. Nat. Gen. part. rep. 2, p. 249 (1802).

Emys dorsualis Spix, Spec. Nov. Testud. Brazil, p. 11 (1824).

Emys scabra Gray, Synopsis Rep., part 1, p. 24 (1831).

Geoclemys callocephalus Gray, Proc. Zool. Soc. London, p. 254 (1863).

Rhinoclemys bellii Gray, Ann. Mag. Nat. Hist. (London), Ser. 3, 12: 183 (1863).

Callopsis dorsalis Gray, Ann. Mag. Nat. Hist. (London), Ser. 3, 12: 183 (1863).

Holotype.—MHNP 9130 (adult female), collected by M. Richard from Cayenne, French Guiana.

Range.—Southeastern Panama, Colombia, and northwestern Ecuador eastward to Trinidad, the Guianas, and northeastern Brazil.

Diagnosis.—A large aquatic species of *Callopsis* with strongly webbed toes, a general lack of spotting on the lower jaw and chin, and a dorsal head pattern ranging from stripes, that run anteriorly from the nape and touch or pass beyond the orbit, to a broad horseshoe-like mark that occurs posterior to the orbit.

Description.—Carapacial length to 290 mm (males 251, females 290), oval, high (D/PL, 0.32–0.47, $\bar{x} = 0.40$; CW/CL, 0.64–0.83, $\bar{x} = 0.73$), somewhat domed; widest at level of marginals 6–7, highest at level of anterior vertebral 3, and notched posteriorly. Sides of carapace bowed to straight, but concave at bridge in some. Posterior marginals strongly serrated and often flared (MW, 11.2–29.0 mm, $\bar{x} = 21.7$; MW/CW, 0.07–0.25, $\bar{x} = 0.17$). General texture of scutes smooth to slightly rough due to granulations and growth rings. Cervical scute bifurcated posteriorly to form a broad to elongated badge-shape. Vertebrals generally wider than long, but the first may be longer than wide. Each vertebral bears a low blunt median keel extending to the posterior carapacial notch; the keel may disappear with

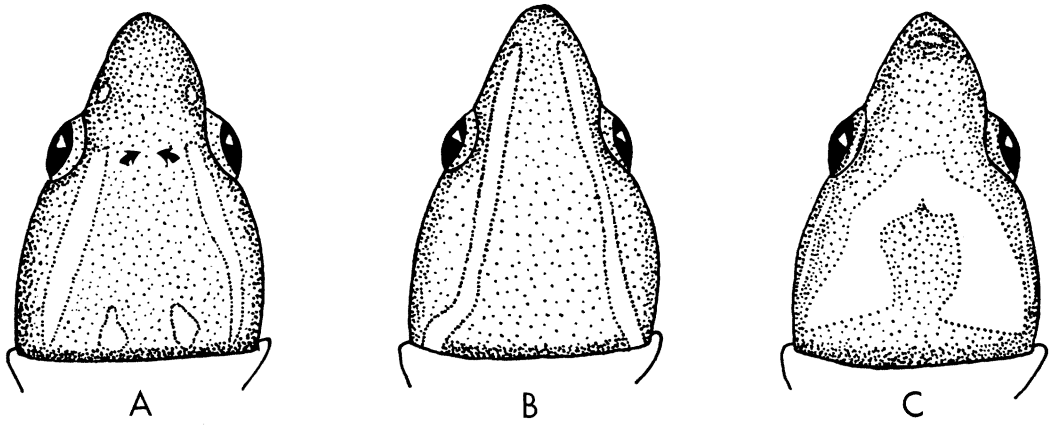

FIG. 1.—Subspecific dorsal head patterns of *Callopsis punctularia*: A) *C. p. punctularia*; B) *C. p. melanosterna*; C) *C. p. diademata*. Arrows indicate possible path of curvature toward unity of head stripes.

age. Carapacial coloration totally dark brown to black in adults, but younger individuals may show some yellow to bronze radiations on each pleural. The undersides of the marginals are yellow with brown blotches or mottlings.

Plastral length to 278 mm (males 233, females 278); PL/CL, 0.84–1.03, $\bar{x} = 0.95$; concave in males and upturned anteriorly in both sexes. The posterior lobe is longer and wider than anterior. The femoral and anal scutes curve slightly toward midline (IFL/IAL, 0.63–2.88, $\bar{x} = 1.01$; AW/AL, 0.86–1.53, $\bar{x} = 1.14$), and the anals have a medial posterior notch. B/PL, 0.35–0.51; $\bar{x} = 0.41$. Plastral formula: Abd. > Pect. > Fem. > An. > Gul. > Hum. GW/GL, 0.50–1.78, $\bar{x} = 0.97$; IGL/IHL, 0.67–4.00, $\bar{x} = 1.72$. In juveniles, each gular scute has three anterior projections. Small axillary and inguinal scutes are present. Plastron coloration red-brown to black with a yellow border and midseam. The bridge is yellow and usually with two large dark blotches.

Head small with the snout only slightly projecting. The upper jaw weakly serrated laterally and notched at tip (straight). Width of lower jaw symphysis less than diameter of the orbit. Coloration dark brown to black. Dorsal head markings variable, ranging from striping to a broad horseshoe-like mark (Fig. 1). The markings are usually red or yellow, but may be pale green in some. The eyelids have a light-colored bar, and there are usually lines between the orbit and tympanum and another from the snout along the upper jaw to the tympanum passing under the orbit. The iris ranges from bronze to bright yellow or white. The jaws are yellow to horn-colored, and the chin is yellow and may be dark-mottled. The neck is yellowish with dark lines.

The digits are strongly webbed, and the foreleg covered in front with large scales (8–12 rows; $\bar{x} = 9.9$). Coloration yellow to reddish with rows of black spots. Hindlimbs dark gray on outside, inside yellowish with black spotting. Tail is yellow to reddish with dark lines.

Males have concave plastra and long tails with the vent beyond the carapacial margin; females have flat to slightly convex plastra and shorter tails with the vent beneath the carapace. Adult females are larger than males.

Callopsis punctularia punctularia (Daudin)

Testudo punctularia Daudin, 1802.
Emys dorsualis Spix, 1824.
Emys scabra Gray, 1831.
Geoclemys callocephalus Gray, 1863.
Rhinoclemys bellii Gray, 1863.
Callopsis dorsalis Gray, 1863.
Rhinoclemmys lunata Gray, Ann. Mag. Nat. Hist. (London), Ser. 4, 11: 144 (1873).
Rhinoclemmys ventricosa Gray, Ann. Mag. Nat. Hist. (London), Ser. 4, 11: 145 (1873).
Geoemyda punctularia punctularia Wettstein, Sitzungsber. Akad. Wiss. Wien Math. Naturwiss. Kl. Abt. 1: 19 (1934).
Geoemyda punctularia lunata Mertens, Senckenbergiana Biol. 35: 6 (1954).

Range.—Atlantic and Caribbean drainages from northeastern Brazil through French Guiana, Guyana, and Surinam to northeastern Venezuela and Trinidad.

TABLE 1.—Significant measurable subspecific characteristics of *Callopsis punctularia*. Significant at $P < .05$ when compared to: (a) *punctularia*, (b) *melanosterna*, (c) *diademata*.

