

Taxonomy, Morphology, and Distribution of *Atractus flammigerus* Boie 1827 (Serpentes: Dipsadidae)

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ABSTRACT: *Atractus flammigerus* was described on the basis of two specimens from Java (in error). Subsequently, its lectotype was designated and the type locality restricted to Paramaribo in Suriname. Although this species has been repeatedly recorded throughout western Amazonia (mainly from Brazil and Peru), all of these records were erroneously assigned to *A. flammigerus* because of a considerable level of confusion with two widespread congeners (*A. snethlageae* and *A. torquatus*). To date, only nine individuals of *A. flammigerus* (sensu stricto) are reported in the literature on the basis of vouchered specimens. During the examination of scientific collections and fieldwork we found 12 additional specimens of this poorly known snake, expanding our knowledge on its morphological variability and distribution. In this paper, we report new localities and data on meristic, morphometric, color pattern in life and, after preservation, macro- and micro-ornamentation of dorsal scales, cranial osteology, and hemipenis morphology of *A. flammigerus*. We provide new diagnostic features and additional data for detailed comparisons with morphologically similar and sympatric congeners, and update the species boundaries of *A. flammigerus*.

Key words: External morphology; Guiana Shield; Hemipenis; Microdermatoglyphics; Osteology; Species boundaries

THE CRYPTOZOIC snakes of the genus *Atractus* Wagler 1828 are distributed widely in the Neotropics, occurring from Panama to Argentina (Giraud and Scrocchi 2000; Myers 2003). *Atractus* is the most species-rich snake genus in the world, encompassing 146 valid species to date (Passos et al. 2016a; Arteaga et al. 2017). A substantial number among these are known only from small series in collections and display relatively restricted distributions (Prudente and Passos 2008; Passos et al. 2009a,b,c,d,e, 2010a,b,c). In the last 10 yr, the taxonomy of the genus has undergone an unprecedented flux on the basis of studies from specific portions of the Andes (Passos et al. 2009a), certain trans-Andean (Passos and Lynch 2011) or cis-Andean (Passos et al. 2010c) provinces, broad biogeographic regions of South America (Passos et al. 2013a), and on species complexes (Passos et al. 2010b). As expected, old names of species poorly characterized in the past have been resurrected or species were rediscovered after many decades because of newly obtained specimens (Passos and Arredondo 2009; Passos et al. 2007a, 2009a, 2010a, 2012, 2013a,b,c). The taxonomic status of several species that were poorly known or hardly diagnosable has been recently improved because of these new samples studied within a comparative framework (including the examination of original types series; Passos et al. 2016b), considering distinct morphological systems (Passos and Prudente 2012; Passos et al. 2013c, 2016a). Such an approach, using rarely explored phenotypic characters, is critical to properly diagnose cryptic taxa and accurately infer species boundaries within this highly speciose genus (Passos et al. 2010b; Prudente and Passos 2010). In this paper, we report new material unambiguously assigned to *Atractus flammigerus* and evaluate the boundaries among closely related species on the basis of the congruence between qualitative and quantitative analyses of putatively independent morphological systems. We also

update the diagnostic features of *A. flammigerus* and provide new comparisons with respect to morphologically similar and sympatric species.

HISTORICAL RESUMÉ

Boie (1827) described *Brachyorrhos flammigerus* on the basis of two specimens erroneously labeled as coming from Java (see Hoogmoed 1980). Schlegel (1837) proposed the synonymy of *B. flammigerus* with *B. badius* Boie 1827 under the combination *Calamaria badia*. Duméril et al. (1854) transferred *C. badia* to the genus *Rabdosoma* Duméril 1854. Jan (1862) recognized many forms as varieties of *R. badium*. Boulenger (1894) redefined the genus *Atractus* and allocated *R. badium* and its varieties, as well as their junior synonyms, to this genus. Boulenger's work influenced all subsequent studies (Amaral 1930; Savage 1960; Peters and Orejas-Miranda 1970; Pérez-Santos and Moreno 1988) in associating those *Atractus* species with 17 dorsal scale rows and a banded color pattern with *A. badius*. Hoogmoed (1980) rediscovered the syntypes of *B. badius*, *B. flammigerus*, and *B. schach* Boie 1827, resurrected them from the synonymy of *A. badius*, and pointed out the distinctive nature of each of them. Hoogmoed (1980) designated a lectotype for *A. flammigerus*, restricting the type locality to Paramaribo, Suriname, on the basis of the origin of the material from Brugmans cabinet. Hoogmoed (1980) reported new localities for *A. flammigerus* in Suriname (Nassau Mountains and Sipaliwini airstrip) and Peru (Paraíso, Iquitos), interpreting *A. flammigerus* as a widespread Amazonian species (Hoogmoed 1980, 1983).

Gasc and Rodrigues (1980) described *Geophis alasukai* on the basis of three specimens from French Guiana (upper Oyapock and Arataye rivers). However, Hoogmoed (1983) considered the types of *G. alasukai* identical to *A. flammigerus*. Cunha and Nascimento (1983) described *A. flammigerus snethlageae* on the basis of nine specimens from eastern Pará, western Maranhão (both regions south of the

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Amazon River), and Amapá (north of the Amazon River) in Brazil. Dixon and Soini (1986) reported two specimens of *A. flammigerus* from the Iquitos region (Moropon and Paraíso) in Peru, apparently following Hoogmoed's concept of the species. Vanzolini (1986) raised *A. snethlageae* to specific rank, without further comments. Chippaux (1986) reported five new specimens of *A. flammigerus* from two localities (Arataye and Cacao) in French Guiana, but did not state where the material was deposited. Martins and Oliveira (1993) followed Vanzolini (1986) and considered *A. snethlageae* as a species, reporting additional specimens from central Amazonia. Silva (1993) reported on *A. flammigerus* from Porto Velho, Brazil. Several authors continue to cite *A. flammigerus* as part of the Peruvian snake fauna (e.g., Carrilo and Icochea 1995; Lehr 2002). Claessen (2001, 2003) accidentally used the combination *G. alasukai* (erroneously considering *A. flammigerus* as a synonym), without explanation. Hoogmoed and Prudente (2003) commented on the taxonomic history of Amazonian species of *Atractus*, reinforcing the synonymy of *G. alasukai* with *A. flammigerus*, as earlier suggested by Hoogmoed (1983). Duellman (2005) reported six individuals of *A. flammigerus* from Cusco Amazonico in Peru, and stated that 14 specimens previously identified as *A. major* by Duellman (1978) from Ecuador (Santa Cecilia and Lago Agrio) are in fact *A. flammigerus*. In contrast, some authors have identified specimens from Amazonian portions (outside the Guiana Shield) of Brazil, Colombia, Ecuador, and Peru to *A. snethlageae* differing from previous identifications in literature or in collections (e.g., Passos et al. 2007b; Passos and Fernandes 2008; Prudente and Passos 2008). However, other authors who worked in the western Amazonian portions of Brazil (Bernarde et al. 2012) and in Peru (Catenazzi et al. 2013) are still reporting the occurrence of *A. flammigerus*. More recently, Schargel et al. (2013) performed morphometric analyses of large-bodied Amazonian species of *Atractus*, corroborating the distinction between *A. flammigerus* (sensu stricto from Suriname) and *A. snethlageae* (sensu lato from outside the Guiana Shield). On the other hand, Schargel et al. (2013) pointed out that *A. snethlageae*, as currently understood, probably represents a species complex deserving a detailed taxonomic study. Therefore, it seemed useful to infer the boundaries of variation and distribution of *A. flammigerus*.

MATERIALS AND METHODS

Specimen and Geographical Data

All specimens of *A. flammigerus*, *A. badius* and *A. snethlageae* examined by us are listed in the Appendix. Institutional acronyms follow Sabaj Pérez (2016). Data from additional specimens of *Atractus* previously examined by us (including *A. latifrons*, *A. schach*, *A. snethlageae*, *A. riveroi*, and *A. torquatus*) can be found in Almeida et al. (2014), Passos et al. (2005, 2007a,b, 2013a), Passos and Fernandes (2008), Prudente and Passos (2008), and Passos and Prudente (2012). Data on external morphology of six specimens of *A. flammigerus* housed in the RMNH and YPM were provided to us by M. Hoogmoed.

Coordinates of localities were acquired in the field using global positioning system devices (in all cases, datum WGS84) and consulting data in museum catalogues or

geographical gazetteers (Stephens and Traylor 1985). When possible, coordinates of records from the literature or in museum databases were obtained using the software Google Earth Pro (v7.1.2, Google Inc., Mountain View, CA).

Measurement Techniques

Terminology for cephalic shields follows Savage (1960) as augmented by Peters (1964), whereas ventral and subcaudal counts follow Dowling (1951). Condition of the loreal scale follows Passos et al. (2007b). Measurements were taken with a dial caliper (± 0.1 mm), except for snout–vent length (SVL) and tail length (TLL), which were measured with a ruler (± 1 mm). Measurements and descriptions of paired cephalic scales are strictly based on the right side of head. Counts of body markings (blotches, spots, and dots) were performed separately for each side of the dorsum because these marks are not always symmetrical. Herein, the term “blotch” refers to broad (two or more scales long and wide) dorsal markings located in the vertebral and paravertebral regions, the term “spot” refers to smaller (between one and two scales long and wide) markings on dorsum or venter, and “dot” refers to any marking smaller than a single scale. Sex was determined by presence/absence of hemipenes determined by a ventral incision at the base of the tail. We examined maxillae of all specimens under a stereoscope, through a narrow lateromedial incision between the supralabials and the maxillary arch. After removing tissues covering the maxillary bone, we counted teeth and empty sockets.

