Molecular systematics and taxonomic revision of the Curve-billed Scythebill complex (Campylorhamphus procurvoides: Dendrocolaptidae), with description of a new species from western Amazonian Brazil

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The morphological attributes distinguishing populations of Campylorhamphus procurvoides⁸ distributed west of the Madeira and south of the Solimões rivers in the Inambari area of endemism (sensu Silva et al. 2005), were first pointed out by Zimmer (1934) when discussing a female (AMNH 309432) from Tefé, in the Brazilian state of Amazonas. Zimmer (1934) could not classify this specimen as C. procurvoides or C. trochilirostris with certainty, although the shape of its pectoral spots was similar to those of birds grouped under C. procurvoides. The next time the Tefé Campylorhamphus was mentioned was by N. Gyldenstolpe (1945a), who studied a female Campylorhamphus (NR 569483) obtained by the Olalla family at Igarapé Grande, upper Juruá River, near Eirunepé, Amazonas, Brazil. Gyldenstolpe concluded that this particular specimen and two males also housed at the NR and collected by the Olallas along the Purus River valley at Lábrea and Jaburú, Amazonas, Brazil (respectively NR 569481 and 569482), closely matched the characters shown by the Tefé specimen discussed by Zimmer (1934), and that, as a whole, these specimens probably represented an undescribed taxon allied to C. procurvoides. Three years later, Todd (1948) studied the Tefé specimen and a series of 19 Campylorhamphus obtained by the collector Samuel M. Klages at six different localities along the Purus, Solimões, and lower Amazon rivers, and concluded that they all belonged, along with the male from the upper Juruá housed at the NR, to the new taxon recognized but not named by Gyldenstolpe (1945a); he then provided a brief description of the new taxon, named Campylorhamphus procurvoides successor Todd 1948 (type locality Nova Olinda, on the left bank of the middle Purus River, Amazonas, Brazil). Subsequently, in his detailed study on the ornithology of the Purus River region in Brazil, Gyldenstolpe (1951) also assigned his Lábrea and Jaburú specimens mentioned above to C. p. successor, without having examined the type series at the CM.

Recently, Portes and Aleixo (2009) showed that the type series of successor consists of a mix of individuals belonging to C. trochilirostris (including the holotype for C. p. successor) and specimens whose plumage characters closely match those of the Tefé, upper Juruá, and Purus specimens discussed, respectively, by Zimmer (1934) and Gyldenstolpe (1945a, 1951). Between 2002 and 2009, five additional specimens with those same characteristics were collected by us and colleagues at four new localities in the Brazilian states of Rondônia and Amazonas and later sequenced for two mtDNA genes. Together, these birds form a statistically well-supported and reciprocally monophyletic group with respect to all other lineages grouped under C. procurvoides. Because the name successor can no longer be applied to birds grouped in this clade, we propose to name them as:

Campylorhamphus gyldenstolpei Tupana Scythebill

arapaçu-do-tupana (Portuguese)



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⁸ Genus Campylorhamphus 8: 445.

Holotype.— Museu Paraense Emílio Goeldi (MPEG) 62267. skin, adult male, skull 100% ossified, no bursa of fabricius; left testis 5 × 3 mm; brood patch present; 38 g with little fat and no molt. Collected (shot) in the understory of creek-side upland (terra-firme) forest by AA and tape-recorded by AW on 4 July 2007 at Tupana Lodge, located at km 158 of the BR 319 road in the municipality of Careiro, Amazonas, Brazil (04° 05' 00.2"S; 60° 39′ 37.8° W); prepared by AA under field number TUP 001. Pectoral muscle tissue preserved in approximately 96% alcohol; field number TUP 001. Hologenetype (Chakrabarty 2010) sequences of the mitochondrial genes cytochrome b (1,076 pb) and NADH subunit 2 (1,041bp) deposited in GenBank (accession numbers KC237252 and KC242874, respectively). Taperecordings of vocalizations archived at the British Library of Natural Sounds under accession number (183248; available at http://www.bl.uk/listentonature/main.html). Digital pictures of the recently collected individual, before preparation, deposited at MPEG.

