

Head color and caruncles of sympatric *Cathartes* vultures (Aves: Cathartidae) in Guyana and their possible function in intra- and interspecific signaling

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Abstract.—The naked heads of *Cathartes* vultures are widely believed to be adaptations for temperature regulation and to reduce plumage fouling during carrion feeding. Bright head color and the elaborate pattern of caruncles on the head and neck skin have a likely function in intra- and interspecific signaling. These integumentary characters have been difficult to study because of extensive postmortem color fading and shrinkage in museum specimens. Here I provide the first detailed description of head color and caruncles of the Greater Yellow-headed Vulture (*C. melambrotus*) from freshly collected specimens and provide comparative notes on sympatric populations of the Turkey Vulture (*C. aura*) and Lesser Yellow-headed Vulture (*C. burrovianus*) from Guyana.

Keywords: caruncles, *Cathartes*, Guyana, head color, intraspecific signaling, vulture

The genus *Cathartes* (Aves: Cathartidae) is composed of three extant species restricted to the Western Hemisphere (Wetmore 1950, 1964). The Turkey Vulture, *Cathartes aura* (Linnaeus 1758), breeds throughout South America and in most of continental North America south of 50° N latitude (Wetmore 1964, Kirk & Mossman 1998). Depending on the taxonomic authority, four to six subspecies of *C. aura* have been recognized on the basis of plumage darkness, wing length, and head color (Hellmayr & Conover 1949, Wetmore 1964, Blake 1977, Kirk & Mossman 1998). Taxonomy of the “yellow-headed” vultures was exceptionally confused (Wetmore 1926, Lehmann 1944, Dugand 1951, 1952) until Wetmore (1964) diagnosed two biological species—

Lesser Yellow-headed Vulture, *C. burrovianus* (Cassin 1845), which occurs in savannahs, grasslands, marshes, and mangrove swamps from eastern Mexico south to Argentina, Brazil, and Uruguay, and the Greater Yellow-headed Vulture, *C. melambrotus* (Wetmore 1964), which is restricted to the lowland humid Amazonian forest biome. Despite its conspicuousness and large geographic range, relatively little is known about the natural history of *C. melambrotus* and even basic information such as its use of olfaction to find carrion was only recently discovered (Graves 1992, Gomez et al. 1994).

Wetmore (1964:1) pinpointed the principal obstacle to diagnosing subspecific taxa and species limits in *Cathartes*, “The color differences of the bare head and neck that separate the species, and in the case of the red-headed group some of the subspe-



Fig. 1. Soft part colors and the morphology and distribution of skin caruncles are difficult to determine in traditional museum specimens: (top) *Cathartes aura ruficollis* (♂, USNM 625337, Abary River, Guyana, 4 April 1999); (middle) *C. burrovianus urubitinga* (♀, USNM 131945, Georgetown, Guyana, 11 July 1891); (bottom) *C. melambrotus* (type, ♂, USNM 483532, Karabo, Guyana, 15 January 1930).

cies, change soon after death to a dull hue discouragingly similar in all.” Not only are soft part colors difficult to discern in traditional museum specimens but the caruncles and papillae on head and neck skin are shriveled and scarcely visible (Fig. 1). These factors and sample size deficiencies caused by the reluctance of collectors to collect carrion-gorged vultures and space constraints for storage of bulky

specimens have resulted in a woefully inadequate resource base for evaluating morphological variation in *Cathartes*.

Head color and caruncle morphology in *Cathartes aura* are known to exhibit geographic variation (Wetmore 1964, Kirk & Mossman 1998) but population studies have not yet been attempted with series of living birds or freshly-collected specimens. Virtually nothing is known about variation in these characters in *C. burrovianus* and *C. melambrotus*. Illustrations and descriptions in standard references suggest that the head and neck color of the two yellow-headed species is identical or nearly so (Houston 1994). Wetmore (1950) provided fairly detailed descriptions of head color of freshly collected specimens of *C. burrovianus* from Panama and Argentina in a paper that has been widely overlooked (Appendix 1). Comparably detailed descriptions of *C. melambrotus* have not been published. The purpose of this paper is to provide descriptions of head color and skin caruncles in *C. melambrotus* (Appendix 2) and comparative notes on sympatric populations of *C. burrovianus urubitinga* and *C. aura ruficollis* from Guyana.