The terminology for micro-ornamentation descriptions follows Price (1982) and Price and Kelly (1989), with a few adaptations. The superficial layer of the dorsal scales was sampled from the middorsal body region of nine individuals of *A. flammigerus*. We removed scale layers (= Oberhäutchen) with forceps and stored them separately in 70% ethyl alcohol. The layers were affixed to metal plates with double-faced carbon tape, then metallized using a Denton vacuum desk IV metallizer. They were photographed using a JEOL JSM 6390LV scanning electron microscope (SEM) under $\times 500$ – $10,000$ magnification and 10–20 kV at the SEM laboratory of the Museu Nacional/UFRJ. Following Price and Kelly (1989), different micro-dermatoglyphics might occur in basal and apical portions of scales. Thus, we describe both scale portions for *A. flammigerus* and compare those with scales of *A. torquatus* (MZUSP 4380, 8205, INPA-R 17665, 17666). The terminology for description of skull osteology follows Cundall and Irish (2008). The head of one individual (MPEG 26222) was scanned on a Skyscan 1173 in vivo high-resolution micro-computed tomography (μ -CT) scan at the nuclear instrumentation laboratory COPPE/UFRJ. The specimen was scanned at 50 kV and 160 μ A and rendered in three dimensions using CTVox for Windows 64 bits, v2.6.

The terminology for hemipenial descriptions follows Dowling and Savage (1960) and Zaher (1999), with a few minor adaptations on the basis of Passos et al. (2013b). Method for preparation of preserved hemipenis was modified from Pesantes (1994) in replacing KOH with distilled water according to Passos et al. (2016a). Before the inflation with petroleum jelly, the organs were placed in an ethyl alcohol (70%) solution with alizarin red for 15–20 min to stain the ornamented calcareous structures according to adaptations from original procedures used by Uzzell (1973).

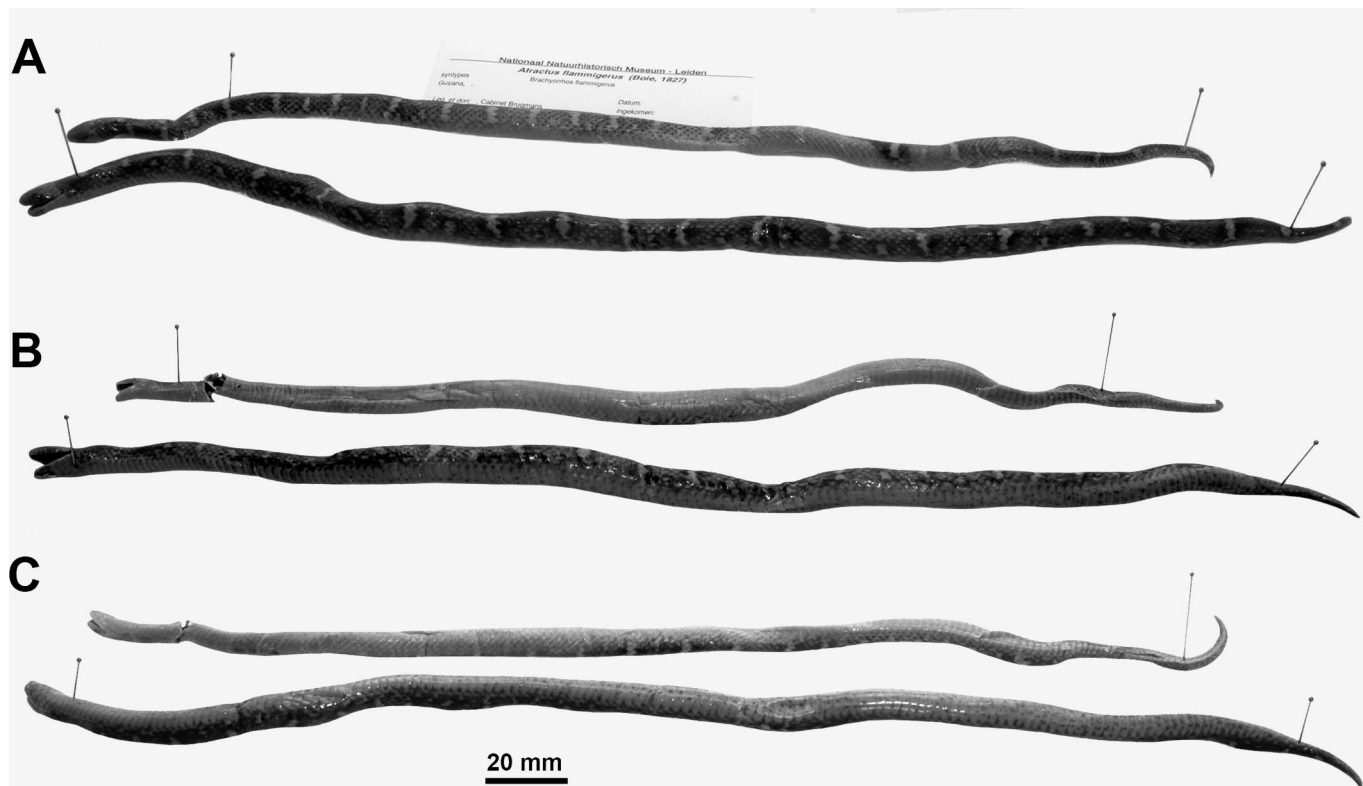


FIG. 1.—Dorsal (A), lateral (B), and ventral (C) views of the lectotype (RMNH 118a; lower) and paralectotype (RMNH 118b; upper) of *Atractus flammigerus*. Photo by C. Pepermans. A color version of this figure is available online.

We follow Passos et al. (2009e, 2010a) with respect to states and terminology of the morphological characters used in diagnosis and description. Mean values are reported \pm 1 SD.

RESULTS

Atractus flammigerus (F. Boie 1827)
Brachyorrhos flammigerus F. Boie 1827:540.
Calamaria badia Schlegel 1837:35. (in part).
Geophis alasukai Gasc & Rodrigues 1980:1122;
 Claessen 2001:223.

Atractus flammigerus Hoogmoed 1980:20; Hoogmoed
 1983:230; Hoogmoed & Prudente 2003:427 (in part).

Types.—Adult female (RMNH 118a, lectotype; RMNH 118b, paralectotype; Fig. 1) from “Guyane,” interpreted by Hoogmoed (1980) as “Guianas,” coming from Brugmans cabinet, donated to RMNH. Hoogmoed (1980) designated the lectotype and restricted the type locality to Paramaribo, Suriname (05°50′N, 55°10′W; sea level).

Diagnosis.—*Atractus flammigerus* is distinguished from all currently recognized congeners by having conspicuous keels on dorsal scale rows of body in immature and mature male and female specimens (Fig. 2). Although this represents an apparent autapomorphy of the species, such a feature might be inconspicuous in immature female individuals and only barely evident in poorly preserved individuals. For that reason, we also provide the following unique combination of morphological characters that can be observed in specimens of any age category or reproductive condition: (1) dorsal scale rows 17/17/17; scales lacking apical

pits but having keels on vertebral and paravertebral series; (2) postoculars two; (3) loreal long, three times height; (4) temporals one plus two; (5) supralabials usually eight, fourth, and fifth contacting eye; (6) infralabials seven or eight, first four contacting chin shields; (7) maxillary teeth usually eight; (8) gular scales comprising three scales (between seventh infralabial and preventrals); (9) preventrals usually three; (10) ventrals 145–156 in females, in males 138–151; (11) subcaudals 19–26 in females, 26–36 in males; (12) in preservative, dorsum uniformly black to brown with a series of 30–43 regular or slightly irregular transverse (never completing a ring) alternate cream or beige bands/blotches along body; (13) venter cream with square or rhomboidal blotches generally forming irregular stripes on the middle or lateral portion of belly; (14) moderately long body size, with females reaching 500 mm and males 380 mm; (15) small to moderately long tail in females (8.6–11.3% SVL) and moderate to long in males (13.1–17.1% SVL); (16) hemipenis strongly bilobed, semicapitate, and semicalyculate.