Diagnosis: Morphology.— Alphanumeric color designations determined through direct comparison with Smithe (1975). Phenotypically, the new species can be unambiguously assigned to the genus Campylorhamphus (Dendrocolaptidae) based on its narrow, long, and curved bill, which distinguishes the genus; within Campylorhamphus it can be placed in the C. procurvoides complex on the basis of its small and narrowly tipped pectoral stripes, which possess a characteristic sagittate format (Zimmer 1934), being nearest to those of specimens assigned to C. p. sanus and C. p. procurvoides, but distinct from all other

members of the complex by a unique combination of size, color, and shape. In comparison with taxa currently grouped under C. procurvoides (sensu Zimmer 1934), the new species can be phenotypically diagnosed as follows: 1) from multostriatus by significantly smaller and sagittate (acutely shaped) whitish pectoral stripes, less pronounced or even absent streaking on the back, narrower head and neck stripes, and belly and back Cinnamon-Brown (33) or Russet (34) (vs. Cinnamon 39); 2) from probatus by narrower and whitish (vs. Pale Horn 92) pectoral stripes, and belly and back Cinnamon-Brown (33) or Russet (34) (vs. Cinnamon 39); 3) from closely related sanus by distinctly larger culmen, wing, and tail measurements (Table 1 in supplementary Information – SI), wider and whitish (vs. Pale Horn 92) pectoral stripes, with a more contrasting black edge (vs. black edge absent), and belly Cinnamon-Brown (33) or Russet (34) (vs. bright Antique Brown 37); and 4) from closely related procurvoides by distinctly broader head, throat, and pectoral stripes, the latter with a more contrasting black edge (vs. black edge absent), and belly Cinnamon-Brown (33) or Russet (34) (vs. Brownish Olive 29). Voice.— The loudsong is immediately distinguished in the field from those of all other members of the complex and, in spectrographic analysis, by the shape and syntax of the notes (described below; see Figs. 1 and 2). Within the C. procurvoides complex, C. gyldenstolpei is the only taxon possessing D note types (characterized by an abrupt frequency peak before its end; Fig. 1D) in its loudsong (Fig. 2C). Genetic divergence.— Separated from its close relatives sanus and procurvoides by approximately 0.8 and 1.2 % sequence divergence, respectively, in the mitochondrial genes cytochrome b and NADH subunit 2 (Fig. 3).

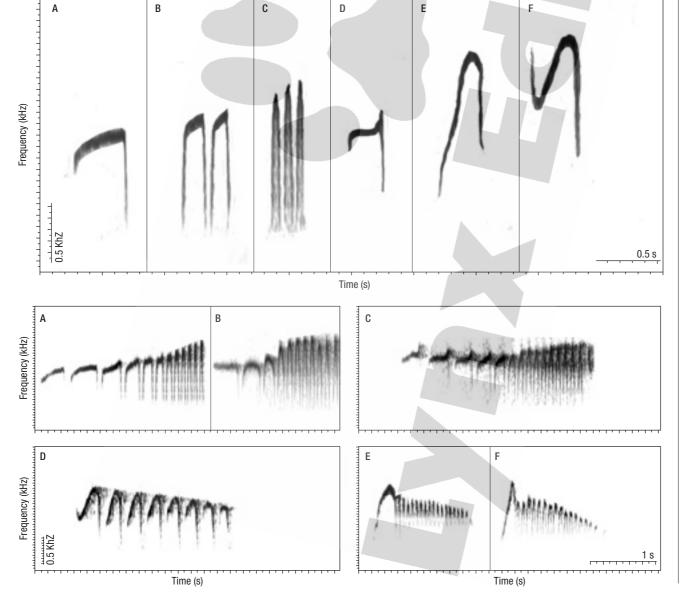


Figure 1. Representative spectrograms of note-types used to diagnose the loudsongs of taxa currently grouped under the polytypic Campylorhamphus procurvoides. Letters refer to the note-type nomenclature used in this study. Notes A, B, and D are restricted to the so-called "procurvoides" group (sensu Marantz et al. 2003; which includes the new taxon gyldenstolpei, described herein), whereas notes E and F are found only in the "multostriatus group" (sensu Marantz et al. 2003).