Methods

Adult specimens of *Cathartes aura ruficollis* (2 ♂♂) and *C. burrovianus urubitinga* (2 ♀♀; 3 ♂♂) were collected from 16 to 21 October 2015 at Dadanawa Ranch, Upper Takutu-Upper Essequibo, Guyana (2° 49.28' N, 59° 31.34' W; 127 m above sea level) for investigations of the gastrointestinal microbiome. The sprawling Dadanawa Ranch hosts several thousand cattle that roam freely in a mosaic of habitats including broad expanses of grassland and scrubby savannah bisected by narrow corridors of riparian forest bordering the Rupununi River and nearby oxbow lakes. Black Vulture (*Coragyps atratus*) was abundant (outnumbering all other cathartids combined by > 50:1) and

Table 1.—Specimens of *Cathartes aura ruficollis*, *C. burrovianus urubitinga*, and *C. melambrotus* collected in the Upper Takutu-Upper Essequibo region of southern Guyana.

Museum number ¹	Species	Sex	Collecting location ²	Reproductive condition ³	Body mass (g)
651995	<i>aura</i>	♂	D	L testis: 6 × 4 mm; R testis: 4 × 3 mm	1150
652005	<i>aura</i>	♂	D	L testis: 7.5 × 6 mm; R testis: 6.5 × 4.5 mm	1250
652028	<i>aura</i>	♀	K	L ovary: 15 × 9 mm, granular, largest ovum 3 mm in diameter	1450
651996	<i>burrovianus</i>	♀	D	Ovary: 11 × 7 mm, granular; oviduct: 4 mm in diameter at cloaca	825
652000	<i>burrovianus</i>	♀	D	Ovary: 11 × 7 mm, largest ova 2 mm in diameter	900
652004	<i>burrovianus</i>	♂	D	L testis: 7 × 4.5 mm; R testis: 6 × 4 mm	875
652018	<i>burrovianus</i>	♂	D	L testis: 4 × 3 mm; R testis: 4 × 3 mm	750
652019	<i>burrovianus</i>	♂	D	L testis: 5 × 4 mm, black; R testis: 5 × 4 mm, black	850
652021	<i>melambrotus</i>	♂	K	L testis: 9 × 6 mm, pale; R testis: 6 × 4 mm, gray	1400
652022	<i>melambrotus</i>	♂	K	L testis: 8 × 6 mm; R testis: 5 × 3 mm	1425
652023	<i>melambrotus</i>	♀	K	Ovary: 10 × 8 mm, granular	1600
652024	<i>melambrotus</i>	♀	K	Ovary: 15 × 12 mm, granular, largest ovum 3 mm in diameter	—
652025	<i>melambrotus</i>	♂	K	L testis: 5 × 4 mm, black; R testis: 4 × 3 mm, black	1450
652026	<i>melambrotus</i>	♀	K	Ovary: 15 × 12 mm, granular; oviduct: 5 mm in diameter at cloaca	1625
652029	<i>melambrotus</i>	♂ ^{4, 5}	K	L testis: 4 × 1.5 mm; R testis: 2 × 1.5 mm	1450
652030	<i>melambrotus</i>	♂ ^{4, 6}	K	L testis: 6 × 3 mm; R testis: 4 × 2 mm	1375
652032	<i>melambrotus</i>	♂ ⁷	K	L testis: 5 × 3 mm; R testis: 4 × 2.5 mm	1300
652299	<i>melambrotus</i>	♂	K	L testis: 7 × 5 mm; R testis: 5 × 3 mm	1750

¹ National Museum of Natural History (USNM), Smithsonian Institution.

² D = Dadanawa Ranch (16–21 October 2015) K = Kanuku Mountains Protected Area (23–29 October 2015).

³ L = left; R = right. USNM 65028 possessed paired ovaries.

⁴ Dark gray pigment on the maxillary and mandibular ramphothecas, indicative of immaturity.

⁵ Bursa (14 × 8 mm).

⁶ Bursa (12 × 7 mm).

⁷ Bursa (10 × 6 mm).

King Vulture (*Sarcoramphus papa*) is seasonally present. *Cathartes melambrotus* occurs regularly in the continuous forest on the southern flanks of the Kanuku Mountains, ~15 km north of the collection site.

Cathartes melambrotus (3 ♀♀; 7 ♂♂) and an additional specimen of *C. aura* (1 ♀) were collected from 23 to 29 October 2015 at a second location that lies 45 km NNE of Dadanawa in the Kanuku Mountains Protected Area, Upper Takutu-Upper Essequibo, Guyana (3° 12.20' N, 59° 24.20' W; 109 m above sea level). This site

was centered on the Rupinuni River in a vast region of old growth forest. *Cathartes melambrotus* was common at this site. Three other cathartids were present in lesser numbers at the collecting site, in descending order of abundance, *Coragyps atratus*, *S. papa*, and *Cathartes aura*.