Comparisons.—*Atractus flammigerus* is unique within the genus *Atractus* in having keels on several dorsal scale rows along the body in males and females (Fig. 2). Immature specimens of *A. flammigerus* (in which keels might not be conspicuous) can be distinguished from morphologically sympatric congeners with 17 rows and banded color pattern (*A. badius*, *A. latifrons*, *A. snethlageae*, *A. schach*, and *A. torquatus*) by having a brown to black dorsum, usually with alternate transverse light bands (vs. dorsum, at least anteriorly, reddish brown with conspicuous dyads formed by two entire black rings separated from each other by a narrow light ring in *A. badius* and *A. latifrons*); postoculars

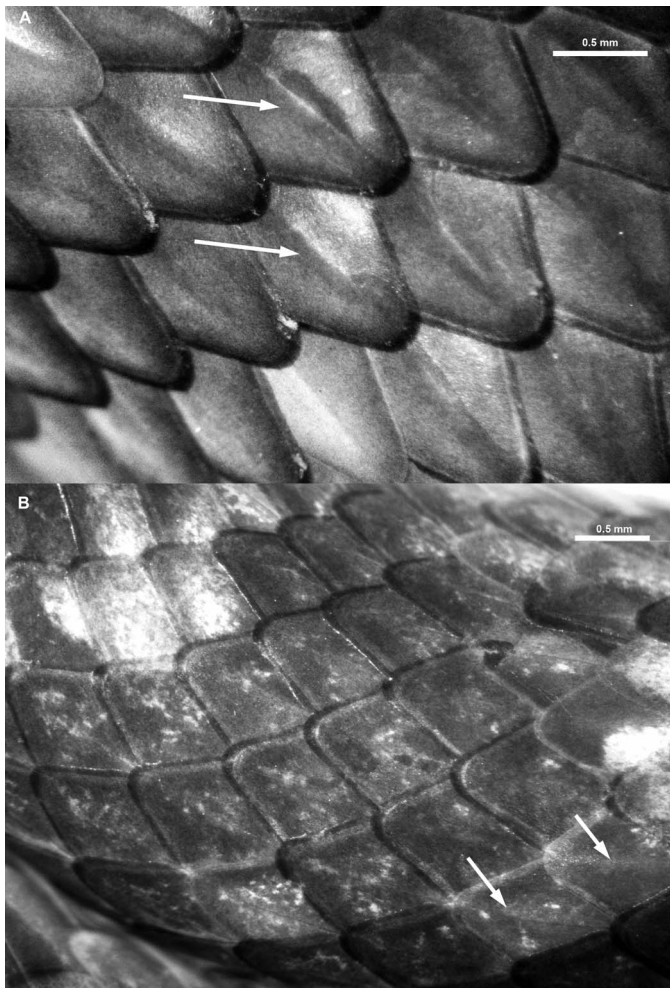


FIG. 2.—Macro-ornamentation of the dorsal scales of a mature male *Atractus flammigerus* (AF 1531-A) from Route de Kaw, French Guiana; and an immature female (QM 613-B) from Matiti, French Guiana. White arrows indicate the conspicuous longitudinal keels.


two, subcaudals 19–26 in females and 26–36 males, snout truncated, and hemipenis strongly bilobed (vs. postocular single in the populations from the Guiana Shield [Passos and Prudente 2012], subcaudals 34–47 in females, 35–53 in males, snout projecting, and hemipenis slightly bilobed in *A. torquatus*); and, usually eight supralabials, eight maxillary teeth, and strongly bilobed hemipenis with laterally expanded basal naked pocket, capitulum shorter than hemipenial body and lacking lobular crests on the asulcate face of hemipenis, and surface of belly cream with squared or rhomboidal blotches generally forming irregular stripes on the middle or lateral portion of belly (vs. usually seven supralabials, seven maxillary teeth, and moderated bilobed hemipenis with narrow and longer naked pocket, capitulum equivalent to hemipenial body and usually with conspicuous lobular crests on the asulcate face of hemipenis, and surface of belly variably pigmented with brown spots or dots but never having squared to rhomboidal blotches in *A. schach* and *A. snethlageae*). *Atractus riveroi* (nonsympatric congener restricted to elevations higher than 1000 m in the Pantepui region of the Guiana Shield; de Fraga et al. 2017) has one morphotype superficially similar to *A. flammigerus* and has supraoccal tubercles (in male specimens) that

perhaps could be confused with keels. Nonetheless, *A. flammigerus* can be distinguished from *A. riveroi* by having 19–26 subcaudals in females and 26–36 in males, and eight maxillary teeth with two postdiastemal teeth (vs. 28–32 subcaudals in females and 34–46 in males, and seven maxillary teeth with a single postdiastemal tooth in *A. riveroi*).


Description of external morphology (n = 13).—Head length twice width, slightly arched in lateral view, rounded in dorsal view; cervical constriction barely distinct; snout truncate in lateral view, rounded in dorsal view; rostral subtriangular in frontal view, wider than high, barely visible in dorsal view; internasals as wide as long; suture sinistral with respect to prefrontal midline suture; prefrontals slightly longer than wide; supraoculars slightly longer than wide; frontal pentagonal, longer than wide; parietals about twice as long as wide; nasals entirely divided; nostril situated between prenasals and postnasals; prenasals about twice as high as long; postnasals slightly higher than long, as long as prenasals; loreals long (about three times longer than high), contacting second, third, and fourth supralabials ventrally, prefrontals dorsally, internasals anteriorly, and eyes posteriorly; pupils round; postoculars two, subequal, slightly longer than high; upper postoculars generally higher and longer than lower postoculars; temporals one plus two; first temporal longer than high; upper posterior temporals usually not fused ($n = 27$ of 30 sides), posteriormost about two times as long as high; supralabials eight (rarely seven), fourth and fifth contacting eye; first two supralabials of similar height, slightly taller than third, and equivalent to fourth and fifth; sixth and seventh usually higher and eighth longer than the other supralabials; symphyisial semicircular, four times as broad as long; infralabials eight, first four contacting chin shields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chin shields contact; chin shields over two times longer than wide; three gular scale rows; two or three preventrals; 17/17/17 dorsal scale rows without apical pits but with conspicuous keels in small mature males and females (immature specimens may show hardly evidence of keels); keels usually evident along vertebral series (vertebral and paravertebral scale rows), forming conspicuous longitudinal ridges; keels occasionally evident after midbody extending to the end of tail, covering seven scale rows above fifth scale row; caudal spine moderately long (slightly longer than last subcaudal), conical, and acuminate.

Color pattern variation in preservative (n = 17).—Dorsum of head medium brown to dark brown, usually uniformly pigmented without light areas on temporal region; posterior region of parietals and occipital area may be pale brown, frequently contrasting with dorsal ground color of body (brown to dark brown); lateral head medium brown or dark brown to dorsal edges of supralabials; supralabials mostly cream, with brown pigment generally restricted to dorsal and posterior regions of each scale; first six supralabials usually uniformly cream in their centers, but sometimes with a few scattered brown dots; occasionally, last two supralabials entirely pigmented with brown or only their posterior regions; infralabials cream with brown spots usually concentrated on first pair of scales and on mesial region of remaining infralabials along the border with chin shields; gular region cream with spots usually restricted to anterior portion of chin shields; very rarely, brown

background completely covering chin shields and margins with third and fourth infralabials; dorsum frequently completely darkened, with the blotches almost indistinct (only distinguishable after alcohol immersion or completely indistinct); most rarely dorsum brown with wide light marks contacting adjacent bands along vertebral region; venter cream with rectangular or rhomboidal brown blotches arranged as two or three irregular longitudinal stripes; brown blotches increasing in size posteriorly and anterior portion of belly generally covered by midline of centralized marks; venter sometimes with scattered brown dots between irregular blotches, both generally more concentrated on posterior regions of body; occasionally, belly almost totally brown by high concentration or expansion of brown blotches and spots; ventral surface of tail mostly brown with few irregular cream spots toward the sides; tail occasionally uniformly brown; dorsal ground color of body and tail brown to dark brown usually covered with a series of 25–37 transversal pale brown to cream transverse bands (one to three scales long); light bands, when present, frequently dark brown bordered and alternated along flanks of body and tail; sometimes bands connected across vertebral region, producing an almost symmetrical dorsal band; first two scale rows cream to pale brown with brown pigmentation from blotch edges or irregular brown dots (Fig. 3).

Color pattern variation in life (n = 7).—Dorsum of head mostly dark brown, except for blotches on the snout region and supralabials usually yellow; dorsal ground color  lack to dark brown with pale brown to reddish brown transverse bands (one to three scales long) alternated along flanks; venter cream strongly scattered with rhomboidal brown blotches; ventral surface of tail almost uniformly brown (Fig. 4).

Microdermatoglyphics of dorsal scales (n = 9).—Basal portion ornamented with lamellate and imbricate cells displaying denticulated apical borders not more than 4 µm distant from each other; denticulations slightly triangular, higher than wide, rarely exceeding 1 µm high; micro-ornamentation on the cell surface composed by slightly distinct pores. Apical portion with layers of lamellate and imbricate cells caudally oriented; cell borders with long and narrow spinulated denticulations (2–4 µm high) that seem to be embedded in the adjacent cell; larger pores barely distinct between denticulations in this portion of the scale.

The microdermatoglyphics of *A. torquatus* (n = 4) differ from those of *A. flammigerus* mostly in the basal portion of the scales, in which denticulations are slightly narrower than those present in *A. flammigerus*; surface micro-ornamentation is markedly punctuate, with much larger pores and closer to each other than the ones present in the basal portion of *A. flammigerus* scales. Apical portion of *A. torquatus* scales differs from *A. flammigerus* by exhibiting conspicuous pores between the spinules and a more regular orientation of imbricate cells (Fig. 5). There are no discrete fixed differences between the micro-ornamentation from *A. flammigerus* and *A. snethlaged* .

Cranial osteology (n = 1).—Skull elongate; laterally the height slightly increases toward posterior end of parietal, where it slightly descends until reaching the exoccipitals.

Premaxilla.—Slightly triangular anteriorly with concave lateral edges expanding dorsally and forming ascendant process, which contacts anteromedial edge of nasals;


laterally, transverse process expands toward maxillary, but not touching it; ventrally, premaxilla expands posteriorly, forming a short vomerian process, which contacts anteroventral tip of septomaxillary but does not contact vomer.

Septomaxillaries.—Anterior edge fits internal angle of nasal process of premaxilla; dorsolaterally projected, comprising a short conchal process approximately trapezoidal, not contacting nasals or prefrontals; attached to frontals posteriorly, forming prokinetic joint; dorsally in contact with vertical lamina of nasals.

Vomers.—Premaxillary process of each vomer slightly expanded anteriorly, delimiting anterior edge of olfactory capsule; premaxillary processes contact each other and septomaxillary dorsally but do not contact premaxilla; caudal processes of vomer expanded posteriorly in medial line, constituting exochoanal fenestra.