Representative spectrograms of loudsongs of taxa currently grouped under the polytypic Campylorhamphus procurvoides and the new taxa described in this volume: A) procurvoides: Venezuela, Rio Grande, El Palmar (LNS-65702_2c); B) sanus: Venezuela, Amazonas, San Carlos (LNS-65706_6); C) gyldenstolpei: Brazil, Amazonas, Tupana Lodge (AW3B3_2b); D) multostriatus: Brazil, Pará, Salobo Road, Carajás (AW5A2_10); E) unnamed taxon described by Portes et al. (2013) in this volume: Brazil, Mato Grosso, Alta Floresta, Rio Cristalino (LNS-106114 24b): and F) probatus: Brazil. Amazonas, Borba, eastern bank of the Madeira River (LNS-127698_3b).

Distribution.— Campylorhamphus gyldenstolpei has been documented from several localities west of the Madeira and south of the Solimões rivers in the Inambari area of endemism (sensu Silva et al. 2005) in Brazil (Fig. 4). The species is likely to be found in the neighboring departments of Loreto (south of the Amazon / Marañón rivers) and Ucayali in Peru near the Brazilian border but so far no records exist (under the name C. procurvoides; Schulenberg et al. 2007).

Description of holotype. — See color illustration. Alphanumeric color designations determined through direct comparison with Smithe (1975). Plumage fresh and unworn, tail and wing not in molt; skull 100% ossified. Head uniformly Sepia (119) with short, light-brownish stripes, including the forehead, lores, and cheeks. Mantle Sepia (219) with thin and rather long light brown streaks restricted to the upper parts, with unmarked lower parts. Primaries, secondaries, and wing coverts Warm Sepia (221A). Tips and inner webs of primaries with a contrasting Fuscous (21) tinge. Lower mantle and upper parts of rump Sepia (219), gradually changing into Warm Sepia (221A) in the lower rump. Rectrices essentially concolor with lower rump. Tail graduated, each rectrix with a stiff shaft, softer at the tips. Throat Sepia (119) heavily streaked with whitish-creamy feathers with a scaly shape. Lower throat and breast Sepia (219) covered with arrow-shaped (i.e., sagitatte) whitish-creamy streaks with thin but contrasting black edges. Upper belly Cinnamon-Brown (33) with some obsolete thin and rather long whitish streaks. Lower belly concolor with upper belly, but unstreaked. Undertail coverts Cinnamon-Brown (33) with feathers with somewhat contrasting whitish shafts. Soft parts in life: Iris dark brown with a contrasting yellow-mustard eyering. Maxilla Burnt Orange (116) with a dark brownish wash around the nostrils: mandible light Burnt Orange (116); tarsi and feet bluish-green. Measurements of holotype: wing 100.7 mm, tail 96.4 mm, tarso-metatarsus 20.8 mm, bill length from the anterior edge of nares 53.3 mm, bill height at nares 6.2 mm, and bill width at nares 5.4 mm.

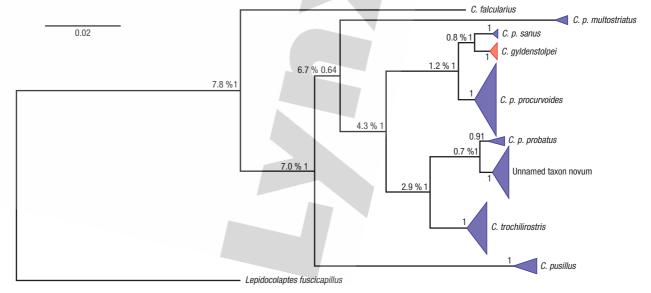
Etymology.— We are pleased to name the new species after the Swedish ornithologist Count Nils Gyldenstolpe, who was the first to characterize the distinctiveness and distribution of the new Campylorhamphus described herein, separating it from all other taxa known at the time grouped under both C. procurvoides and C. trochilirostris (Gyldenstolpe 1945a, 1951). Furthermore, the name of the new species represents a tribute to Gyldenstolpe's great contribution to Neotropical, and particularly Amazonian, ornithology, as shown by his unique and thorough monographs on the birds of northern Bolivia and the upper Juruá and Purus rivers in Brazil (Gyldenstolpe 1945a,b, 1951).

