

New Cryptic Species of *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia

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A new species of *Atractus*, previously reported as a disjunct population of *A. zidoki* south of the Amazon River, differs from all congeners in having an undivided sulcus spermaticus. Herein, we restrict the concept of *A. zidoki* to populations north of the Amazon River, provide a detailed description of its everted hemipenis, and describe a new species to accommodate the population occurring to the south of the Amazon River. Additionally, we briefly discuss intraspecific variation and the systematic value of the hemipenis structure in snakes, mainly with respect to the genus *Atractus*.

Uma nova espécie de *Atractus*, reportada previamente como uma população disjunta de *A. zidoki* ao sul do Rio Amazonas, difere de todos congêneres por apresentar o sulco espermático simples. Aqui nós restringimos o conceito de *A. zidoki* às populações ao norte do Rio Amazonas, fornecemos uma descrição acurada do seu hemipênis evertido e descrevemos uma nova espécie para acomodar a população ao sul do Rio Amazonas. Adicionalmente, nós discutimos brevemente a variação intra-específica e o valor sistemático de estruturas hemipenianas das serpentes, sobretudo com respeito ao gênero *Atractus*.

THE cryptozoic and fossorial snake genus *Atractus* is widely distributed in South America, occurring from Panama to Argentina (Giraud and Scrocchi, 2000; Myers, 2003). This genus currently comprises about 125 species, most of them exhibiting restricted distribution or local endemism (Myers, 2003; Passos and Fernandes, 2008; Prudente and Passos, 2008; Passos et al., 2009a, 2009b). The taxonomy of *Atractus* has been based mostly on color pattern, cephalic plate contact, and meristic characters (Savage, 1960; Roze, 1961; Hoogmoed, 1980; Passos et al., 2005, 2007a; Prudente and Santos-Costa, 2006; Passos and Arredondo, 2009); however, internal morphology (e.g., hemipenis and osteology) has also been shown recently to be informative regarding species-level decisions (Passos et al., 2009c, 2009d, 2010).

In the course of the study of Amazonian species of *Atractus*, we found a cryptic species, formerly identified as *A. zidoki* (Cunha and Nascimento, 1984), which is distinguished from all congeners by having an undivided sulcus spermaticus. Therefore, we describe it as new and restrict the concept of *Atractus zidoki* for populations occurring north of the Amazon River.

MATERIALS AND METHODS

We used characters from meristics, morphometry, dentition, and hemipenis morphology. Terminology for *Atractus* cephalic shields follows Savage (1960), and the method of counting ventral scales follows Dowling (1951). The condition of the loreal scale follows Passos et al. (2007b). Sex was determined by the presence or absence of hemipenis through a ventral incision at the base of the tail. Terminology for hemipenis description follows Dowling and Savage (1960) and Zaher (1999). Techniques for hemipenis preparation follow Pesantes (1994). We defined mature individuals through inspection of the flaccid oviducts, oviductal eggs, and ovarian follicles greater than 1 mm in females (modified from Shine, 1988), and opaque and convoluted

testicles in males (Shine, 1994). Measurements were taken with a dial caliper to the nearest 0.1 mm under a stereoscope, except for snout–vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest millimeter.

Atractus hoogmoedi, new species

Figures 1–3

Atractus zidoki.—Cunha and Nascimento, 1984:220 (part).

Holotype.—MPEG 13268, immature male, Brazil, state of Pará, municipality of Capitão Poço, 04°45'S, 47°04'W, ca. 48 m elev., at locality of Santa Luzia, 1975, F. Nascimento.

Paratypes.—MPEG 13265 (adult female) and MPEG 13266 (immature male), both with same data as holotype.

Diagnosis.—*Atractus hoogmoedi* is distinguished from all species of *Atractus* by having an undivided sulcus spermaticus. Among congeners, *Atractus hoogmoedi* shares only with *A. guerrerói*, *A. steyermarki*, and *A. zidoki* a unlobed hemipenis. *Atractus hoogmoedi* differs from the first two by having apical pits and supra-anal tubercles in the male specimens (vs. absence of apical pits and supra-anal tubercles). The new species differs from *A. zidoki* by having 170–171 ventral scales in males and 180 in the single female and an undivided sulcus spermaticus (vs. 173–187 in males and 196–200 in females and bifurcated sulcus spermaticus).