Vulture heads were photographed soon after the animals were euthanized. Body mass was measured with a spring balance to the nearest 5 g. Reproductive condition of specimens was determined during specimen necropsy (Table 1). All specimens were examined for the presence of a bursa

of Fabricius, a small diverticulum of the proctodeal region of the cloaca that is found only in immature birds (Glick 1983). Specimens were also examined for the occurrence of dark gray pigment on the maxillary ramphotheca, a character that is associated with immaturity (hatching year or second year) in *C. aura* populations in eastern North America (Henckel 1981). Topography of the head and neck follows the terminology of Lucas & Stettenheim (1972; see Fig. 5). Caruncle length was measured from the skin surface (Baldwin et al. 1931) of specimens preserved in 10% formalin. Color descriptions were based on photographs of specimens taken under variable light conditions without background color standards. For this reason, I use general color descriptions rather than quantitative color descriptions (e.g., Munsell color system). All specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Results and Discussion

Comparison of Cathartes melambrotus and C. burrovianus.—Head and neck color of sympatric populations of the two yellow-headed vultures in Guyana exhibit significant differences that are readily apparent in the hand. The facial skin of *C. melambrotus* is marked with a vibrant lemon yellow to chrome yellow swath extending from the nasal and mandibular malar regions posterior to the ear opening and ventrally to the upper submalar region (Fig. 2; Appendix 2). Head and neck color of adult males ($n = 4$) and females ($n = 3$) were similar. The yellow facial swath was slightly paler and more restricted in extent in two immature males (USNM 652029, 652030) that possessed a cloacal bursa and gray markings on the maxillary ramphotheca. Head color in a third immature male (USNM 652032) with a bursa and an unmarked ivory-colored bill resembled

that of adult males. The postorbital region, hindcrown, and dorsal neck of the most immature-appearing specimen (USNM 653029) were more heavily feathered with short bristle-like filoplumes than in the other immatures and adults.

The color of the facial swath in adult *C. burrovianus* is richer in tone, varying from deep yellow to yellowish orange. In contrast to *C. melambrotus*, the yellow and orange pigments in *C. burrovianus* do not extend beyond the malar mandibular region to the submalar region (Figs. 2, 3; Appendix 1). The presence of bright yellow pigment on the throat of adult *C. melambrotus* is useful for discriminating the two yellow-headed species at a distance (Fig. 4). Both yellow-headed species possess a dark facial stripe between the eye and ear opening that is densely feathered with short black filoplumes.

Caruncles are small fleshy eminences or protuberances of the skin (Lucas & Stettenheim 1972). Both yellow-headed vultures possess transverse rows of small wart-like caruncles on the hindcrown and bare portions of the neck (Figs. 2, 3). In *C. melambrotus*, the largest caruncles (protruding 2.5–3.0 mm from the skin) occur on the lower lateral neck. The two immatures with gray bill markings and bursas (USNM 652029, 652030) had fewer caruncles on the posterior crown and anterior portion of the dorsal neck but caruncle development on the lateral neck region was similar to that of adult males.

Caruncles are more widely distributed in *C. burrovianus*, extending laterally from the dorsal neck to the anterior ventral neck and anteriorly to the ear opening in the postorbital region. Caruncle size in the two species overlaps but those on the lower lateral neck in *C. burrovianus* tend to be longer, more pendulous, and are more likely to be stalked with elongated bulbous tips. The extent to which caruncles are erectile in living individuals of *C. burrovianus* and *C. melambrotus* is unknown.