Character	*C. p. punctularia*			*C. p. melanosterna*			*C. p. diademata*		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
W/L 2nd V	65	1.07 (b)	0.11	18	0.94 (a, c)	0.08	5	1.05 (b)	0.06
W/L 2nd Pl	75	1.36 (b, c)	0.09	22	1.28 (a, c)	0.09	5	1.46 (a, b)	0.14
MW/CW	59	0.18 (b)	0.03	18	0.15 (a)	0.03	5	0.17	0.03
GW/GL	77	0.99 (b)	0.14	23	0.91 (a)	0.17	5	0.88	0.22
IGL/IHL	77	1.54 (b)	0.55	23	2.28 (a)	0.82	5	1.63	0.53
CW/CL	65	0.75 (b)	0.03	18	0.68 (a, c)	0.02	5	0.74 (b)	0.03
B/PL	79	0.40 (b)	0.02	23	0.43 (a, c)	0.03	5	0.40 (b)	0.01
IFL/IAL	78	0.96 (b)	0.26	23	1.24 (a, c)	0.24	5	0.84 (b)	0.11

Diagnosis.—A medium-sized subspecies of *Callopsis punctularia* with a dorsal head pattern of an oblique yellow to red stripe on each side running posteriorly from above the orbit to above the tympanum (these stripes may exhibit any degree of variation between total separation to transverse jointure just behind the orbits), two light blotches on the nape, and a light spot on the snout in front of each orbit (Fig. 1).

Description.—Essentially like that of the species, but carapace length to only 205 mm (males 201, females 205), pleurals with light radiations in young, plastral length to 205 mm (males 203, females 205), iris bronze, and yellow or red head-striping. Head pattern as given in diagnosis (Fig. 1). For mensural characteristics see Table 1.

Remarks.—Gray (1863) described the species *Rhinoclemys bellii* from tropical America as having a "head with a spot on each side of the nose and of the occipit and with a sinuous urn-shaped band on the crown, over the orbit and temples.... The figure differs from any species... by the superciliary bands being united by a short transverse band in front between the eyes." Later, Gray (1873*a*) described another new turtle, *Rhinoclemmys lunata*, as having "a spot on each side of the nose and occipit, and a streak on each side of the head, united across the forehead." It is obvious from these descriptions that *bellii* and *lunata* are identical and, as such, *R. lunata* becomes a synonym of *R. bellii*. I examined the types of *R. lunata* (BMNH 1946.1.22.69, 70) and found they match the description of *R. bellii*. Unfortunately the type of *R. bellii* is not known to exist. Wermuth and Mertens (1961) placed the species *Rhinoclemmys ventricosa* Gray, 1973, in synonymy with *R. lunata*. I also examined its type (BMNH 1947.3.5.49), a headless female shell, and although it is recognizable as a *Callopsis punctularia*, it cannot for certain be identified as a *lunata*. However, the status of these names is really academic, because I have examined specimens of *C. punctularia* showing every intermediate stage in the transverse unification of the head stripes from total separation to united, as described above. These specimens were from throughout much of the northern range of *Callopsis p. punctularia* (Trinidad: BMNH 1917.9.27.1; TTM 7383–84, 7397; UF/FSM 3636. Guyana: AMNH 8080, 61530; MCZ 45537; PCHP 141, 1092; UMMZ 83648–50, 83749–50, 83753; USNM 164180. Surinam: AMNH 8652; ANSP 16690; BMNH 1946.1.22.69, 70, 1866.8.14.231; MCZ 1888; NMW 18796; RMNH 3311, 9352; French Guiana: MHNP 2023), and Lescure et al. (see Fretey, 1975) also encountered all of the intermediate head patterns among the French Guiana specimens they examined; these indicate that both *bellii* and *lunata* are only head pattern variants of *C. p. punctularia*. Measurable characters of

both *lunata* and *ventricosa* also fall within the ranges of those of *C. p. punctularia*. Boulenger (1889) also recognized the *lunata* head pattern (he apparently overlooked *R. bellii*) as only a variant of *C. punctularia* and treated both *lunata* and *ventricosa* as synonyms.

No integration between *C. p. punctularia* and the other two subspecies occurs as they are widely separated geographically, with *C. p. punctularia* occurring only west to the mouth of the Orinoco River in eastern Venezuela, and *C. p. melanosterna* and *C. p. diademata* being found generally west of Sierra Nevada de Merida in northwestern Venezuela.

Specimens examined (145).—Brazil (19): AMNH 62584; CAS 13479, 49287, 49290; CM 3145; KU 127253; 130263–64; MCZ 2601, 2627 (3), 4061; SMF 57960; USNM 28978, 65106–08, 65115. French Guiana (10): PCHP 297, MHNP 2023, 5297, 9126–30; SMF 47845; UF/FSM 33125. Guyana (23): AMNH 8080, 61527, 61530, 61534; BMNH 1862.12.15.37; MCZ 45537; PCHP 141, 502, 1092; MHNP 2046, 5297; UMMZ 53978, 83648–50, 83749–50, S-46668–69; USNM 85022, 89408, 164180. Surinam (54): AMNH 8652–53; ANSP 344, 16690; BMNH 1866.8.14. 228–231, 1946.1.22.69–70, 1946.4.4.70–71, 1947. 3.5.49; CM 44423; MCZ 1888, 46579; NMW 18792(2), 18793(2), 18794, 18796–97; PCHP 296, 389, 396, 796, 882; RMNH 45, 2827, 3308–11, 9352, 134731, 15972, 15998–99, Field #693, unnumbered (12); UF/FSM 33124, 33128; USNM 86861. Trinidad (23): AMNH 73143, 78963; BMNH 1876.1.31.12, 1917.9.27.1; FMNH 53657–62; PCHP 345; SMF 7664; TTM 7381–84, 7397–98; UF/FSM 3636, 6691, 33126; USNM 166103, 198632. Venezuela (2): AMNH 65542, BMNH 1871.12.13.2. Locality unknown (14): AMNH 17793, 44613; BMNH 1865.11.30.2, 1947. 3.5.50, unnumbered (2); MHNP 2021, 4099, 7937; SMF 7658, 45485–87; USNM 104343.

Callopsis punctularia melanosterna (Gray)

Geoclemmys melanosterna Gray, Proc. Zool. Soc. London, p. 205 (1861).

Emys dorsalis (non Spix) Gray, Cat. Shield Rep., p. 32 (1855).

Callopsis melanosterna Gray, Ann. Mag. Nat. Hist. (London), Ser. 3, 12: 183 (1863).

Nicoria punctularia var. *melanosterna* Boulenger, Cat. Chel., Rhynch., Croc. British Mus., p. 124 (1889).

Cotypes.—BMNH 1947.3.4.8 (dry adult female), collected by J. O. Goodridge from Rio Buonaventura, Colombia; BMNH 1947.3.5.51 (dry juvenile), collector unknown, from Cherunha (corrected from Chirambira by Medem, 1958), Gulf of Darien, Colombia.

Range.—Caribbean drainages of southeastern Panama and northern Colombia, and Pacific drainages of western Colombia and northwestern Ecuador.