Along with *A. zidoki*, the new species shares apical pits and supra-anal tubercles exclusively with *A. alphonsehoegi*, *A. caxiuana*, *A. collaris*, *A. gaigeae*, *A. limitaneus*, and possibly *A. surucucu* (Prudente and Passos, 2008). *Atractus hoogmoedi* differs from these species by having a single hemipenis and short loreal scale (vs. bilobed hemipenis and moderate to long loreal scale). Based on easily observed characters, *Atractus hoogmoedi* can be distinguished from *A. alphonsehoegi*, *A. collaris*, *A. gaigeae*, and *A. limitaneus* by having the loreal scale in contact with second and third supralabials

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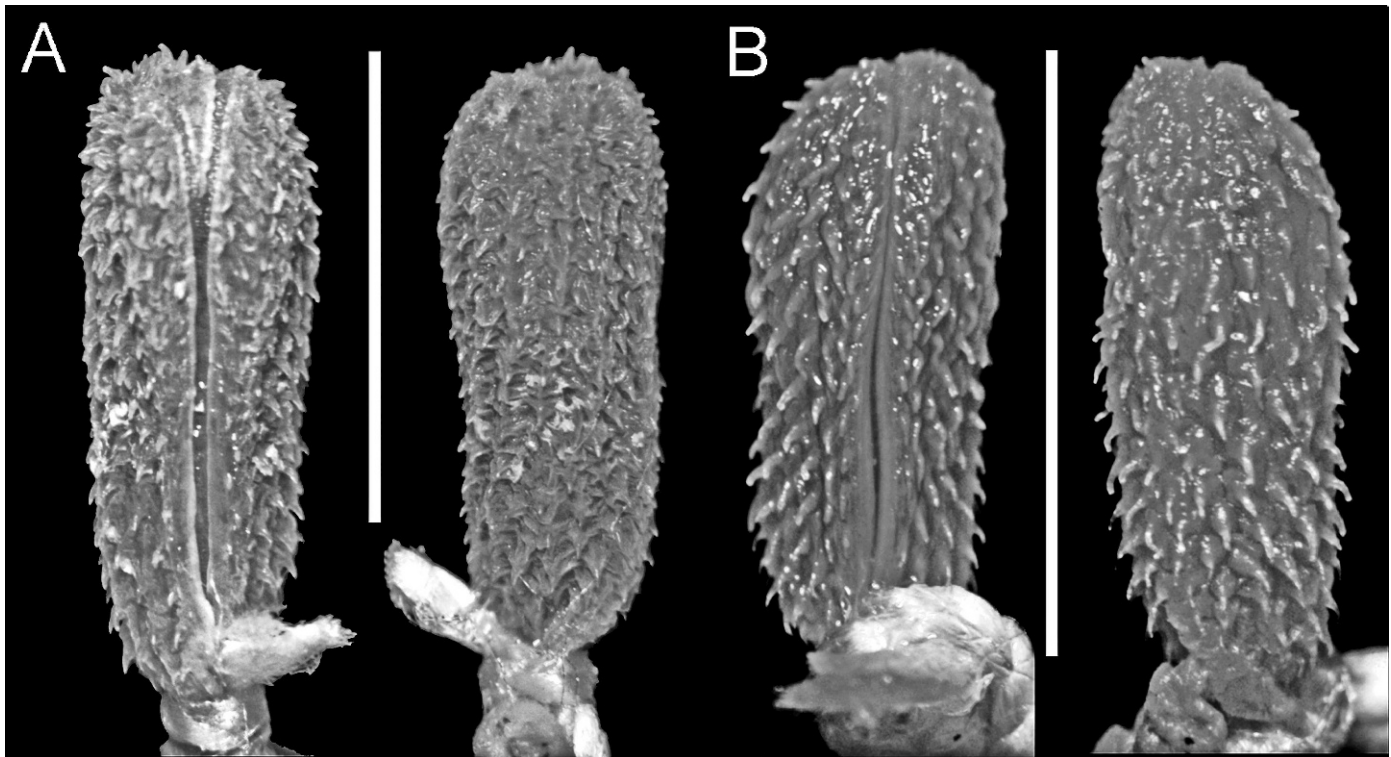


Fig. 1. Sulcate (right) and asulcate (left) sides of the hemipenis (A) of *Atractus zidoki* (IBSP 24772) and (B) *Atractus hoogmoedi*, new species (MPEG 13268). Scale = 10 mm.

and five maxillary teeth (vs. first supralabial contacting loreal scale and six or seven maxillary teeth); from *A. caxiuana* by postnasal preventing internasal-loreal contact (vs. internasal contacting loreal); and from *A. surucucu* by a creamish white tail (vs. uniformly black tail).