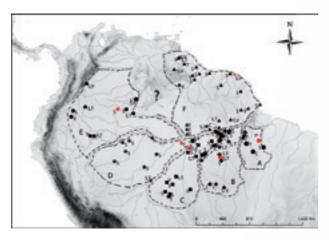
REMARKS

Type series.— The allotype of C. gyldenstolpei is MPEG 68870, skin, adult female, ovary 7×3 mm with ova minute, convoluted oviduct, no molt; collected (shot) and tape-recorded in the understory of terra-firme forest by AA on 29 September 2009 at Tupana Lodge (same locality as the holotype); prepared by M. Santa-Brígida under field number TUP 059. Tissue samples deposited at MPEG and mitochondrial cytochrome b and NADH subunit

2 sequences deposited in GenBank (KC237250 and KC242872, respectively). Tape-recordings of vocalizations archived at Xeno-canto under accession numbers (XC107627; available http://www.xeno-canto.org/107627). Paratypes of C. gyldenstolpei are the following fourteen specimens: MPEG 60081: skin, adult male, left testes 7 × 5 mm, molt; carcass preserved in 70% ethyl alcohol under field number CUJ 25; collected (shot) on 10 March 2006 by AA in the understory of terra-firme forest at Reserva de Desenvolvimento Sustentável do Cujubim, ca. 390 km SW of Jutai (05° 13' 11.5"S; 69° 19' 00.0"W), Amazonas, Brazil, and prepared by Fabíola Poletto; tissue sample deposited at MPEG and mitochondrial cytochrome b and NADH subunit 2 sequences deposited in GenBank (KC237251 and KC242873, respectively). MZUSP 76641: skin, adult male with well developed gonads; collected by Luís Fábio Silveira and Fábio Olmos at Estação Ecológica Antônio Mujica Nava (09º 24' S; 64º 56' W), Rondônia, Brazil, on 12 February 2002; tissue sample deposited at Instituto de Biologia da Universidade de São Paulo (IB-USP). INPA 1630: skin, male, Campos do Tupana (ca. 120 km south of Manaus: 4°09'S; 60°08'W), Amazonas, on 6 July 2007, collected by M. Cohn-Haft; tissue sample deposited at INPA. NR 569483: skin, female, Igarapé Grande (ca. 15 km north of Eirunepé: 6°38'S; 69°50'W; coordinates from Gyldenstolpe 1945a), Amazonas, Brazil, 30 August 1936, collected by A. M. Olalla and crew. NR 569481: skin, male, Lábrea (ca. 7°18'S; 64°35'W; coordinates from Gyldenstolpe 1951), right bank of the Purus River, Amazonas, Brazil, 7 January 1936, collected by A. M. Olalla and crew. NR 569482: male, Jaburú (ca. 5°36'S; 64°12'W; coordinates from Gyldenstolpe 1951), left bank of the Purus River, Amazonas, Brazil, 10 December 1935, collected by A. M. Olalla and crew. AMNH 309432: female, Santo Isidoro, Tefé (ca. 3°22'S; 64°42'W; coordinates from Paynter and Traylor 1991), Amazonas, Brazil, 31 July 1928, collected by A. M. Olalla and crew. CM 96192: male, São Paulo de Olivença (ca. 3°27'S; 68°48'W; coordinates from Paynter and Traylor 1991), Amazonas, Brazil, 2 April 1923, collected by Samuel M. Klages. CM 91898: male, Nova Olinda (ca. 5°40'S; 64°18'W; coordinates from Gyldenstolpe 1951), left bank of the Purus River, Amazonas, Brazil, 14 July 1922, collected by Samuel M. Klages. CM 86702, 87386, and 87857: males, Hyutanaan (ca. 7°40'S; 68°45'W; coordinates from Gyldenstolpe 1951), right bank of the Purus River, Amazonas, Brazil, collected, respectively, on 26 December 1921, 19 January 1922, and 9 February 1922 by Samuel M. Klages. CM 99363: male, Caviana (coordinates not located), south bank of the Solimões River, Amazonas, Brazil, 30 May 1924, collected by Samuel M. Klages. UMMZ 150237 (ex-CM 93949): male, Arimã (ca. 5°47'S; 63°38'W; coordinates from Gyldenstolpe 1951), right bank of the Purus River, Amazonas, Brazil, 9 November 1922, collected by Samuel M. Klages. Variation in the type series: The most noticeable variation in the type series pertains to the chest and belly color of the different specimens, which ranges