Diagnosis.—A large subspecies (290 mm) of *Callopsis punctularia* with a dorsal head pattern consisting of an oblique pale green to orange (or reddish) stripe on each side running posteriorly from in front of the orbit to above the tympanum and there curving downward toward the posterior side of the tympanum; with no light blotches on the snout in front of the orbits or on the nape; and with the oblique stripes never united across the forehead (Fig. 1).

Description.—Essentially like that of the species, but with a bright white or yellow iris, pleurals with light radiations in young, and a head pattern as given under diagnosis (Fig. 1). For mensural characteristics see Table 1.

Remarks.—Medem (1962, and personal communication 1974) remarked on an interesting phenomenon regarding the head-stripe coloration of Colombian *C. p. melanosterna*. Those living in a freshwater habitat always have red stripes, whereas those living in brackish waters close to to Pacific Coast show green to greenish stripes. Populations intermediate (intergrade?) between the two possess orange stripes. There are no morphological differences, although red-striped turtles seem to grow larger. These differences cannot be seen in preserved specimens due to bleaching out of the pigments. This situation needs additional field study to determine the cause of these color differences.

Specimens examined (31).—Ecuador (2): BMNH 1901.3.29.3, 1902.5.27.8. Colombia (10): BMNH 1947.3.4.8, 1947.3.5.51; FMNH 73782–85, 73787, 74887; SMF 51726; USNM 117458. Panama (16): AGJR 78; AMNH 45064; KU 80607, 107890–95, 107897–900, 108331; MVZ 83216; USNM 167224. Locality unknown (3): SMF 45485–87.

Callopsis punctularia diademata (Mertens)

Geomyda punctularia diademata Mertens, Senckenbergiana Biol., 35: 4 (1954).

Holotype.—SMF 48141 (adult female), from "Hamburg Aquarium," April, 1954. Type locality Maracay, Venezuela.

Range.—Caribbean drainage of eastern Colombia and northwestern Venezuela.

Diagnosis.—A slightly smaller subspecies of *Callopsis punctularia* with a dorsal head pattern consisting of a large yellow horseshoe-shaped figure located medially just behind the orbit with the apex pointing anteriorly and the long arms running posteriorly, flaring laterally, and centrally enclosing a dark area; a light blotch on the snout in front of each orbit, and no light blotches on the nape (Fig. 1).

Description.—Essentially like that of the species, but the somewhat flattened carapace to only 208 mm (males 163, females 208), and with some yellow about the seams. Plastral length to 200 mm (males 147, females 200). Iris greenish to bronze. Head pattern as given in diagnosis (Fig. 1). For mensural characteristics, see Table 1.

Remarks.—The head pattern of *C. p. diademata* is very different from that of its nearest relative, *C. p. melanosterna*, and there are a number of mensural character differences (Table 1). Also, although the geographic ranges overlap, or are extremely close, no evidence of intergradation has been found. These observations seem to suggest that *C. p. diademata* may actually represent a full species. However, since only the type series of five individuals and color transparencies of several others have been examined, I am reluctant to elevate *C. p. diademata* to specific rank at this time. Its relationship needs further study.

Specimens examined.—Venezuela (5): SMF 48141–44, 58408.

Comparisons.—Basic comparisons between the subspecies of *C. punctularia* are given in Figure 1 and Table 1. Comparisons with *C. funerea* and *C. nasuta* are presented under those species. The aquatic *Chrysemys* have a prefrontal arrow head pattern with a wide red temporal bar and complex plastral patterns. The side-neck turtles (Chelidae, Pelomedusidae) have an intergular scute present on the plastron.

Callopsis pulcherrima (Gray)

Emys pulcherrimus Gray, Cat. Shield Rep., p. 25 (1855).

Nicoria punctularia var. *pulcherrima* Boulenger, Cat. Chel., Rhynch., Croc. British Mus., p. 125 (1889).

Holotype.—BMNH 1947.3.5.52 (dry juvenile), collector and date unknown, from "Mexico"; here restricted to vicinity of San Marcos, Guerrero, Mexico.

Range.—Guirocoba, southern Sonora (and possibly Chihuahua), southward through western Mexico, western Guatemala, El Salvador, western Honduras, and the Pacific coastal areas of Nicaragua and Costa Rica to just South of San Jose. The questionable Chihuahuan specimen (USNM 104626; a shell of a female collected by Hobart M. Smith, 11 October 1938, at the Rio Santa Mario near Progresso) has been tentatively identified as *Callopsis pulcherrima* by Dr. John M. Legler and the author, but the habitat of the area seems wrong for this species.

Diagnosis.—A terrestrial lowland species of *Callopsis* with little or no digital webbing, a notched (unhooked) upper jaw, a flattened to high-domed carapace, with bright red or yellow pleural markings, a series of red lines on the snout, and a prefrontal arrow pattern on the dorsal snout.

Description.—Carapacial length to 206 mm (males 181, females 206), oval, flattened and broader in the northern parts of the range and higher domed southward (D/CL, 0.31–0.53, $\bar{x} = 0.42$; CW/CL, 0.65–0.84, $\bar{x} = 0.78$), widest at level of marginals 6–7, highest at seam between vertebrals 203. Carapacial sides straight to slightly bowed. Posterior marginals slightly serrated and, in some, flared (MW, 9.0–31.0 mm, $\bar{x} = 19.2$; MW/CW, 0.08–0.26, $\bar{x} = 0.16$). General texture of scutes rough due to growth rings. Cervical scute narrow and rectangular, or bifurcated posteriorly to form an elongated badge-shape. Each vertebral wider than long and with a blunt median keel. Carapace notched posteriorly. General coloration brown with variable patterns (see species diagnoses). Pleural patterns range from unicolor to a single dark-bordered yellow or red spot, or to bright yellow or red lines or ocelli (Fig. 2). The vertebrals may be unicolor, dark-flecked, or with well developed red or yellow lines (Fig. 2). Upper surface of each marginal may be unicolor or dark-speckled, or have light bars or a large ocellus; the undersides are brown with from one to three yellow bars. The patterns become more colorful and pronounced southward. The reds and yellows fade in preservative.

Plastral length to 213 mm (males 185, females 213); PL/CL, 0.88–1.06, $\bar{x} = 0.95$; concave in males, and slightly upturned anteriorly in females. The posterior lobe is longer and wider than the anterior. Femoral and anal scutes are curved toward midline (IFL/IAL, 0.56–2.23, $\bar{x} = 1.09$, AW/AL, 0.84–2.83, $\bar{x} = 1.22$), and the anals have a wide medial notch. B/PL, 0.39–0.49; $\bar{x} = 0.44$.