Description of holotype.—Male, SVL 160 mm, CL 27 mm; tail 16.8% of SVL; head length 6.6 mm (4% SVL), head width 3.7 mm (56% of head length); rostrorobital distance 1.7 mm; nasorobital distance 1.1 mm; interorbital distance 1.6 mm; head arched in lateral view, subtriangular in dorsal view; canthus rostralis well marked in lateral view; snout short and truncate in lateral view, round in dorsal view; head indistinct from neck; rostral subtriangular in frontal view, 1.4 mm wide, 0.9 mm high, well visible in dorsal view; internasal 0.6 mm long, as wide as long; internasal suture sinistral with respect to prefrontal suture; prefrontal 1.2 mm long, as wide as long; supraocular sub-rectangular, 0.9 mm long, 0.4 mm wide; frontal sub-triangular, 1.9 mm long, 1.5 mm wide, with anterior apex projected; parietal 3.2 mm long, 1.7 mm wide; nasal divided; nostril restricted prenasal to postnasal; postnasal hexagonal, 0.6 mm long, about as long as wide, slightly higher than prenasal; loreal short, as long as high, smaller than postnasal, contacting second and third supralabials; eye diameter 1.0 mm; pupil round; two postoculars; upper postocular longer (0.3 mm) and higher (0.5 mm) than lower postocular; temporals 1+2; anterior temporal 1.3 mm long, 0.3 mm high; anterior; upper posterior elongate (2.2 mm long), six times longer than high; seven supralabials, third and fourth contacting orbit; first three supralabials with similar size, and smaller than fourth supralabial; sixth higher and seventh supralabial longer than remaining supralabials; symphyisial subtriangular, 0.5 mm wide, 0.3 mm long; seven infralabials, first three

contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields 1.8 mm long, 0.3 mm wide; four gular scale rows; four preventrals; 17/17/17 dorsal scale rows; dorsal with apical pits and supra-anal tubercles, and lacking keels; caudal spine long, robust, conical, and rhomboid. Maxilla arched in dorsal view, with three prediastemal and two postdiastemal teeth; prediastemal teeth large, well spaced, curved, decreasing posteriorly, angular in cross section, robust at base and narrower at the apex; maxillary diastema long; postdiastemal teeth with half the size of the prediastemal teeth; lateral process of maxilla well developed with posterior projection.

Color of holotype in preservative.—Dorsal ground color of head light brown with variegate cream blotches; rostral, internasals, and anterior portion of prefrontals creamish white; head with two cream spots posteriorly, one on each side, not contacting one another in the median portion, forming an incomplete occipital collar that covers the posterior part of parietals, upper and lower posterior temporals, posterior part of seventh supralabial, and first occipitals; background of head brown with variegate cream blotches to dorsal edges of supralabials; supralabials creamish white, except for brown pigmentation covering posterior suture of scales; mental region creamish white, except for brown dots collapsed on symphyisial, anterior region of chinshields, and infralabial sutures; preventrals and gular region creamish white; venter and tail creamish white with lateral edges dark brown, forming a regular paraventral stripe; dorsum of body with a dark brown collar on neck (three scales long), with branches directed downward, connected to cephalic cap through parietal suture; dorsal ground color light brown with vertebral line (one scale wide)

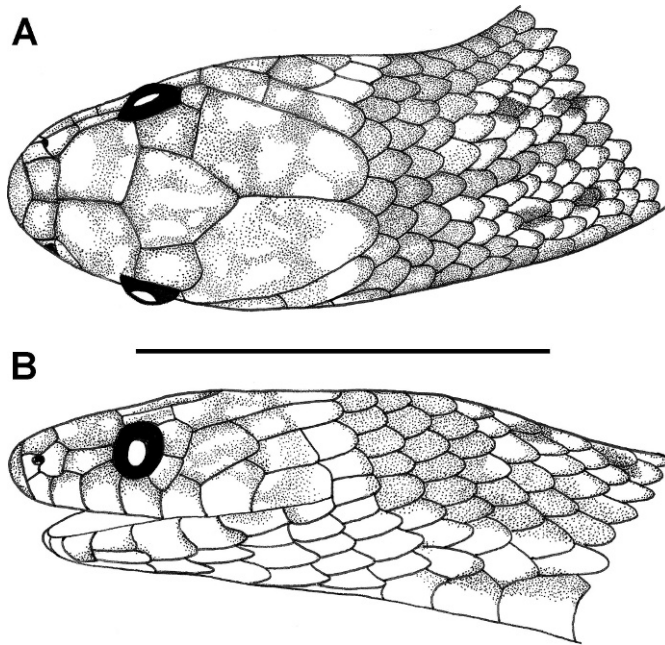


Fig. 2. Dorsal (A) and lateral (B) views of the head of the paratype of *Atractus hoogmoedi*, new species (MPEG 13266), with SVL 165 mm and CL 29 mm. Scale = 5 mm.