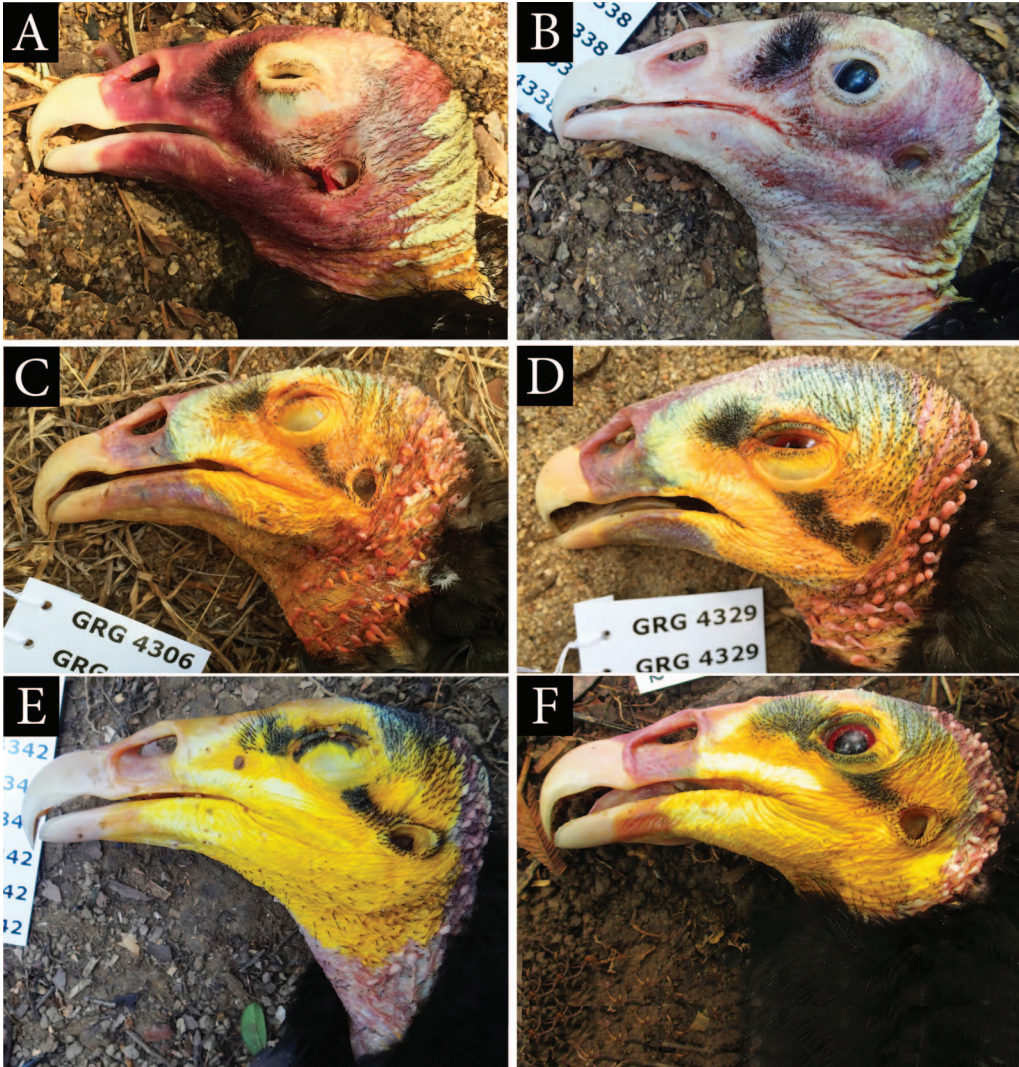


Fig. 2. Heads of three sympatric species of *Cathartes* vultures occurring in southern Guyana (sex; museum number)—(A) *C. aura* (♂, USNM 651995); (B) *C. aura* (♀, USNM 652028); (C) *C. burrovianus* (♀, USNM 651996); (D) *C. burrovianus* (♂, USNM 652019); (E) *melambrotus* (♂ immature, USNM 652032); (F) *C. melambrotus* (♂, USNM 652022). Photographs (B, E, F) courtesy of Christopher M. Milensky.

The dorsal and lateral neck skin in *C. melambrotus* is flesh colored, pale grayish purple, or pale pinkish purple studded with white, pinkish white, or pale pink caruncles (Figs. 2, 3). There were no consistent differences between males and females in the color of neck skin or caruncles. Within-individual variation in caruncle color was nil in *C. melambrotus*. Neck skin in *C. burrovianus* is yellowish orange to reddish

orange and studded with orange, reddish-orange, rose, reddish-purple or yellow caruncles. In contrast to *C. melambrotus*, caruncles in male and female *C. burrovianus* may be multicolored (Fig. 3D).