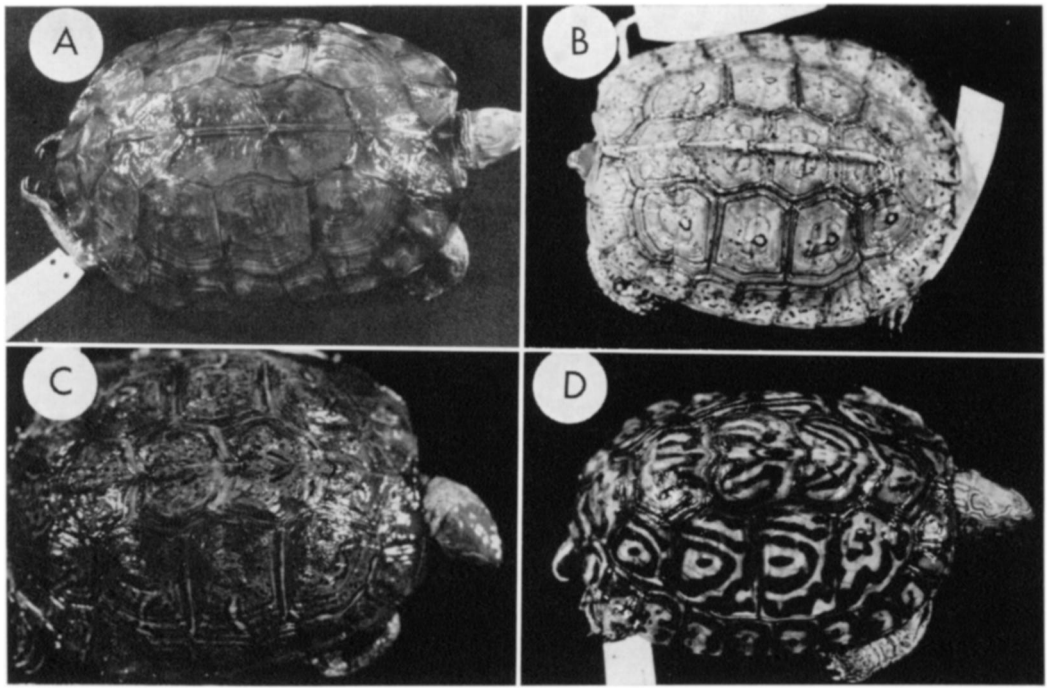

FIG. 2.—Subspecific carapacial patterns of *Callopsis pulcherrima*: A) Holotype of *C. p. rogerbarbouri* (AMNH 63760); B) *C. p. pulcherrima* (UF/FSM 33131): C) *C. p. incisa* (USNM 128098); D) *C. p. manni* (PCHP 392).

Plastral formula: Abd. > Pect. > Fem. > An. > Gul. > Hum. GW/GL, 0.61–1.21, $\bar{x} = 0.90$; IGL/IHL, 0.63–4.16, $\bar{x} = 1.83$. In juveniles each gular scute may have two or three anterior projections. Small axillary and inguinal scutes are present. Plastron yellow with a narrow-to-wide central dark blotch (Fig. 3). The seams may be dark-bordered. The bridge is either completely brown or has a yellow bar separating the brown pigment from the carapace (Fig. 3).

Head small with the snout only slightly projecting. Upper jaw slightly serrated laterally and notched, sometimes with cusps, at the tip (straight). Width of lower jaw symphysis less than diameter of the orbit. Coloration olive to brown. There is a series of red stripes on the head: (1) a middorsal stripe running forward from between the orbits to the dorsal tip of the snout where it meets two other stripes, one from each orbit, to form a prefrontal arrow (the lateral stripes may extend through the orbit to the nape, and each of these three stripes may be discontinuous in some specimens); (2) a stripe running from each nostril to the corresponding orbit; (3) a stripe running posteriorly from below the nostrils along the upper jaw under the orbit to the tympanum; and (4) several stripes (usually two or three) from the orbit to the tympanum. There is usually a red spot and dark mottling on the tympanum. Iris gray to bluish-green, bronze, or in some reddish. The jaws and chin are yellow, and the lower jaw and chin may contain red lines, large black spots, or ocelli.

The digits are only slightly webbed, if at all. The forelegs are covered with large scales (8–15 rows; $\bar{x} = 10.7$), and are red or yellow with rows of black spots (the bright colors fade in preservative). Hindlimbs with smaller scales, olive to brown outside and yellow or reddish inside with small black spots. The tail is red or yellow with dark dorsal lines.

In comparison to females, males are smaller, have concave plastra, and longer tails with the vent beyond the carapacial margin.

Callopsis pulcherrima pulcherrima (Gray)

Emys pulcherrimus Gray, 1855.

Nicoria punctularia var. *pulcherrima* Boulenger, 1889.

Range.—Vicinity of Acapulco on the Pacific Coast of Guerrero, Mexico.

Diagnosis.—A subspecies of *Callopsis*

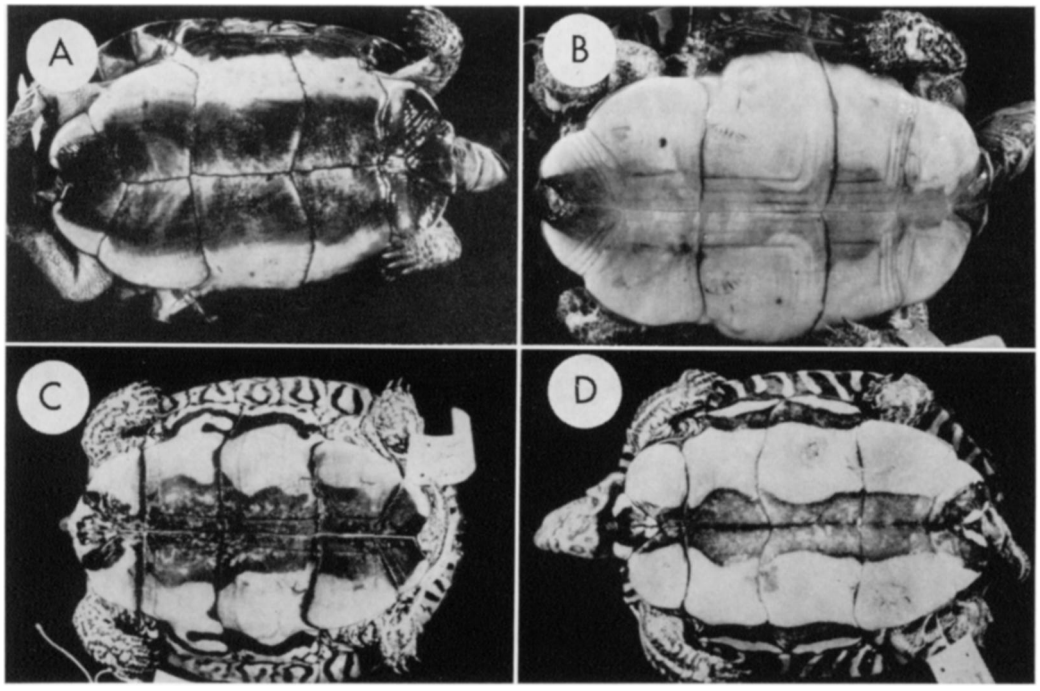

FIG. 3.—Subspecific plastral and bridge patterns of *Callopsis pulcherrima*: A) Holotype of *C. p. rogerbarbouri* (AMNH 63760); B) *C. p. incisa* (USNM 128098); C) *C. p. pulcherrima* (UF/FSM 33131); D) *C. p. manni* (PCHP 392).

pulcherrima with a low, wide brown carapace with dark flecks; a single, central, dark-bordered red or yellow spot in each pleural (Fig. 2); the undersides of the marginals with two or three light bars; a yellow plastron with a narrow, dark, central blotch which may be forked on the gulars and anals; and a bridge pattern consisting of a yellow and a black transverse bar (Fig. 3).