extending from dark brown collar to the end of tail; longitudinal series of paired paravertebral dark brown dots barely distinct; dots arranged in an “X” shape, cream bordered, on sixth to eighth scale rows; second and third scale rows dark brown, constituting generally a dorsolateral line extending to tail; first dorsal scale row cream, comprising a conspicuous paraventral stripe limited proximally and distally by dark pigmentation.

Variation.—Largest male SVL 165 mm, CL 29 mm; female SVL 224 mm, CL 24 mm; tail 16.8–17.6% ($n = 2$) of SVL in males, 10.1% in female; 170–171 ($n = 2$) ventrals in males, 180 in female; 37–40 ($n = 2$) subcaudals in males, 27–28 ($n = 2$ sides) in female; 8–10 ($\bar{x} = 8.7$; SD = 0.8; $n = 6$ sides) dorsal scale rows in the level of second subcaudal; 2.7–3.4 mm ($\bar{x} = 3.0$; SD = 0.4; $n = 3$) midbody diameter. The paratypes differ from the holotype by more conspicuous (76/74 in both) paravertebral dots; MPEG 13266 with dots irregularly arranged and/or with triangular shape, without cream border.

Hemipenis comparisons.—In order to improve diagnosis between *Atractus hoogmoedi* and *A. zidoki* we provide detailed descriptions of their organs.

Atractus zidoki: Retracted organ extending to the level of ninth subcaudal. Hemipenis unlobed, non-capitate and non-calyculate; organ cylindrical with round apex; organ ornamented with small hooked spines; spines arranged in vertical series, forming longitudinal crests; longitudinal crests conspicuous on asulcate and lateral sides of hemipenis; sulcus spermaticus margins bordered by a thick area distally; sulcus spermaticus bifurcated on distal portion of the organ, near to hemipenial tip; branches of sulcus spermaticus with centrolineal orientation, reaching hemipenis apex; sulcus spermaticus smooth, deep, and bordered with spinules; organ entirely covered with small hooked spines; spines dispersed on basal portion of hemipenial body and concentrated distally; basal naked pocket restricted to

basal portion of hemipenial body on the asulcate side of the organ; proximal region of organ with disperse spinules (Fig. 1A).

Atractus hoogmoedi: Retracted organ extending to the level of eighth subcaudal. Hemipenis unlobed, non-capitate and non-calyculate; organ cylindrical with round apex; organ entirely covered with small hooked spines; tip of organ ornamented with small papillae; sulcus spermaticus undivided, centrolineal, reaching hemipenis apex; sulcus spermaticus margin stout, deep, and bordered with spinules; basal naked pocket restricted to basal portion of hemipenial body in the asulcate side of the organ; proximal region of organ with longitudinal plicae and disperse spinules (Fig. 1B).

Distribution.—Known only from the locality of Santa Luzia, Municipality of Capitão Poço, State of Pará, Brazil (Fig. 4).

Etymology.—The specific epithet “*hoogmoedi*” honors Marinus Steven Hoogmoed for his extensive contributions in the study of Amazonia herpetofauna, especially with respect to the genus *Atractus*.

DISCUSSION

Gasc and Rodrigues (1979) described *Atractus zidoki* based on two specimens from Trois Sauts in the state of Oyapock, French Guyana, distinguishing it by its apical pits, supra-anal tubercles, and unlobed hemipenis (vs. absence of apical pits, supra-anal tubercles, and bilobed hemipenis in the other species of *Atractus*). Subsequently, Hoogmoed (1980) reported seven additional specimens of *A. zidoki* from Surinam and Guyana, which match the original species description, although the meristic variation (number of ventrals and subcaudals) of *A. zidoki* was increased considerably. Cunha and Nascimento (1983) made the first report of *A. zidoki* for Brazil on the basis of a single specimen from Serra do Navio in the state of Amapá (north of the Amazon River). Subsequently, Cunha and Nascimento (1984) reported three additional specimens of *A. zidoki* from Capitão Poço in the state of Pará, Brazil (south of the Amazon River), with similar characteristics to those of the individual reported from Serra do Navio. Nonetheless, Cunha and Nascimento (1984) noted that specimens occurring south of the Amazon River have fewer ventral scales compared with populations occurring to the north of the river (e.g., Serra do Navio, Surinam, and French Guyana samples). Cunha and Nascimento (1984) failed to find any other characters that would support taxonomic recognition of the specimens south of the Amazon River.