Yellow and orange pigments in *C. burrovianus* and *C. melambrotus* were relatively vibrant for 2–3 weeks following saturation in 10% formalin. However, only faint traces of yellow were visible 12 weeks



Fig. 3. Skin caruncles of sympatric species of *Cathartes* vultures occurring in southern Guyana—(upper row) hindcrown of *C. aura* (♀, USNM 652028); (middle left) side of head centered posterior to ear opening of *C. burrovianus* (♂, USNM 652019); (middle right) side of neck below the ear opening of *C. burrovianus* showing multicolored caruncles (♂, USNM 652018); (bottom left) hindcrown and dorsal neck of *C. melambrotus* (♂, USNM 652299); (bottom right) side of throat of *C. melambrotus* (♂, USNM 652021). Photographs (upper left, bottom left) courtesy of Christopher M. Milensky.

after preservation. The identity of the yellow pigment is unknown, but lutein, which appears yellow at low concentrations and reddish-orange at high concentrations, has been extracted from the yellow facial skin of the distantly related

Egyptian Vulture, *Neophron percnopterus* (Negro et al. 2002). By comparison the slate blue pigment on the crowns of *C. burrovianus* and *C. melambrotus* was still strongly visible 12 weeks after preservation.



Fig. 4. *Cathartes melambrotus* photographed on the Rupununi River, Upper Takutu-Upper Essequibo, Guyana ($3^{\circ} 12.3' N$, $59^{\circ} 24.3' W$). The bright yellow throat of adults separates this species under field conditions from the frequently confused *C. burrovianus*.

Cathartes aura ruficollis.—Little is known about geographic or sexual variation in head color in this widespread taxon that ranges from Panama southward east of the Andes to northern Argentina, Uruguay, and southern Brazil. Wetmore (1964:7) offered a composite description of head color without locality data, “. . . in life, head and neck dull red, with several distinct transverse yellowish white or greenish white lines across the posterior surface of the crown and the nape; adult usually with an irregular area of yellowish white in the center of the crown.”

Head color in the three recently collected specimens (2 ♂♂, 1 ♀) from

Guyana ranged from dull pinkish red to garnet red (Fig. 2A, B). This variation is likely a response to handling. Captured individuals of *C. aura septentrionalis* from eastern North America reportedly enter a defensive stupor during which the head and neck color changes from red to light red, gray, and nearly white (Henckel 1981). These color changes reverse when the birds are released. Flushing and fading of head color is caused, respectively, by vasodilation and vasoconstriction of subcutaneous capillaries (Arad et al. 1989). During vasoconstriction, the skin assumes the color of the whitish collagen fibers in the subcutaneous connective tissue. The red color during vasodilation is due to hemoglobin rather than carotenoid pigments in the skin, although small amounts of carotenoid pigments have been detected in blood plasma of the Andean Condor (*Vultur gryphus*) and Black Vulture (*Coragyps atratus*) (Blanco et al. 2013).

Specimens of *C. aura ruficollis* from Guyana exhibit slightly elevated patches of creamy white skin on the anterior half of the crown and on the dorsal neck (Figs. 2, 3). The crown patch is composed of a broad pad of smooth skin marked by three or four deep transverse folds or creases. The white patch is virtually devoid of black filoplumes and is smoother and less wrinkled than the reddish skin flanking it fore and aft. The dorsal neck patch, which is separated from the crown patch by a transverse band of reddish skin, extends from the posterior crown to the feather line on the lower neck. The dorsal neck patch is composed of 4–6 major transverse bands and 2–3 minor bands of creamy white skin separated by deep creases or folds. The transverse bands become progressively narrower from the crown to the feather line; the skin between the posterior bands is dull pale yellow to buffy yellow. Unlike the mostly smooth crown patch, the white neck bands are stippled with filoplumes to the same extent as the

adjacent reddish skin. As far as is known, all populations of *C. aura ruficollis* possess creamy white crown and neck patches. Likewise, all known populations lack the white caruncles on the orbital and nasal regions of the facial skin that are characteristic of adult *C. a. septentrionalis* of eastern North America (Kirk & Mossman 1998) and *C. a. aura* of Jamaica (Gosse 1847).

None of the *Cathartes* specimens collected in October 2015 in the Upper Takutu-Upper Essequibo region of Guyana exhibited gonadal activity consistent with breeding (Table 1). The degree to which head color and caruncle morphology varies seasonally with breeding condition or ephemerally during social interactions remains to be investigated.

Conclusions

Social behavior, modes of communication and competitive interactions among *Cathartes* vultures are poorly known (Audubon 1834, Loftin & Tyson 1965, Wallace & Temple 1987, Houston 1988, Gomez et al. 1994, Kirk & Houston 1995). Owing to the absence of a syrinx (Miskimen 1957), vocalizations in the genus are limited to low-frequency hissing and coughing and whining inhalations and exhalations (Audubon 1834, Pemberton 1925, Lynch 2006). The acoustic pathways available for communication in other diurnal raptors have been evolutionarily lost in this specialized clade of carrion scavengers.