Nasals.—Trapezoidal with dorsal edges convex; medial anterior edges contacting ascendant process of premaxilla and do not contact frontals posteriorly; do not compose prokinetic joint; small process originating on the posterior-lateral margin, but not touching prefrontals; vertical lamina single, ventrally in contact with middorsal surface of septomaxillary.

Frontals.—Trapezoidal in dorsal view, contacting prefrontals anterolaterally, parietal posteriorly and postorbital ventrolaterally; ventrally expanded anteriorly into septomaxillary process and in contact with septomaxilla at prokinetic joint, which is composed exclusively of these two bones, because the frontals do not contact nasals; anteriorly, supra- and subolfactory laminae converge medially, forming a single interolfactory pillar, restricted to the internal anterior portion of frontal.

Parietal.—Pentagonal, comprising  (two-thirds???)2/3 the skull in dorsal view; anterior edge concave and attached to frontals; small anterolateral projections articulating with postorbital bone and exceeding their lateral limits dorsally; posteriorly, sutured to supraoccipitals, posterolaterally to prootics, and ventromedially to parabasisphenoid; dorsal surface smooth with two parietal crests that converge posteriorly until reaching anterior edge of supraoccipitals.

Supraoccipitals.—Fused and pentagonal, contacting parietal anteriorly, prootics laterally and exoccipitals posteriorly; anterior edge concave; lateral margins contacting supratemporal edge medially; dorsally with an oblique crest, which makes its posterior portion ventrally positioned.

Exoccipitals.—Trapezoidal, comprising dorsal edge of foramen magnum; each exoccipital contacting basioccipital ventrally and prootic laterally; two foramina ventrolaterally located at each exoccipital.

Basioccipital.—Pentagonal, contributing to posterior portion of braincase floor, as well as medial portion of occipital condyle; contacts parabasisphenoid complex anteriorly, prootics and exoccipitals laterally, and atlas posteriorly, where it composes ventral edge of foramen magnum.

Parabasisphenoid.—Triangular, contacting frontals dorsal-anteriorly, parietal and prootic laterally, and basioccipital posteriorly.

Prootics.—Irregular, contacting parietal dorsally and anterolaterally, parabasisphenoid and basioccipital ventrally, supraoccipital posterodorsally, exoccipital posterolaterally; anterior portion of supratemporal lies on its dorsal surface; ventrolateral surface of each prootic pierced by two

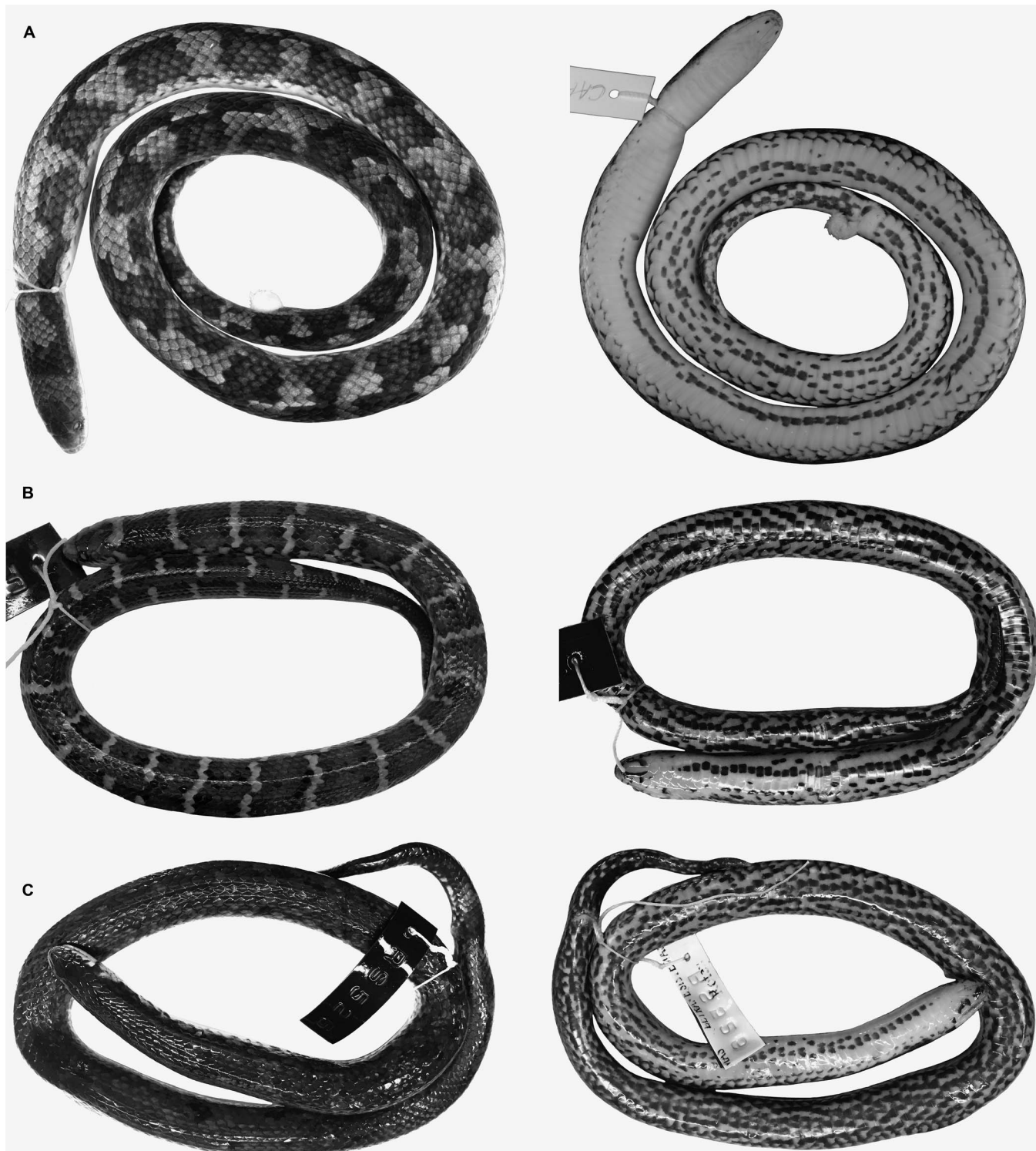


FIG. 3.—Pattern variation of *Atractus flammigerus*, in preservative, from Montagne Cacao, French Guiana (CAHE 09-A) and Ferreira Gomes (IEPA-FL 469-B) and Pedra Branca do Amapari (IEPA-RS 562-C), the ultimate two localities in the state of Amapá, Brazil. Dorsal views in left column, ventral views in right column.

foramina; posterior region with small enlargement on the insertion of columela auris at foramen ovale.

Prefrontals.—Contacting frontal in its posterolateral portion, and maxillary and palatine ventrally; lateral descending lamina enlarged dorsally, with reduction of size in its ventral half; ventrally, with enlarged process supported by

palatine; anterior lamina concave, with medial process toward prokinetic joint (but not touching it) and pierced by lacrimal foramen, which crosses prefrontal ventrally.

Postorbitals.—Small and slender, delimiting orbital cavity posteriorly; composed of vertical portion and dorsal process horizontally oriented in broad contact with antero-