Description.—Essentially like that of the species, but carapace length to 166 mm (males 145, females 166) and profile low (D/PL, 0.31–0.48, $\bar{x} = 0.38$). Plastral length to 146 mm (males 127, females 146). Stripes of head pattern usually discontinuous. Carapacial and plastral patterns as given in diagnosis (Figs. 2, 3). For mensural characteristics see Table 2.

Specimens examined (7).—Guerrero (5): AMNH 79094; FMNH 196793; UF/FSM 11224, 24714, 33131. Locality unknown (2): BMNH 1882.11.23.12, 1947.3.5.52.

Remarks.—Smith and Taylor (1950) restricted the type locality of *C. p. pulcherrima* to Presidio de Mazatlán, Sinaloa, Mexico, and recent descriptions of the race have all been based on this northern form. Having previously examined a number of *C. pulcherrima* from Colima northward, when I first saw specimens from Guerrero I thought them to be a new race. However, after examining the holotype of *C. pulcherrima* (BMNH 1947.3.5.52) it became apparent that the Guerrero population was the type race and that the more northern form represented an unnamed subspecies.

I name this new turtle in honor of my former advisor and teacher Dr. Roger W. Barbour, University of Kentucky, for his many contributions to the study of vertebrate animals.

Callopsis pulcherrima ***rogerbarbouri*** subsp. nov.

Holotype.—AMNH 63760, adult female; Guirocoba, Sonora, Mexico; obtained between 15 June and 15 October 1941 by John W. Hilton.

Paratypes.—AMNH 63759, 63761 (adult males), 64520 (adult female shell), same collection data as holotype; MVZ 50912

TABLE 2.—Significant measurable subspecific characteristics of *Callopsis pulcherrima*. Significant at $P < .05$ when compared to: (a) *manni*, (b) *incisa*, (c) *pulcherrima*, (d) *rogerbarbouri*.

Character	*C. p. manni*			*C. p. incisa*			*C. p. pulcherrima*			*C. p. rogerbarbouri*		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
W/L 1st V	28	1.25 (b, c, d)	0.10	51	1.16 (a)	0.12	6	1.10 (a)	0.15	40	1.12 (a)	0.17
W/L 2nd V	24	1.16 (b)	0.16	42	1.27 (a)	0.16	3	1.22	0.09	31	1.23	0.11
W/L 2nd Pl	27	1.57 (b, d)	0.13	50	1.45 (a, d)	0.18	6	1.46 (d)	0.10	41	1.35 (a, b, c)	0.11
MW	24	13.84 (b, c, d)	3.08	41	20.36 (a)	4.22	6	21.98 (a)	1.82	31	21.67 (a)	4.48
MW/CW	22	0.12 (b, c, d)	0.03	41	0.16 (a, d)	0.04	3	0.20 (a)	0.01	31	0.19 (a, b)	0.04
GW/GL	28	0.83 (b)	0.09	38	0.95 (a, c, d)	0.13	5	0.81 (b)	0.13	39	0.83 (b)	0.13
IGL/IHL	28	1.98 (b)	0.52	38	1.59 (a, c, d)	0.61	5	2.22 (b)	0.36	39	2.13 (b)	0.84
CW/CL	24	0.78 (d)	0.03	42	0.79 (d)	0.03	3	0.75	0.05	32	0.75 (a, b)	0.04
D/CL	22	0.44 (c, d)	0.03	42	0.43 (c, d)	0.05	3	0.36 (a, b)	0.03	32	0.38 (a, b)	0.05
IFL/IAL	28	0.97 (b, c)	0.15	34	1.23 (a, d)	0.29	5	1.20 (a)	0.17	39	0.96 (b)	0.29

(juvenile), collected 13 August 1950 by Richard G. Zweifel; MVZ 50913 (adult female), collected 17 August 1950 by Kenneth S. Norris. All paratypes are from the type locality.

Diagnosis.—A subspecies of *Callopsis pulcherrima* ranging from southern Sonora southward through Colima on the west coast of Mexico and having a low, wide, brown carapace with no pleural markings (or occasionally only a faint reddish stripe or spot; Fig. 2); the undersides of each marginal with one light bar; a yellow plastron with a wide, dark (often faded) central blotch; and a totally dark-colored bridge (Fig. 3).

Description (from all specimens examined).—Carapace length to 202 mm (males 176, females 202), oval, flattened (D/CL, 0.31–0.48, $\bar{x} = 0.38$; CW/CL, 0.65–0.84, $\bar{x} = 0.75$), widest at level of marginals 6–7, highest at seam between vertebrals 2–3. Carapacial sides straight to bowed. Posterior marginals slightly serrated and somewhat flared (MW, 13.0–28.0 mm, $\bar{x} = 21.7$; MW/CW, 0.10–0.26, $\bar{x} = 0.18$). General texture of scutes rough due to growth rings. Cervical scute narrow to broad, and slightly bifurcated posteriorly to form a badge-shape. Each vertebral wider than long and with a blunt median keel. Carapace notched posteriorly. General coloration brown with usually no light markings on the pleurals, but, in some, a single faded red stripe or spot (Fig. 2). Some small black flecks may occur on all carapacial scutes. Undersides of marginals brown with a single central yellow bar.

Plastral length to 200 mm (males 150, females 200); PL/CL, 0.87–1.01, $\bar{x} = 0.94$; concave in males, and slightly upturned anteriorly in females. Posterior plastral lobe is longer and wider than the anterior. The femoral and anal scutes are curved toward midline (IFL/IAL, 0.56–2.23, $\bar{x} = 1.00$; AW/AL, 0.93–1.34, $\bar{x} = 1.20$). Anals with a wide posterior medial notch. B/PL, 0.39–0.46; $\bar{x} = 0.44$. Plastral formula: Abd. > Pect. > Fem. > An. > Gul. > Hum. GW/GL, 0.66–1.16, $\bar{x} = 0.83$; IGL/IHL, 1.15–4.16, $\bar{x} = 2.13$. Small axillary and inguinal scutes are present. Plastron yellow with a wide, often faded, central

brown blotch (Fig. 3). The seams may be dark bordered. The bridge is completely brown.

Head small with the snout only slightly projecting. Upper jaw slightly serrated laterally and notched, sometimes with cusps, at the tip (straight). Width of lower jaw symphysis less than diameter of orbit. Coloration brown with red stripes crossing the snout (2 or 3), forming a prefrontal arrow, and running from the nostrils to the orbit and from the orbit to the tympanum (this head pattern is the same as that described for the species). Iris gray to bluish-green. Jaws and chin are yellow and unmarked.

Digits only slightly webbed, if at all. Forelegs covered with large scales (9–13 rows; $\bar{x} = 10.8$), and are red with rows of black spots. Hindlimbs with smaller scales, brown outside and reddish inside with small black spots. The tail is brownish with red dorsal lines.

Males have concave plastra, and longer tails with the vent beyond the carapacial margin; females have flat plastra, slightly upturned anteriorly, and shorter tails with the vent beneath the carapace.