According to our sample, *Atractus zidoki* and *A. hoogmoedi* differ in the number of ventral scales (170–171 in males and 180 in female of *A. hoogmoedi*, vs. 178–187 in males and 196–200 in females of *A. zidoki*). Although Hoogmoed (1980) reported an individual (sex was not stated, but it is presumably a male based on the low count) of *A. zidoki* with 173 ventral scales, close to the range found in the male specimens of *A. hoogmoedi*, the hemipenis of both species diverge in the bifurcation of the sulcus spermaticus and in the general ornamentation (Fig. 1). Within the subfamily Dipsadinae (*sensu* Zaher et al., 2009), a single sulcus spermaticus is found also only in the genus *Adelphicos* (Campbell and Ford, 1982). However, both conditions appear to be homoplastic since the sulcus spermaticus of

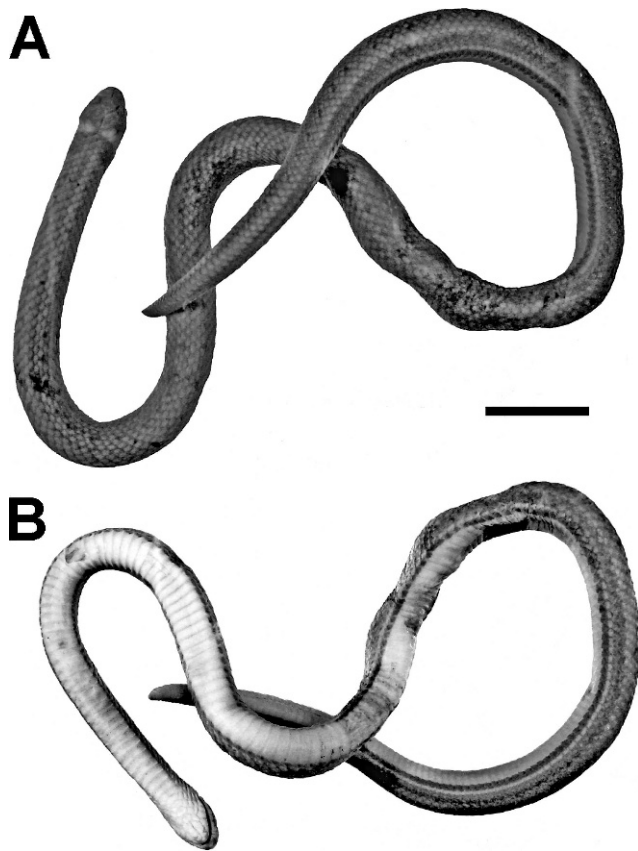


Fig. 3. Dorsal (A) and ventral (B) views of the holotype of *Atractus hoogmoedi*, new species (MPEG 13268). Scale = 2.5 mm.

Adelphicos have a centrifugal orientation diverging on the basal portion of the hemipenis, while *Atractus hoogmoedi* has a median sulcus spermaticus. As the hemipenis of *A. zidoki* has a median sulcus spermaticus with distal bifurcation of the branches, we believe that the loss of the sulcus spermaticus branches in *A. hoogmoedi* is an autapomorphy of the species (P. Passos, unpubl.).

The hemipenis structure is used widely in squamate systematics, both for alpha level taxonomy and for constructing phylogenetic hypotheses (Dowling and Savage, 1960; Dowling, 1967; Arnold, 1986; Keogh, 1999; Zaher, 1999). Hemipenis differences between taxa may arise from a variety of phenomena, including non-homologous evolution of associated character systems, direct selection, development of physical isolating mechanisms, and pleiotropic events (Arnold, 1986). Sources of hemipenis differences are based on seasonal (Vences et al., 1999), ontogenetic or individual (Shine et al., 2000), intraspecific (Inger and Marx, 1962), and interspecific (Presch, 1978) variation. While individual variation produces differences primarily in the size of the organ associated with reproductive success (Shine et al., 2000), seasonal variation of the hemipenis reflects micro-ornamentation modifications related to hormonal cycles during the breeding season, and has been found only in some lizard families (Böhme, 1971; Vences et al., 1999). In snakes, the seasonal changes of the male reproductive organs are hormonally controlled, similar to other reptiles, but differ from them essentially in reproductive cycles affecting size of testis and the thickness of efferent passages (Volsøe, 1944).