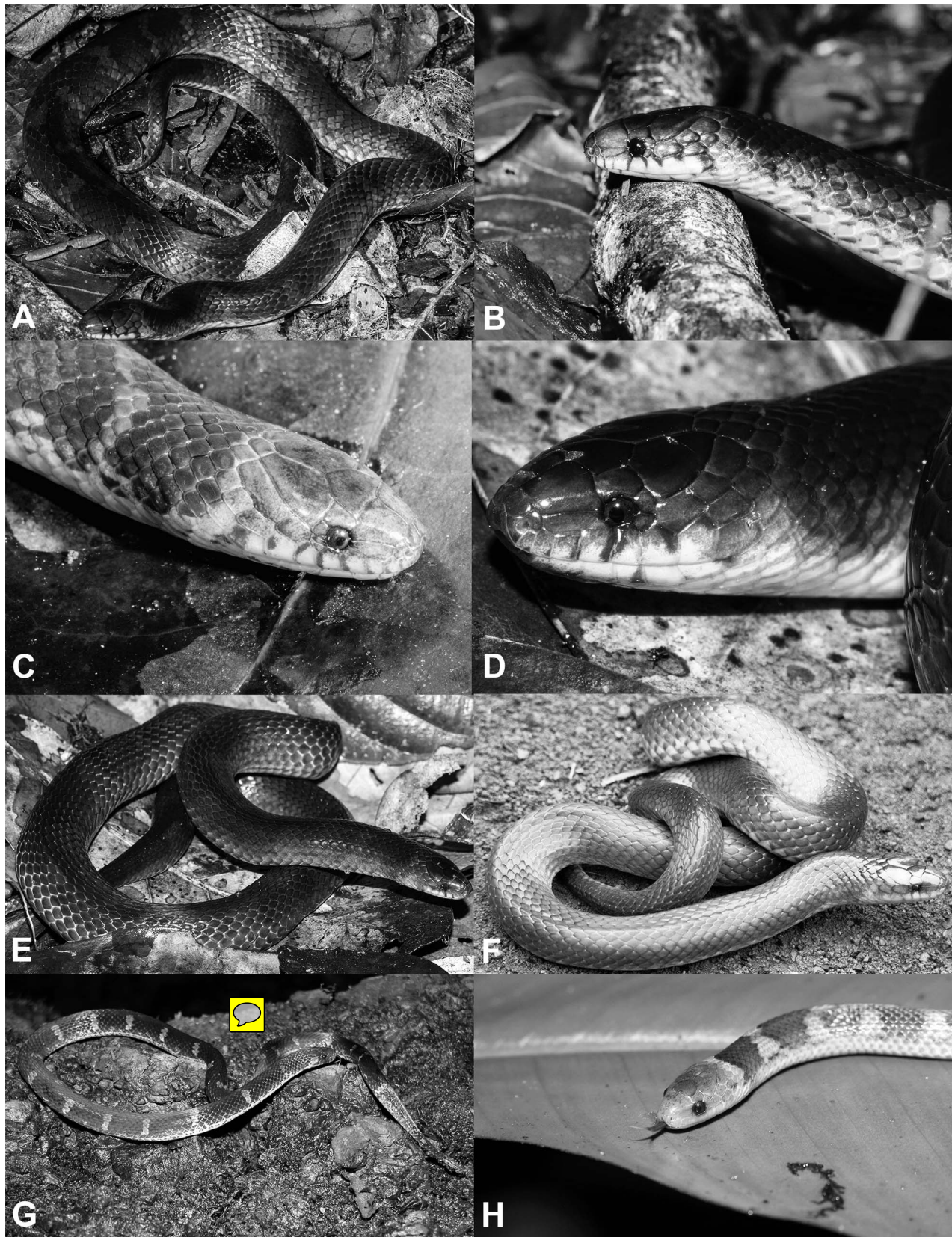


FIG. 4.—General view in life of the body of *Atractus flammigerus* from Mont Itoupé (AF 3546–A, B and AF 3721–C, both males), Reserve Naturelle de la Trinité (AF 1151–D, E, male and F, female MNHN uncatalogued), Roura, Route de Kaw (G, H, specimens not collected, sex undetermined), French Guiana. Photos A–E by A. Fouquet, F. Starace, and G, H by P. Macquere. A color version of this figure is available online.

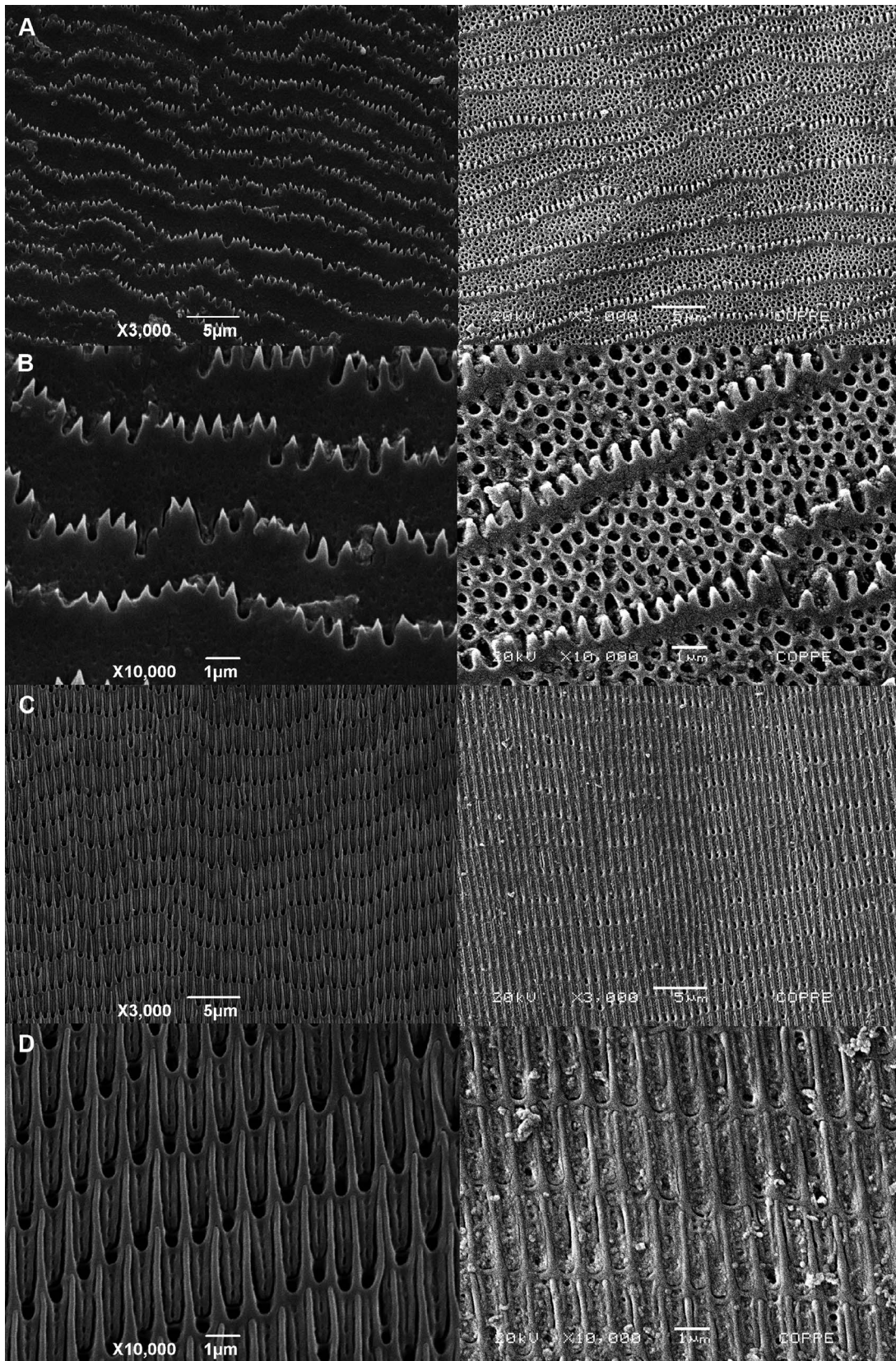


FIG. 5.—Microdermatoglyphics of the dorsal scales of *Atractus flamnigerus* (MPEG 26222 left column) and *Atractus torquatus* (INPA-H 17665 right column) from the basal portion at $\times 3000$ (A) and $\times 10,000$ (B), and the apical portion at $\times 3000$ (C) and $\times 10,000$ (D).

lateral processes of parietal and, on its anterior tip, a narrow contact with posterolateral portion of frontal.

Columela auris.—Small and slender bone inserted in fenestra ovalis, composed of posterolateral portion of prootics and anterolateral portion of exoccipitals; it crosses the fenestra ovalis toward quadrate, attaching to process located at its medial portion.

Maxillaries.—In lateral view, extends from the anterior tip of nasals to posterior portion of frontals; posterior tip of maxilla attached to anterior tip of ectopterygoid; two medial processes, palatine process at medial portion with dorsal contact with prefrontal and ectopterygoid process at posterior portion in contact with ectopterygoid; lateral surface concave and pierced by single foramen; seven (right) to eight (left) posteriorly curved teeth.

Palatines.—Slightly shorter than maxillaries, in anterodorsal contact with prefrontal; posterior tip slightly forked and attached ventrally to anterodorsal tip of pterygoid; maxillary process of palatine located laterally, not contacting palatine process of maxilla, and supporting ventral portion of prefrontal bone dorsally; five teeth; choanal process absent.

Pterygoids.—Each pterygoid located posterior to palatine, with its posterior portion enlarged and exceeding posterior limits of the skull; 14 teeth, smaller than those in maxillary and palatine and decreasing in size posteriorly; ectopterygoid fits to dorsal surface of pterygoid approximately in a gap between fifth and sixth teeth and extending to level of third tooth.

Ectopterygoids.—Anterior portion bifurcated and attached to ectopterygoid process of maxilla, exceeding maxillary row of teeth and reaching sixth or seventh tooth; ventrally, attached to dorsomedial portion of pterygoid.

Supratemporals.—Short and elongated, ventrally attached to posterior portion of prootics and posteriorly reaching posterior portion of exoccipitals, but not contacting them; in narrow medial contact with lateral edges of supraoccipital and in posterodorsal contact with quadrate.

Quadrates.—Elongated and vertically positioned; proximal portion enlarged, medially articulated with posterodorsal portion of supratemporal; distally slightly enlarged, articulating with glenoid cavity of retroarticular process of mandible; lateral lamina twined, facing to posterior portion of skull and with a short articulatory process posteriorly.

Compound bone.—Connected to skull through the glenoid cavity posteriorly; anterior portion projected as a tapering process that inserts into dentary and extends until level of sixth tooth; lateral lamina concave, its midventral portion contacting angular; mandibular fossa relatively deep, with one anterior internal foramen; surangular and prearticular crests equally high; anterolateral portion with one foramen on each bone; retroarticular process short and rounded, medially curved.

Dentaries.—With nine teeth decreasing gradually in size posteriorly; posterolaterally, in contact with compound bone, where it is forked; one process dorsally extended and the other ventrally extended, and slightly longer than the first; anterior end of compound bone fits into such processes; mentonian foramen located laterally at level of gap between fifth and sixth teeth; posteromedial end of dentary contacts anterior tip of angular and anterior half of splenial; Meckel's groove opening at level of fourth tooth and extending posteriorly through entire dentary.

Splenials.—Anterior portion fits into dentary through tapering process, until the gap between fifth and sixth teeth, with its posterior end attached to angular; posterior region pierced by milohyoid foramen.