Bare head and neck skin of *Cathartes* vultures are believed to be adaptations to reduce plumage fouling during carrion feeding (Darwin 1845) and for temperature regulation (Arad et al. 1989). The function of bright skin color and the elaborate patterns of skin caruncles has not been explicitly addressed. I hypothesize that both characters are likely adaptations for individual recognition and intra- and

interspecific signaling of age and dominance status. Vivid skin ornamentation in *Cathartes* may compensate in some respects for the inability to communicate with modulated high-frequency syringeal vocalizations.

Further advances in our understanding of the age, sexual, and geographic variation in head and neck color and the morphology of caruncles are unlikely to come from additional study of existing museum collections. Investigators should strive to obtain photographic documentation of head and neck color and caruncle morphology from vouchered population samples of all *Cathartes* species from as many breeding localities as is practicable.

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Appendix 1

Descriptions of soft part colors of *Cathartes burrovianus* (Wetmore 1950: 417).

Soft part colors of a freshly-collected female *C. b. burrovianus* obtained at El Rincón, Panama.

“Cere, forepart of crown to center of eyes, nape, back of head, and throat dull orange-red; center of crown dull bluish gray; sides of head from posterior loreal space through eye and ear, including the area down to below the gape, bright orange; lores greenish yellow; spot in front of and slightly above eye dull bluish gray; sides and front of neck, including the area covered by papillae dull yellowish orange; iris red.”

Soft part colors of a freshly-collected adult male *Cathartes burrovianus urubtinga* obtained at Las Palmas, Chaco, Argentina.

“The bill was cream buff, shading to vinaceous buff on a broad area that extended onto the forehead, behind the nostrils; side of the head in general, including eyelids, deep chrome; center of crown dark Tyrian blue, bordered on either side by a broad band of stone green; skin of throat posteriorly deep chrome, becoming paler forward, to shade into olive buff toward base of bill; space between mandibular rami spotted with dark Tyrian blue; a dull spot of slate blue beneath the nostrils on either side; iris carmine; tarsus cartridge buff, shading to neutral gray on toes, where the interscutal spaces have a scurfy whitish appearance.”

Appendix 2

Description of head color and caruncle distribution in a freshly collected specimen of *Cathartes melambrotus* (♂ adult, USNM 652022; Fig. 2F) from

the Kanuku Mountains Protected Area, Upper Takutu-Upper Essequibo, Guyana. (3° 12.20' N; 59° 24.20' W)

The maxillary and mandibular ramphotheca are ivory colored. Fleshy skin surrounding the nostrils varies from fleshy pink to pinkish red. This color extends along the nasal arch and forehead to a point perpendicular to the middle of the eyes. The forehead is tinted or dappled with creamy yellow. The lateral margins of the nasal arch shade from fleshy pink to creamy yellow or buffy yellow before merging with chrome yellow on the upper eye lid and the nasal region. A patch of short black filoplumes overlying grayish skin occurs anterior to the eye. The orbital region is pale yellow to chrome yellow; the eyelids are rimmed with a slate gray line beneath the eyelash filoplumes. The transversely-furrowed skin of the crown is slate blue shading to pinkish purple on the posterior edge of the crown. Crown furrows relax when the neck is extended.

Skin at the anterior margins of the nasal and malar regions adjacent to the ramphotheca is pinkish buff or pinkish red becoming chrome yellow about half way to the rictus. The sides of the face (posterior edge of nasal, maxillary and mandibular malar, suborbital, hyoid, postorbital) and upper throat (upper parts of the submalar regions) are chrome yellow. The chrome yellow skin on the sides of the face and upper throat are softly wrinkled and wattle-like (Fig. 3F). A narrow strip of flesh-color skin extends up the ventral midline of the anterior neck separating the chrome yellow facial patches. A contrasting diagonal band of slate-gray skin extends from the lower eyelid to the ear opening. This band is lightly to densely feathered with short black filoplumes. The rear portions of the crown, anterior dorsal neck, and lateral neck regions are pale pinkish purple. Transverse rows (12 or more) of caruncles extend from the rear of the crown to the feathered margins of the bare skin on the anterior dorsal neck. The largest caruncles (protruding 3.0 mm from the skin) occur on the lower lateral neck. These are somewhat flattened and tab-shaped. On average, caruncles are paler than the surrounding skin. Short black filoplumes are scattered on the lower throat and neck skin but are not embedded in the largest caruncles. The iris is carmine red.