Specimens examined (40).—Mexico (40): Sonora (6): AMNH 63759–61, 64520, MVZ 50912–13. Chihuahua? (1): USNM 104626. Sinaloa (7): ANSP 343; KU 43617, 75656; LACM 105334; MVZ 67432; UMMZ 120422; USL 12620. Nayarit (3): CAS 91961; MSU 10718; MHNP 1898-235. Jalisco (1): UINHM 41474. Colima (19): AMNH 12611; PCHP 1091; MHNP 9982; UF/FSM 33132–35; UMMZ 80338–49. Locality unknown (3): CHE 289; SMF 7656–57.

Callopsis pulcherrima incisa (Bocourt)

Emys incisa Bocourt, Ann. Sci. Nat. Zool., Paris, Ser. 5, 10: 121 (1868).

Rhinoclemmys bocourti Gray, Ann. Mag. Nat. Hist. (London), Ser. 4, 12: 111 (1873).

Rhinoclemmys frontalis Gray, Ann. Mag. Nat. Hist. (London), Ser. 4, 12: 144 (1873).

Nicoria punctularia var. *incisa* Boulenger, Cat. Chel., Rhynch., Croc. British Mus., p. 125 (1889).

Holotype.—MHNP 9131 (dry adult female), collector and date unknown, from "montagne Conchavoua," La Union, El Salvador.

Range.—Vicinity of Tehuantepec, Oaxaca, Mexico, southward through western Guatemala, western Honduras, El Salvador, and Pacific Nicaragua to Lake Managua.

Diagnosis.—A subspecies of *Callopsis pulcherrima* with a medium to high-domed brown carapace with dark flecks; a dark-bordered red or yellow stripe or large ocellus on each pleural (Fig. 2); the undersides of the marginals with a single light bar; a yellow plastron with a narrow, dark central blotch unforked on the gulars and anals; and a brown bridge (Fig. 3).

Description.—Essentially like that of species. Carapacial length to 206 mm (males 181, females 206) and profile high (D/PL, 0.34–0.52, $\bar{x} = 0.43$). Plastral length to 213 mm (males 170, females 213). Prefrontal arrow usually sharply pointed. Carapacial and plastral patterns as given in diagnosis (Figs. 2, 3). For mensural characteristics see Table 2.

Remarks.—Gray (1873*b*) described and named the turtle *Rhinoclemmys bocourti* on the basis of a color plate of a living adult presented in Duméril and Bocourt (1870). Unfortunately, the type is not known to exist, but the color plate clearly shows this animal to be an example of *C. p. incisa*.

I examined the holotype of *Rhinoclemmys frontalis* Gray, 1873 (BMNH 1947.3.5.53) and found it also to be a *C. p. incisa*. Boulenger (1889) likewise placed *R. frontalis* in the synonymy of *incisa*.

Specimens examined (59).—Mexico (1): Chiapas (1): BMNH 1881.9.30.3. Guatemala (6): KU 59795; PCHP 1087; RAM (1), UMMZ 107879–81. El Salvador (20): FMNH 65021; LACM 61173; MHNP 9131; SMF 42197–200, 43048, 43050–52, 43164, 44301–02, 51972–74, 51978, 57546; TCWC 22311. Honduras (28): CM 57186; LACM 48350, 48352–53; LSU 28508; MCZ 49742–48; PCHP 145, 390; TCWC 17367, 19233, 22312, 23650, 23826; TU 18191, UF/FSM 33122; USNM 102888–93, 128098. Nicaragua (1): KU 85528. Locality unknown (3): BMNH 1883.4.5.61, 1947.3.5.53; SMF 58047.

Callopsis pulcherrima manni (Dunn)

Geoemyda manni Dunn, Proc. New England Zool. Club 12: 33 (1930).

Geoemyda pulcherrima manni Wettstein, Sitzungsber. Akad. Wiss. Wien Math. Naturwiss. Kl. Abt. 1: 15 (1934).

Holotype.—MCZ 29097 (adult female), collected by E. R. Dunn, 1930, from "San Jose, Costa Rica."

Range.—Lake Nicaragua in southwestern Nicaragua southward in Pacific Costa Rica to vicinity of San Jose.

Diagnosis.—A subspecies of *Callopsis pulcherrima* with a high-domed brown carapace; several large red or yellow ocelli on each pleural (Fig. 2); the undersides of the marginals with two light bars; a yellow plastron with a narrow, dark, central blotch which may be forked on the gulars and anals; and a bridge pattern consisting of a yellow and a black transverse bar (Fig. 3).

Description.—Essentially like that of species, but carapacial length to 182 mm (males 159, females 182) and profile high (D/PL, 0.39–0.53, $\bar{x} = 0.44$). Plastral length to 182 mm (males 147, females 182). Chin and ventral aspect of neck with large black spots. Carapacial and plastral patterns as given in diagnosis (Figs. 2, 3). For mensural characteristics see Table 2.

Specimens examined (29).—Nicaragua (10): AMNH 95946; 96941 (2); KU 85526–27; MCZ 54976–78; PCHP 181; TCWC 17369. Costa Rica (16): CU 9658, 9661; KU 43613–14, 67459, 102540–41; LACM 9349, MCZ 29097; PCHP 391–92; MHNP 5363, TCWC 17368; UF/FSM 33129–30; USNM 198633. Locality unknown (3): CM 58877; PCHP 144; MHNP 7958.

Intergrade C. pulcherrima *specimens examined* (24).—*C. p. pulcherrima* × *C. p. incisa* (21): Mexico (21): Oaxaca (10): AMNH 68150–53; BMNH 1879.1.9.12; MHNP 6217; USNM 46305, 46313–14, 135981. Chiapas (11): MCZ 5033; UINHM 86880; UMMZ 87731–36; USNM 109093–95. *C. p. incisa* × *C. p. manni* (3): Nicaragua (3): KU 101927, 113020; TTM 7434.

Comparisons.—*Callopsis pulcherrima* is most like *C. rubida* which has a broad asymmetrical horseshoe-like mark on the crown and a hooked upper jaw. *Callopsis areolata* has a plain yellow bridge and a broad yellow or red stripe ending behind the orbit. The terrestrial box turtles, *Terrapene*, are high-domed and have a hinged plastron. Several Mexican *Chrysemys* resemble *C. pulcherrima* in carapacial shape, but have intricate plastral patterns, numerous wide yellow lines on the head, and a broad red or orange stripe on the temple.

Callopsis rubida (Cope)

Chelopus rubidus Cope, Proc. Am. Philos. Soc. 11: 148 (1869).

Cotypes.—USNM 45612–13 (alcoholic parts and shells of adult females) and USNM 45614 (alcoholic juvenile), collected by Francis Sumichrast from Tuchitan, Tehuantepec, Mexico.

Range.—West coast of Mexico from Chamela, Jalisco, southward through Michoacan, and from Totolapan, Oaxaca, southward through western Chiapas.

Diagnosis.—A lowland species of *Callopsis* with little or no digital webbing, a hooked (unnotched) upper jaw, a flattened carapace with few pleural markings, and a broad red or yellow horseshoe-shaped mark on the crown.