It has been largely noticed that the hemipenis differs from other organ systems in its ability to retain changes through evolutionary time, and thus it is inherently more stable than many other morphological features used in systematic assessments (Dowling and Savage, 1960; Dowling, 1967; Arnold, 1986; Keogh, 1999). Dowling (1967) pointed out that the hemipenis structure, unlike other characters (teeth, skull, or scutellation), has no obvious correlation with the ecology, food habits, or locomotion of the animal. Consequently, the hemipenis may yield better data on the phylogenetic relationships than other habit- or habit-correlated characteristics (Dowling, 1967). As in other internal system organs, the hemipenis structures are less likely to be affected by strong selective forces acting on external characters (Arnold, 1986). Moreover, individual males usually possess hemipenis compatibility with the morphology of as many female cloaca as possible within local populations to increase their fitness (Arnold, 1986; Keogh, 1999). Despite the widespread use of hemipenis differences as an important source of characters for higher categories of snake phylogeny (Dowling and Duellman, 1978; McDowell, 1987; Keogh, 1999; Zaher, 1999), their use for inferring species boundaries has been somewhat limited by the highly conservative nature of traits at generic levels (McDowell, 1974, 1975; Branch, 1986; Guo et al., 1999; Keogh, 1999).

On the other hand, intraspecific variation is reported for some species of snakes with respect to size, shape, and hemipenis microornamentation (Inger and Marx, 1962; Keiser, 1974; MacDowell, 1979; Cole and Hardy, 1981; Zaher and Prudente, 1999; Shine et al., 2000; Schargel and Castoe, 2003). However, to our knowledge, variation of lobular and sulcus spermaticus conditions of the snake hemipenis is still restricted to Indo-Malayan island populations of *Calamaria lumbricoidea* (Inger and Marx, 1962). Although Inger and Marx (1962) highlighted that intraspecific differences on the hemipenial shape and ornamentation were accompanied by variation of the cloaca form of females, this surprising variation is apparently exclusive to this species and does not discount these structures as taxonomic characters in other species of *Calamaria* or other genera (Inger and Marx, 1962, 1965). Another basis for hemipenis variation may also come from preparation bias of partially protruded organs of preserved specimens (Dowling, 2002). Despite the recent discussion regarding the preparation bias of preserved hemipenis (see also Myers and Cadle, 2003 and Zaher and Prudente, 2003 for other points of view), this artifact (when identified) is more than likely constrained to features such as lobular shape, orientation, or microornamentation (Dowling, 2004).

Within the genus *Atractus*, the intraspecific variation of the hemipenial characters, when observed, is concentrated on micro- and macro-ornamentation structures like spinules, spines, and papillae and/or calyces and flounces respectively (Schargel and Castoe, 2003; Zaher et al., 2005; Passos, 2008). Even so, there is the possibility of bias in the preparation of preserved hemipenis, as outlined by Dowling (2004), mainly with respect to partially everted organs in the field. Based on the preparation of about 200 hemipenis of the preserved specimens of *Atractus* following Dowling's recommendations, the junior author has found that macro-ornamentation structures such as calyces and flounces may be also permanently affected by the time of immersion in formalin and/or concentration of the solution of semi-everted organs during