Angulars.—Triangular, with tapering projection directed posteriorly and anterodorsal process that extends above splenial until reaching posterodorsal tip of dentary dorsally; dorsal process originates at level of eighth tooth; anteroventral portion of angular pierced by milohyoid foramen (Fig. 6).

Hemipenial morphology (n = 9).—Organs in situ (entirely retracted; $n = 2$) extend to subcaudals 10–11 and bifurcate at level of eighth or ninth subcaudal. Fully everted and almost maximally expanded hemipenes ($n = 9$) render a strongly bilobed, semicapitate, and semicalyculate; lobular region wider than hemipenial body; lobes cylindrical, slightly attenuate and centrifugally oriented; lobes symmetrical (AF1591, AF 3546, QM 199, MPEG 26222, and CAHE 09) or with left lobe slightly longer than right (AF 3721 and AF 805); lobes covered with spinulate calyces along basal region on both sides of hemipenis; spinules gradually replaced by papillae toward apices of lobes; spinules occasionally almost reaching the tip of organ (MPEG 26222); asulcate and most of sulcate side of hemipenis usually displaying irregular calyces not forming flounces; rarely, capitulum in its basal and lateral regions on the asulcate side of capitulum with regular flounces (AF 3721); calyces sometimes deeper, but maintaining with high concentration (AF 805); capitular groove well defined on asulcate side and less evident on sulcate side; capitulum varying from 30% to 40% length of hemipenial body; hemipenial body elliptical with large scattered hooked spines; hemipenial body sometimes with slightly expanded base and absence of spinulate calyces on the basal region of lobes (IEPA-RS 562; supposed anomalous organ; S1 in the supplemental materials available online); larger spines generally located laterally below sulcus spermaticus bifurcation; sulcus spermaticus bifurcates at about the half length of the organ with each branch centrifugally oriented, running almost to the tip of lobes; sulcus spermaticus margins relatively narrow at level of division and very expanded above capitular crotch; sulcus spermaticus bordered by spinules from base of organ to apices of lobes; concentration of spinules increasing on proximal region of organs with fewer large spines and nude areas; basal naked pocket restricted to most basal region of hemipenial body and laterally expanded; proximal region of hemipenis with longitudinal plicae and dispersed spinules (Figs. 7, 8).

Quantitative variation (n = 17).—Largest male 380 mm SVL, 61 mm TLL; largest female 500 mm SVL, 51 mm TLL; tail 13.1–17.1% SVL in males, 8.6–11.3% SVL in females; ventrals 138–151 (mean = 144.8 ± 4.1 ; $n = 12$) in males, 145–156 (mean = 151 ± 4.9 ; $n = 5$) in females; subcaudals 26–36 (mean = 32.2 ± 2.6 ; $n = 12$) in males, 19–34 (mean = 23 ± 2.6 ; $n = 5$) in females; supralabials seven ($n = 2$ sides) or eight ($n = 32$ sides); infralabials seven ($n = 19$ sides) or eight ($n = 15$ sides); prementals two ($n = 1$) or three ($n = 11$); adult midbody diameter 7.2–17.2 mm; maxillary teeth seven ($n = 4$ sides) or eight ($n = 24$ sides).

Distribution (n = 18).—*Atractus flammigerus* seems endemic to the eastern part of the Guiana Shield (sensu Hoogmoed 1983), occurring from Paramaribo, Suriname

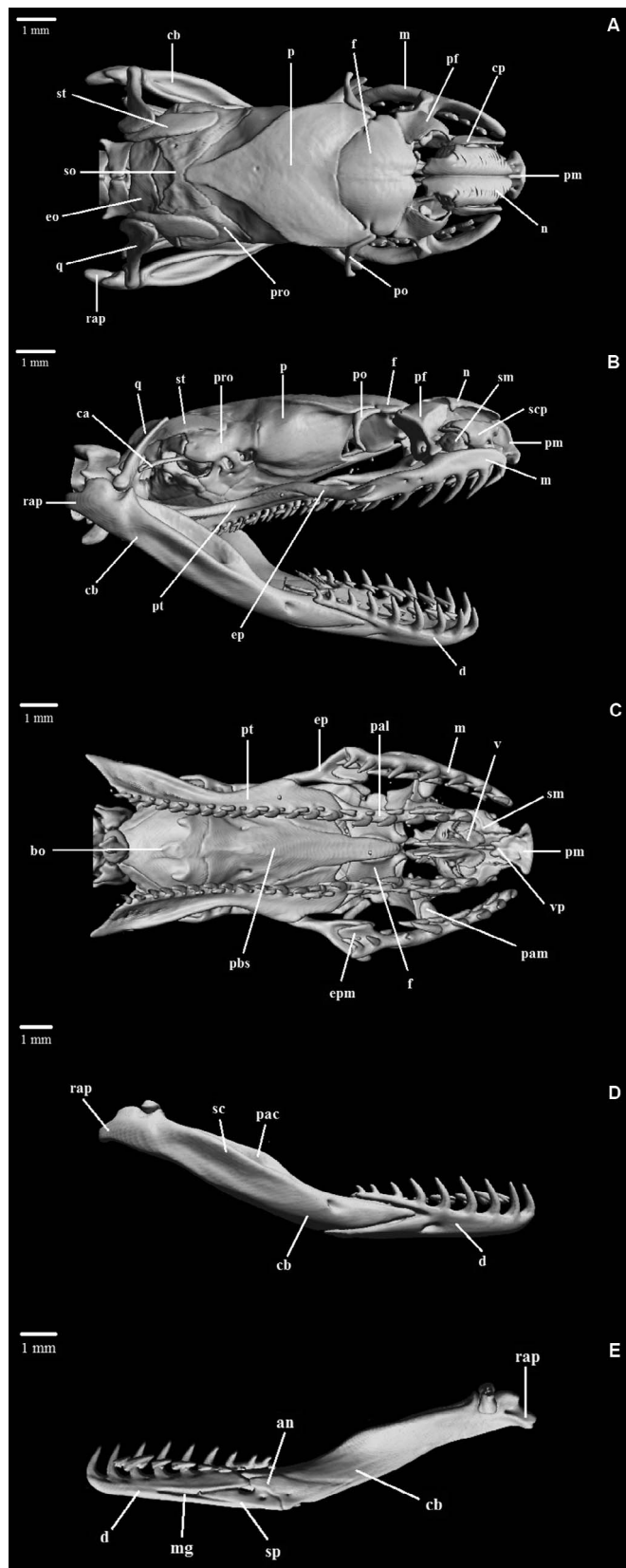


FIG. 6.—Dorsal (A), lateral (B), and ventral (C) views of the skull and lateral (D) and medial (E) views of mandible of *Atractus flammigerus* on the basis of a microcomputed tomography scan of a specimen (MPEG 26222) from Laranjal do Jari, Amapá, Brazil. Abbreviations are as follows: pm = premaxilla, n = nasal, pf = prefrontal, scp = conchal process of septomaxilla,

(05°49'44"N, 55°09'44"W) to Laranjal do Jari, Amapá, Brazil (00°49'56"S, 52°24'37"W), on the left bank of the Jarí River (a tributary of Amazonas River), including all of French Guiana and eastern Suriname. *Atractus flammigerus* occurs in lowland rainforest from 0 to 600 m above sea level (Fig. 9).

DISCUSSION

Atractus flammigerus has been confused with several congeners (i.e., *A. badius*, *A. schach*, *A. snethlageae*, and *A. torquatus*) for almost 200 yr since its first mention in the famous unpublished monograph entitled “Erpétologie de Java” (see Hoogmoed 1980 for details). Despite its earlier nomenclatural problems, Hoogmoed (1980) stabilized the taxonomy and provided accurate diagnoses for most *Atractus* species occurring in the Guiana Shield, with the exception of *A. flammigerus*. Hoogmoed (1980) identified a specimen from Loreto in the Peruvian Amazon as *A. flammigerus* and, even after the formal description of *A. snethlageae* by Cunha and Nascimento (1983), the majority of authors continued to use the name *A. flammigerus* for specimens from western Amazonia (mostly in Brazil and Peru; Silva 1993; Carillo and Icochea 1995; Lehr 2002; Duellman 2005). This confusion was probably attributable to the similarities between these two species in dorsal color pattern and meristics, exacerbated by the broader concept of *A. flammigerus* when it was resurrected. More recently, a series of papers has identified Amazonian populations outside the Guiana Shield as *A. snethlageae* rather than *A. flammigerus* (Passos et al. 2005; Passos and Fernandes 2008; Prudente and Passos 2008). Although *A. snethlageae* likely represents a species complex (Schargel et al. 2013), we first need to accurately diagnose it from those species with which it was previously confused, and second, to distinguish among divergent lineages within *A. snethlageae* (sensu lato). Notwithstanding, our results indicate that the presence of conspicuous keels in several dorsal scale rows of *A. flammigerus* represent a putative autapomorphy for the species (Fig. 2), although this character is less conspicuous in immature females (Fig. 2B) and might be indistinguishable in poorly preserved specimens. In such circumstances, beyond the meristic characters used by Schargel et al. (2013) to distinguish between these two species (e.g., number of supralabials), which show a certain level of overlap within *A. snethlageae* (sensu lato), we could utilize other less traditional morphological characters of hemipenial morphology, such as longitudinal shortening and lateral distention of the basal naked pocket of the hemipenis, hemipenial body longer than capitulum, and absence of lobular crests on the asulcate face of hemipenis (Figs. 7, 8). The only external morphological character of *A. flammigerus* that does not appear to overlap with *A. snethlageae* (sensu lato), however, is the ventral color pattern of cream with squared or rhomboidal blotches generally forming irregular or barely regular stripes (Schar-

m = maxilla, f = frontal, p = parietal, po = postocular, cb = compound bone, pro = prootic, so = supraoccipital, eo = exoccipital, rap = retroarticular process, sm = septomaxilla, st = supratemporal, q = quadrate, ca = columella, pt = pterygoid, ep = ectopterygoid, d = dentary, pal = palatine, v = vomerian process, pam = palatine process, epm = ectopterygoid process, pbs = parabasiptenoid, pt = pterygoid, and bo = basioccipital.