Description.—Carapacial length to 230 mm (males 230, females 179), oval, flattened to slightly domed (D/CL, 0.31–0.50, $\bar{x} = 0.40$; CW/CL, 0.68–0.83, $\bar{x} = 0.76$), widest at level of marginals 6–7, highest at seam between vertebrals 2–3 or anterior vertebral 3, and slightly notched posteriorly. Sides of carapace often with a concavity at level of the bridge. Posterior marginals serrated and often flared; lateral marginals may also be flared (MW, 6.2–31.8 mm, $\bar{x} = 15.8$; MW/CW, 0.07–0.28, $\bar{x} = 0.16$). General texture of scutes rough due to growth rings. Cervical scute often bifurcated posteriorly to form an elongated badge-shape. Vertebrals wider than long and with a blunt median keel on each. Carapacial coloration in life yellow-brown with dark seams and dark mottling on each scute to entirely dark brown. A yellow spot may be present along the keel of each vertebral and on each pleural. The upper surface of each marginal usually has a rectangular-to-square yellow blotch; the undersides are brown with either a central yellow bar or yellow mottling. In preservative the yellow markings bleach to gray or cream.

Plastral length to 218 mm (males 218, females 179); PL/CL, 0.86–1.06, $\bar{x} = 0.95$; concave in males and slightly upturned anteriorly in both sexes. The posterior lobe is longer and wider than the anterior. Femoral and anal scutes are curved gradually toward the midline (IFL/IAL, 0.41–2.03, $\bar{x} = 0.71$; AW/AL, 0.76–1.86, $\bar{x} = 1.11$). The anals are widely notched posteriorly. B/Pl, 0.40–0.49; $\bar{x} = 0.44$. Plastral formula: Abd. > Pect. > An. > Gul. > Fem. > Hum. GW/GL, 0.69–1.65, $\bar{x} = 0.90$; IGL/IHL, 0.75–3.51, $\bar{x} = 1.87$. In juveniles, each gular may have three anterior projections. Small axillary and inguinal scutes are present. The plastron is yellow with a brown central blotch, and the bridge is brown.

Head with a well-developed snout. Upper jaw weakly serrated laterally and hooked at the tip (unnotched). Width of lawer jaw symphysis approximately equal to diameter of the orbit. Coloration olive to red with a highly variable broad yellow-to-red horseshoe-shaped mark on the crown. There are usually several light bars across the snout, another between the orbit and tympanum, and yet another from the corner of the mouth to the tympanum. The tympanum is light-

spotted or mottled. The iris is yellow to red. The jaws and chin are yellow with small dark vermiculation or stipples. The neck is yellow to red with numerous narrow black stripes.

The digits are only slightly webbed, if at all. The forelegs are covered with large scales (8–13 rows; $\bar{x} = 9.9$). The coloration is yellow to red with black spots and vermiculations. Hind limbs also with some large scales; olive to gray outside, yellowish inside. The tail is yellow with fine, dark, dorsal stripes. The yellow or red skin markings bleach to white or gray in preservative.

Males have concave plastra and longer tails with the vent beyond the carapacial margin.

Callopsis rubida rubida (Cope)

Chelopus rubidus Cope, 1869.

Rhinoclemmys mexicana Gray, Proc. Zool. Soc. London, p. 659 (1870).

Geomyda rubida rubida Mosimann and Rabb, Occas. Pap. Mus. Zool. Univ. Michigan no. 548, p. 2 (1953).

Range.—Western Oaxaca and Chiapas, Mexico.

Diagnosis.—A subspecies of *Callopsis rubida* with a uniform light brown carapace with dark mottlings; a gular scute approximately twice as long as the humeral; marginal scutes little flared laterally; and an elongated temporal spot.

Description.—Essentially like that of the species; but with a higher profile, a dark-bordered yellow spot on each pleural, and the vertebrals, pleurals and marginals colored the same intensity of brown. For mensural characters see Table 3.

Specimens examined (53).—Oaxaca (52): AMNH 66096, 89769, 97206, 100934, 106690; ANSP 285, 333–34, 336–41; BMNH 1879.1.7.9, 1881.9.30.4, 1903.9.30.3, 1947.3.4.34, 1947.3.5.60–61, KU 38059, 70965–66, 155017; LACM 61172; MVZ 78373–74; TCWC 17365, 23793; UF/FSM 24713, 33121; UINHM 9984–85, 9987–88, 35628; USNM 45612–14, 46283–84, 46295, 50986, 72341, 109096–99, 109216, 113276–77, 029579. Chiapas (1): LSU 24208.

Callopsis rubida perixantha (Mosimann and Rabb)

Geoemyda rubida perixantha Mosimann and Rabb, Occas. Pap. Mus. Zool. Univ. Michigan no. 548, p. 1 (1953).

Holotype.—UMMZ 80336 (adult female), collected by James A. Oliver, 13 July 1935, 8 km S Tecoman, Colima, Mexico.

TABLE 3.—Statistically significant ($P < .01$) subspecific characteristics of *Callopsis rubida*.

Character	*C. r. rubida*			*C. r. perixantha*		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
W/L 1st V	51	1.03	0.11	24	1.12	0.14
W/L 2nd Pl	51	1.36	0.14	24	1.22	0.12
MW	45	14.83	3.93	20	19.18	4.69
MW/CW	45	0.14	0.03	20	0.20	0.04
IGL/IHL	51	2.08	0.64	24	1.44	0.41
D/CL	45	0.40	0.03	21	0.38	0.02
Foreleg Scale Rows	38	9.24	1.09	24	10.96	0.98
Oval Temp. Spot	1	(2.5%)		23	(100%)	
Elongate Temp. Spot	39	(97.5%)		0	(0%)	

Range.—Southwestern Jalisco through Colima and western Michoacan, Mexico.

Diagnosis.—A subspecies of *Callopsis rubida* with the marginal scutes uniform light brown without dark mottlings; pleural scutes darker brown than the vertebrals and marginals; a gular scute only slightly longer than the humeral; lateral marginal scutes projecting outward (flared); and an oval temporal spot.

Description.—Essentially like that of the species, but with a lower profile, carapacial length to 156 mm (males 141, females 156), a dark-bordered yellow spot on each pleural, and the pleurals always darker than the vertebrals and marginals. For mensural characters see Table 3.

Specimens examined (24).—Colima (16): ANSP 342, 15259–60; CAS 14085; CHE 288; FMNH 1634; MCZ 6914, 7823; MVZ 72129; PCHP 140; SMF 7661; UF/FSM 33127; UMMZ 80335–37; USNM 55702. Michoacan (5): FMNH 39136–37; MCZ 53278; UMMZ 104333, 104335. Jalisco (3): MSU 11016–18.