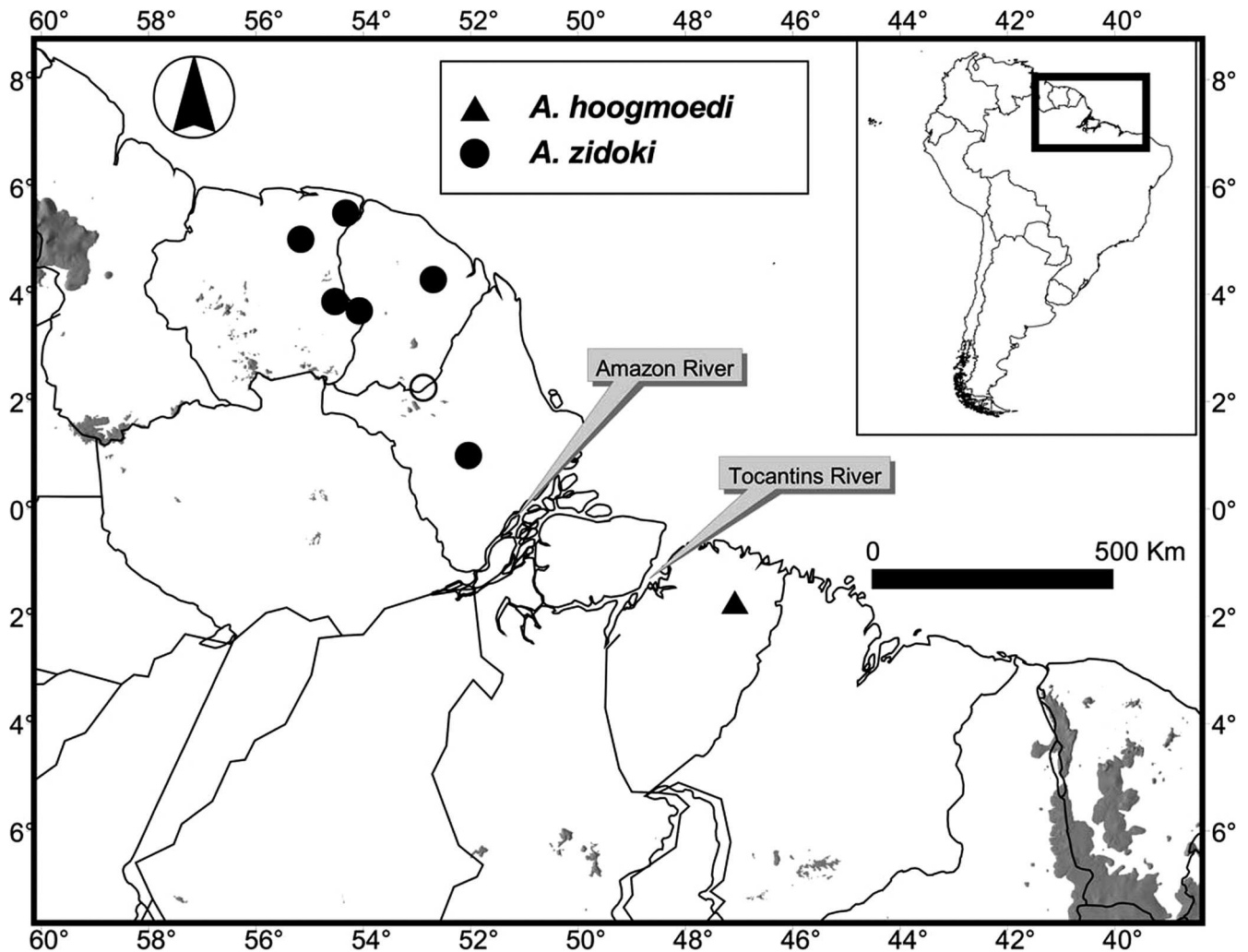


Fig. 4. Geographic distribution of *Atractus zidoki* and *A. hoogmoedi*, new species.

the preservation process. Nonetheless, no intraspecific variation on sulcus spermaticus division and/or orientation was observed for any species of *Atractus*. Besides the organs from *Atractus hoogmoedi* ($n = 2$) and *A. zidoki* ($n = 4$) examined by us, there are two other specimens of *A. zidoki* showing the bifurcated condition of the sulcus spermaticus previously cited in the literature (Gasc and Rodrigues, 1979:553–54; Hoogmoed, 1980:30). Therefore, the available evidence suggests that single and bifurcate conditions are apparently fixed in *A. hoogmoedi* and *A. zidoki*, respectively. Regardless of the relatively small sample, it represents about 60% of known males of the former and all the known males of the latter species. Given the scarcity of both species in museum collections and the difficulties encountered when seeking permission for preparing organs from rare species, the samples reported on herein provide consistent evidence for species diagnosis, and we can reliably confirm these two conditions as diagnostic characters.

All remaining external and internal characters examined for *Atractus hoogmoedi* and *A. zidoki* are comparable or overlap one another's range of variation, and for that reason, cannot be used to distinguish them. Nonetheless, the southern record for *Atractus zidoki* (Serra do Navio) is about 500 km (airline) northwest from the type locality of *A. hoogmoedi* (Capitão Poço), with the Amazon River mouth

separating them (Fig. 4). In this sense, we speculate that reorientation of the Amazonian drainage system in the late Miocene by marine incursions (Lovejoy et al., 2006 and references therein) or in the late Pliocene (Gregory-Wodzicky, 2000 and references therein) to Pleistocene (Lundberg et al., 1998 and references therein) by the Andes uplift, could represent a vicariant episode for the ancestral stock of *A. hoogmoedi* and *A. zidoki*.