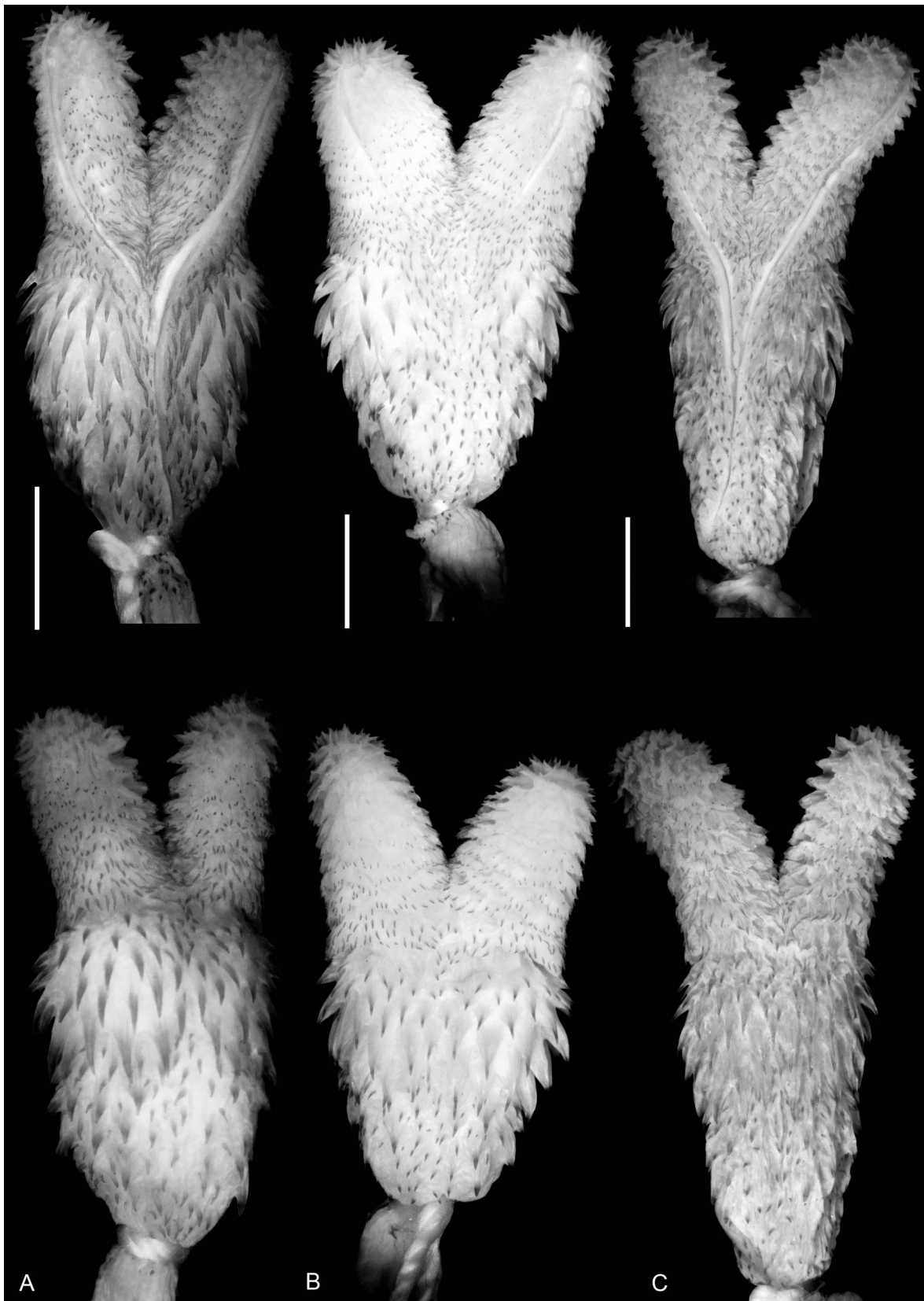


FIG. 7.—Hemipenial morphology variation of *Atractus flammigerus* in sulcate (upper row) and asulcate (lower row) sides of specimens from Saint Georges de l'Oyapock (QM 299-A), Mont Itoupé (AF 3546-B), and Route de Kaw (AF 1531-C), French Guiana.

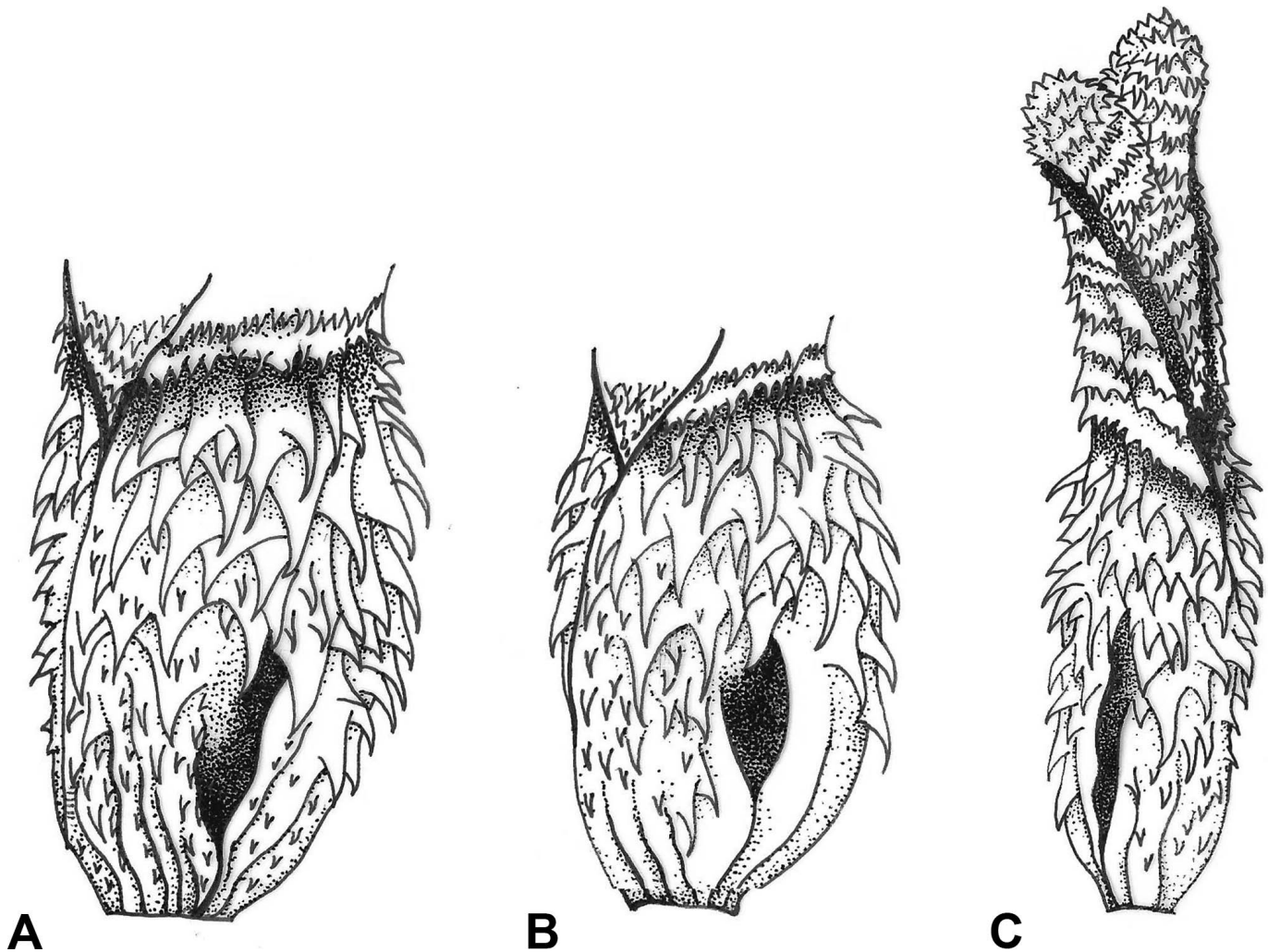


FIG. 8.—Comparisons between hemipenial morphologies of *Atractus flammigerus* (AF 1591 and AF 0805–A, B, respectively) from Roura, Route de Kaw, French Guiana; and *Atractus snethlageae* (INPA-H 31930-C) from Parque Nacional do Pico da Neblina, São Gabriel da Cachoeira, Amazonas, Brazil.

gel et al. 2013). With respect to the specimens currently housed in museum collections, *A. flammigerus* has been frequently misidentified as one of the morphotypes of the polychromatic *A. torquatus* (see fig. 5G, H in Passos and Prudente 2012), another sympatric congener with 17 dorsal scale rows, eight supralabial scales, large body size, and occasionally having two postocular scales. Both species can be easily distinguished on the basis of some underexplored morphological characters, however, such as the conspicuous pores in the micro-ornamentation pattern of the dorsal scales (Fig. 5) and the postorbital bone anterior to the opening of the optic foramen (Fig. 6 vs. Fig. 2.101B in Cundall and Irish 2008), or even using other characters such as the level of bilobation and capitulation of the hemipenis (fig. 7 vs. fig. 9 in Passos and Prudente 2012).