Comparisons.—The only other terrestrial species of *Callopsis* occurring in Mexico are *C. areolata* and *C. pulcherrima*. *Callopsis areolata* is different in having a yellow bridge, high-domed olive carapace, and a striped head pattern; *C. pulcherrima* is very similar to *C. rubida* but has several narrow red lines across the snout, a dorsal red prefrontal arrow-pattern on the head, and a notched upper jaw. The terrestrial box turtles, *Terrapene*, are high-domed and have a hinged plastron. Several species of Mexican *Chrysemys* resemble *C. rubida* in carapacial shape, but have more intricate carapacial and plastral patterns, numerous

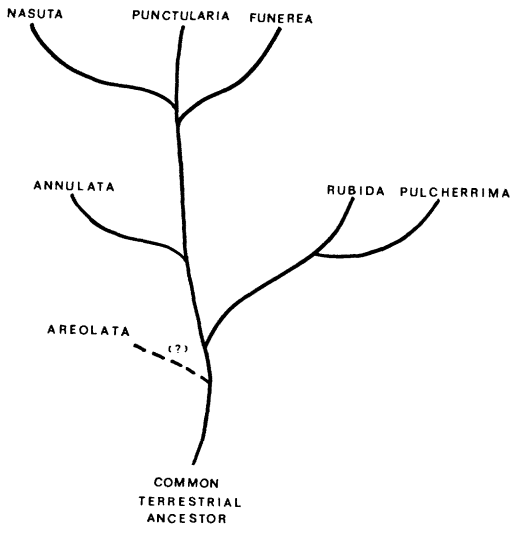

FIG. 4.—Suggested relationships of *Callopsis*.

lines on the head and neck, and usually a broad red or orange stripe on the temple.

Remarks.—Mosimann and Rabb (1953) referred *Rhinoclemmys mexicana* (Gray, 1870) to *C. r. rubida* on the basis of the colored plate published by Gray (1871). Examination of the types of *R. mexicana* (BMNH 1947.3.4.34; 1947.3.5.60, 61) has confirmed this designation as their coloration, patterns, and ratios all fall within the variation shown by other *C. r. rubida*. Also, these specimens are from San Juan del Rio, Oaxaca, well south of the range of *C. r. perixantha*.

Callopsis rubida has yet to be collected from Guerrero, but probably occurs there in the coastal lowlands. Turtles from this area may prove to be intergrades between the existing subspecies.

RELATIONSHIPS

When the morphological characteristics of the shell and the patterns of the head, carapace, plastron, and bridge are taken into consideration, the genus *Callopsis* can be divided into three groups: (1) the *pulcherrima-rubida* group of terrestrial turtles; (2) the *punctularia* group of aquatic and terrestrial species (including *C. annulata*, *C. funerea*, and *C. nasuta*); and (3) *C. areolata*.

Callopsis rubida is most closely related to *C. p. pulcherrima* and *C. p. rogerbarbouri*, with which it shares a relatively low carapace and similar carapacial and plastral patterns; *C. rubida* and *C. p. rogerbarbouri* also have the same bridge coloration. In the northern part of its range, *C. p. incisa* also shares the bridge and plastral patterns, and is somewhat flattened; however, populations from the southern part of its range have more colorful carapaces and deeper shells, possibly due to genetic influence from *C. p. manni*. The most divergent characters of these two species are the head patterns, plastral scute formulae, and the notched *versus* hooked upper jaws. The jaw adaptations are probably due to different feeding habits.

Turtles of the *punctularia* group share similarly structured carapaces and carapacial, plastral, bridge, and head patterns (the head pattern of *C. p. diademata* probably evolved from that of *C. p. melanosterna*). All have a notched upper jaw except the terrestrial *C. annulata*. *Callopsis nasuta* and *C. punctularia* have identical plastral formulas, while *C. annulata* differs only in having the humeral longer than the gular, and *C. funerea* has the gular longer than the anal. *Callopsis funerea* and *C. punctularia* are the only *Callopsis* with a choanal papilla (McDowell, 1964).

Callopsis areolata has similarities with both groups, but its ovoid carapace and plain bridge are unique. It shares its head pattern and plastral formula with the *punctularia* group, but is closer to *pulcherrima* and *rubida* in its plastral and carapacial patterns. It is hoped that later electrophoretic and karyotype studies will reveal its exact relationships.

Callopsis is the only batagurine genus in the Americas, and is most closely related to the Asiatic genera *Cyclemys* and *Melanochelys* (McDowell, 1964). Zoogeographically, its origins are also probably Asiatic. McDowell (1964) believed the Eocene fossil turtle *Echmatemys pusilla* Hay, 1908, from the Bridger B of Grizzly Buttes, Wyoming, to be a *Callopsis*. This might indicate a southward migration of turtles that had crossed the Bering land bridge from Asia. A hypothetical evolutionary tree for *Callopsis* is presented in Figure 4.

Such a radiation could have occurred if a common terrestrial ancestor invaded the lowlands of western Mexico during the Oligocene or early Miocene and then proceeded southward into Central America along two dispersal routes: one along the west-coast lowlands, and a second along the east-coast lowlands after having crossed the Isthmus of Tehuantepec north of the Chiapas and Guatemalan highlands (such dispersal routes are discussed and illustrated by Savage, 1966). The *pulcherrima-rubida* line arose in the savanna areas on the west coast of Mexico, and *C. areolata* on the east coast. When the ancestral line entered the tropical rainforests of Central America, *C. annulata* evolved. Up to this time there had been little or no competition for niches from other terrestrial turtles, but now the first *Geochelone* land tortoises (Testudinidae) were met. The *Geochelone* were well established in Central and South America by at least the early Miocene (Auffenberg, 1971) and apparently provided too much competition for the neophyte *Callopsis*. This competition, plus the separation of Central and South America by the Panamanian marine portal from the Eocene to Pliocene, temporarily stopped the southward dispersal of *Callopsis*. Once the terrestrial niches were closed, the only possible new adaptive zone was aquatic. It is doubtful that *Chrysemys* reached Central America before the late Pliocene or Pleistocene, as their earliest fossils are from Miocene-Pliocene deposits in North America (Ernst and Barbour, 1972), and thus the Emydidae aquatic niches would have been open. Those *Callopsis* which first became semiaquatic and later aquatic probably found little competition from the bottom dwelling chelydrids and kinosternids (if they were present in Central America at that time), and some radiated into *C. funerea*. After the close of the marine portal in Panama, the *Callopsis* dispersed into South America. The terrestrial *C. annulata* invaded the lowland forests of western Colombia (Choco) and northern Ecuador, but was probably confined there because of competition from the already widespread *Geochelone*. The aquatic *Callopsis* entered southern Panama and northern South America where it became *C. punctularia*. *Callopsis nasuta* is the most specialized aquatic *Callopsis* and probably arose from *punctularia* which invaded the swift-flowing, deep rivers of western Colombia and northern Ecuador. Further invasion of South America was checked by competition from aquatic pleurodirans (Chelidae, Pelomedusidae) which had been present since the late Miocene or early Pliocene (Simpson, 1942). The ancestral North American population apparently died out during the Pleistocene, leaving *Callopsis* in its present range.

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MATING BELLOWS OF THE GALAPAGOS TORTOISE, *GEOCHELONE ELEPHANTOPUS*

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THE low-pitched sound produced by male giant tortoises during mating has been described by several authors (DeSola, 1930; Evans, 1949; Van Denburgh, 1914) as a "roar" or "bellow," but has not previously been quantified. Campbell and Evans (1967) produced the first sonagrams of chelonian sounds from recordings of a male *Geochelone carbonaria* that was following and attempting to mount a female. Subsequently, Campbell and Evans (1972) analyzed vocalizations of two additional turtle species and described correlated behavior in a short review of the general