The incidence of cryptic species of *Atractus* remains underestimated, but several species should be recognized on the basis of analysis of internal characters (Passos, 2008). In the face of the highly conservative nature of the external morphology within the genus, except for color pattern characters (Schargel and Castoe, 2003), the species delimitation has turned out to be a hard task for several species (Passos, 2008). Even so, recent studies still diagnose *Atractus* species on the basis of slight nuances of color pattern, cephalic plate contact, and meristic characters, even for taxa that are susceptible to strong polymorphism or with overlapping species ranges (Silva, 2004; Esqueda and La Marca, 2005). Meanwhile, major relevant information, useful for systematic studies, can be extracted from other classes of characters (e.g., hemipenial features). For that reason, we strongly recommended that a description of the hemipenis should be included (when possible) in future

accounts of *Atractus* in order to provide an adequate number of diagnostic characters, thus guaranteeing a robust species identification for this complicated and highly diverse genus.

MATERIAL EXAMINED

Institutional abbreviations are listed at <http://www.asih.org/codons.pdf>, except the following institutions. Colombia—Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Bogotá, D.C.; Museo de la Universidad La Salle (MLS), Bogotá, D.C.; Ecuador—Museo de Zoología, Pontificia Universidad Católica de Ecuador (QCAZ), Quito; Brazil—Instituto Butantan (IBSP), São Paulo, SP; Instituto de Medicina Tropical de Manaus (IMTM).

Atractus alphonsehoegi ($n = 9$).—Brazil: Maranhão: Santa Inês: MPEG 10874; Pará: Viseu: Km 75 from Bragança—Viseu Highway: Bela Vista: MPEG 14928 (holotype); Augusto Corrêa: Fazenda Cacoal: MPEG 9949 (paratype); Bragança: Parada Bom Jesus: MPEG 2221, 8573, 8667 (paratypes); Colonia Nova: MZUSP 8378, Km 224 (formerly Km 74) from BR 316 Highway: MPEG 10093 (paratype); Santa Rosa: Estrada de Vigia: MPEG 12593.

Atractus caxiuana ($n = 3$).—Brazil: Pará: Melgaço: Floresta Nacional de Caxiuana: MPEG 19657 (holotype), MPEG 19964, 20128 (paratypes).

Atractus collaris ($n = 12$).—Colombia: Amazonas: La Pedrera: ICN 10112–13; Caquetá: Florencia: MLS 1324, 2782; Parque Natural Nacional Kaparú: ICN 8144. Ecuador: Napo: Pozo Petrolero Zabalo: EPN 5216; Orellana: Yasuní: QCAZ 5980; Sucumbíos: Cuyabeno: QCAZ 983, 986, 1042. Peru: Loreto: Iquitos, Maynas: MHNSM 2310; Ucayali: Coronel Portillo, Pucallpa: MHNSM 3083.

Atractus gaigeae ($n = 10$).—Ecuador: Napo: Estación Biológica Sacha: EPN (not catalogued); Loreto: USNM 217622; Mouth of Río Coca: USNM 217621; Pastaza: Cotopaza: EPN 8693 (paratype); Misión: EPN 752; Motalvo: USNM 217627; Río Bobonaza: EPN 5217; Río Canambo, near mouth of Río Romarizo: USNM 217624; Río Conambo, near mouth of Río Shione: USNM 217625; Río Rutuno, tributary of Río Bobonaza: USNM 217626.

Atractus hoogmoedi ($n = 3$).—Brazil: Pará: Capitão Poço: Santa Luzia: MPEG 13268 (holotype and everted hemipenis), MPEG 13265 (paratype), MPEG 13266 (paratype and retracted hemipenis).

Atractus limitaneus ($n = 1$).—Colombia: Amazonas: La Pedrera: IBSP 9196 (holotype).

Atractus surucucu ($n = 3$).—Brazil: Roraima: Serra do Surucucu: MPEG 19146 (holotype), MPEG 18436–37 (paratypes).

Atractus zidoki ($n = 11$).—Brazil: Amapá: Serra do Navio: IBSP 24112, 24772 (everted hemipenis), 27393, MPEG 16437 (retracted hemipenis), 23225 (everted hemipenis), 23226, 23227, 23228, MZUSP 2840, MZUSP (not catalogued), IMTM 450 (retracted hemipenis).

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