Many of the New World snake groups have undergone dramatic taxonomic changes in the last few years through phylogenies on the basis of molecular data (Pyron et al. 2015, 2016) or by complementing molecular evidence with phenotypic characters to better diagnose each of the recognized taxa (Torres-Carvajal et al. 2012, 2015; Pyron and Wallach 2014). In contrast, most changes to *Atractus* were made on the basis of qualitative and quantitative phenotypic characters or a correspondence between both data sets (Passos et al. 2016a and references therein). Despite the inclusion of some species of *Atractus* in several molecular studies intending to improve the high-level classification of snakes (Zaher et al. 2009, 2014; Graziotin et al. 2012; Pyron et al. 2013, 2015; Figueroa et al. 2016), none of these hypotheses covered more than 10% of the



TABLE 1.—Selected qualitative diagnostic features from microdermatoglyphics of the dorsal scales of sympatric *Atractus flammigerus* (MPEG 26222) and *Atractus torquatus* (INPA-H 17655).

Oberhäutchen	<i>Atractus flammigerus</i> (n = 9)	<i>Atractus torquatus</i> (n = 4)
Basal portion at $\times 3000$	Pores indistinct	Pores well evident
Basal portion at $\times 10,000$	Barely evident and scarcely distributed pores	Conspicuous and highly concentrated pores
Apical portion at $\times 3000$ and $\times 10,000$	Cells irregularly oriented	Cells more regularly oriented

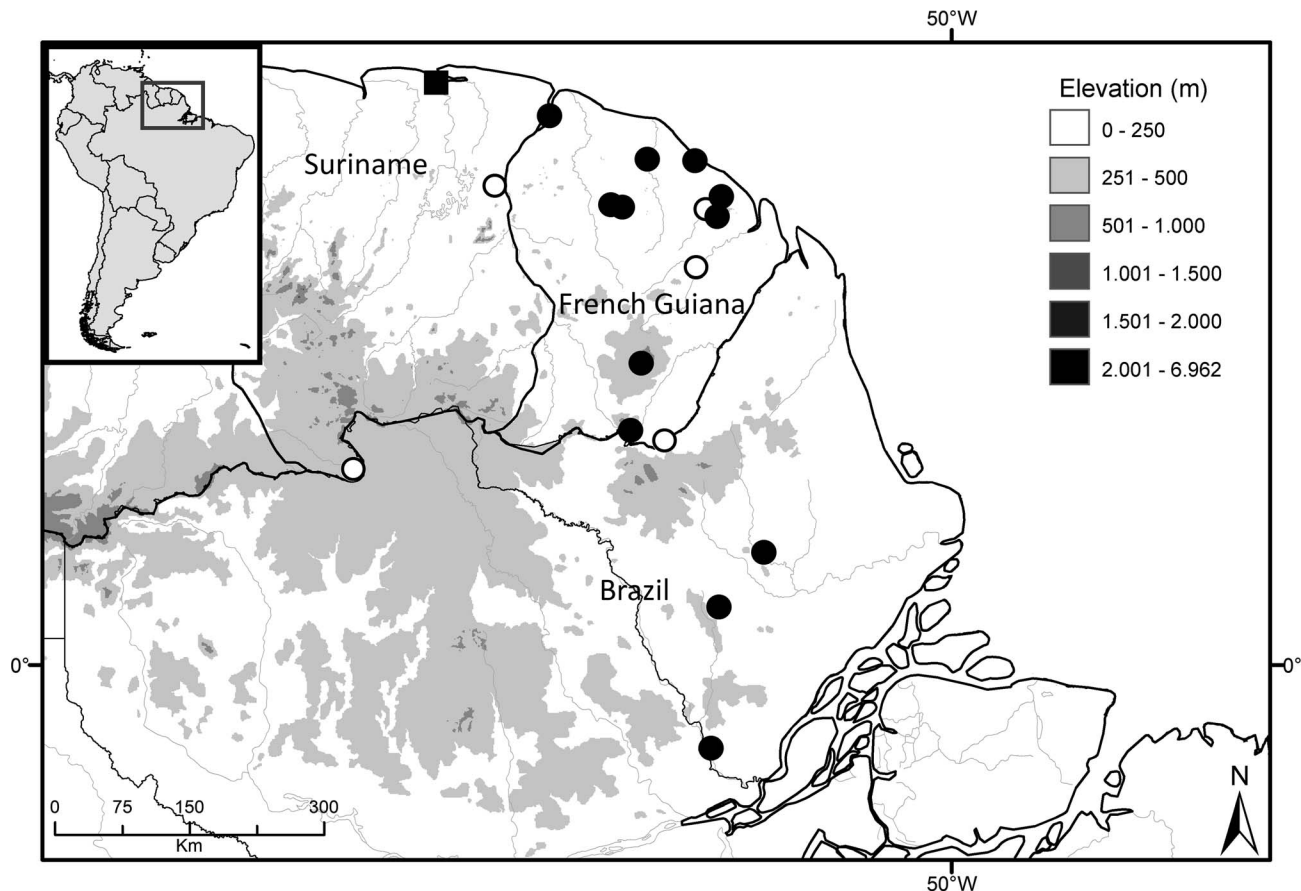


FIG. 9.—Geographic distribution of *Atractus flammigerus* in South America (inset). Filled circles represent examined specimens, open circles represent literature records, and the type locality is marked with filled square. The literature records are from Gasc and Rodrigues (1980) and Chippaux (1986).

current generic diversity. Recently, a phylogenetic hypothesis based uniquely on mitochondrial genes has improved considerably the number of terminals of *Atractus*, with about 30% (Arteaga et al. 2017). However, all of these analyses are plagued by sequence identification problems or even chimeras (= mixture of sequence as a single terminal) created between distinct and nonclosely related species (P. Passos, personal observation). Both systematic constraints—the apparent scarcity of tissue samples in collections and current misidentifications—might be attributable to those taxa not yet well delimited or even diagnosed in the literature, such as *A. flammigerus*. Many problems might be overcome by simple examination of the voucher specimens on which the sequences in GenBank were based, and for which unambiguous diagnoses exist (e.g., *A. serranus*, *A. trihedrurus*, and *A. zebrinus*; Passos et al. 2010c). In such cases, using little-explored phenotypic characters could facilitate recognition of a given species in this complex group of snakes by examination of certain unique traits (e.g., scale micro-ornamentation). We realize that obtaining high-quality images from SEM and μ -CT for many species might be impractical. This effort is currently in progress, however, and we hope those data will be available soon for most of the valid species of *Atractus*.

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SUPPLEMENTAL MATERIALS

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-16-00086.S1>.

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APPENDIX

Specimens Examined

Specimens from which we prepared the hemipenes and microdermatoglyphics are identified with an asterisk and by a degree symbol, respectively.

***Atractus badius* (n = 15).**—FRENCH GUIANA: unknown locality: (MZUSP not catalogued); Cayenne: (USNM 438); Montsinéry: Bagne des Annamites: (QM 237); Saint-Laurent du Maroni: Chutes Voltaire: Chemin Crique Voltaire: (AF 1735); Roura: Route de Kaw (AF 1319, 2550), PK 10: (AF 1764); Kourou: Matiti: (QM 78, 249); Matoury: Route du Galion: (AF 1370); Roura: Ecole: (AF 1297); Saül: (AF 1558).

***Atractus flammigerus* (n = 17).**—BRAZIL: Amapá: Laranjal do Jari: Jari River: (MPEG 26222*°); Pedra Branca do Amapari: Rio Cuxi, Reserva de Desenvolvimento Sustentável do Rio Iratapuru: (IEPA-RS 526*); Ferreira Gomes: Igarapé Santo Antônio, Unidade de Conservação: Floresta Nacional do Amapá (IEPA-FL 469*). FRENCH GUIANA: Kourou: Matiti: (QM 613°), Roura: Route de Kaw (AF 0805*°, 1531*°), Camopi: Mont Itoupé: (AF 3546*°, 3721°), Montagne Cacao: (CAHE 09*°), Saint Georges de l'Oyapock: (QM 299*°), Saint Elie: Reserve Naturelle de la Trinité: Camp Aya (AF 1151°). SURINAME: “Guyane”: unknown locality (restricted by Paramaribo, Suriname by Hoogmoed 1980): (RMNH 118a,b; lectotype and paralectotype of *Brachyorrhos flammigerus*); Sipaliwini: Nassau Mountains: (RMNH 13571*–72); Sipaliwini: airstrip (YPM 5912); Suriname: Paramaribo: (RMNH 13573).

***Atractus snethlageae* (n = 13).**—BRAZIL: Amazonas: São Gabriel da Cachoeira: Parque Nacional do Pico da Neblina: (INPA-H 31930*); Maranhão: Nova Vida: (MPEG 14986, 15422 paratypes); PARÁ: Ananindeua: Lago Azul: BR-316 Highway: (MPEG 16383, 16385, 16387 paratypes); Belém: Mosqueiro Island: (MPEG 2595 paratypes), Santa Bárbara: Benevides: road to Moesqueiro Island: (MPEG 3955 paratype), São João da Pratinha: (MPEG 10137* paratype), Viseu: Colônia Nova: BR-316 Highway, 10 km from Gurupi River: (MPEG 10131 holotype), Bela Vista: (MPEG 2543, 6845, 15973 paratypes).

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