Figure 3. Bayesian estimate of the phylogeny of the genus Campylorhamphus based on two mitochondrial genes (cyt b and ND2). Numbers refer to posterior probability values and genetic distances (% of average uncorrected p sequence divergence) between sister groups associated with the labeled nodes. Note the polyphyly of taxa currently grouped as subspecies of C. procurvoides (multostriatus, probatus, procurvoides, and sanus) and the new taxon gyldenstolpei and a second previously unnamed taxon described by Portes et al. (2013) in this volume. High support values (i.e., 1) associated with nodes grouping procurvoides. sanus and gyldenstolpei are consistent with their recognition as species-level taxa.





from Cinnamon-Brown (33) to Russet (34), with a nearly Amber (36) tinge in some specimens (AMNH 309342, CM 91898, NR 569481, NR 569482, MZUSP 76641, MPEG 60081). Apparently, this variation has no geographical, seasonal, ontogenetic, or sexual basis, since series of adult male and female specimens collected between July and September at the same or nearby localities (such as Tupana) varied noticeably in chest and belly color (MPEG 62267, MPEG 68870, and INPA 1630). The same applies to the color of the throat and pectoral spots, which range from pure white (CM 86702, CM 87857, MPEG 60081) to whitish with a Buff (24) hue (NR 569481, NR 569482, NR 569483, CM 87386), with the tendency of the contrasting black edge to be more conspicuous in the birds with whiter pectoral spots; three male specimens collected at the same locality (Hyutanaãn) between late December and early February exhibited both white (CM 86702 and CM 87857) and more buffy (CM 87386) spots, therefore suggesting that the variation in this character is of an individual nature. Head color varied less, with most specimens being Fuscous (21), although UMMZ 150237 (ex-CM 93949) and NR 569482 had conspicuously faded head coloration, with an overall Raw Umber (23) color. Therefore, it is more likely that all aforementioned variation in plumage color has an individual basis that could possibly be explained by differences in the amount of wear due to differences in foraging and roosting, for example. No specimens in the type series exhibit signs of immaturity, with all those for which age-related data are available being full adults based on skull ossification and gonad development data (MZUSP 76641, MPEG 60081, MPEG 62267, MPEG 68870, and INPA 1630).

Ecology and behavior.— Campylorhamphus gyldenstolpei, like other members of the C. procurvoides complex, forages alone or in pairs in the understory and sometimes midstory of terra firme forest, usually found along forest creeks, and will occasionally join mixed-species flocks that pass through its territory. The species seems particularly tied to terra firme forest growing on sandy soils such as at Tupana Lodge and Reserva de Desenvolvimento Sustentável do Cujubim, where the local forest possesses a dense understory dominated by short Lepidocaryum sp. palm trees. Its nest and eggs remain unknown.

Vocalizations.— When compared to loudsongs of other taxa in the C. procurvoides complex, the loudsong of gyldenstolpei is unique, mainly in the shape and syntax of the note. Within the complex, this vocalization typically consists of three note types (B, C, and D; Fig. 1), with D note types being found only in C. gyldenstolpei. Note syntax for a typical loudsong of C. gyldenstolpei is as follows: an introductory sequence of 2-4 D notes, followed by 1-4 B notes, and terminating with 6-12 C notes (N = 8, Figs. 1 and 2c). This loudsong type contrasts with that of other members of the C. procurvoides complex, whereby the syntax is similar between procurvoides and sanus (including only note types A, B, and C), varying only in the number of each note type

Hence, the loudsong of sanus normally includes an introductory sequence of 1-2 A notes, followed by 2-3 B notes, and concluding with 4-9 C notes (N = 3, Figs. 1 and 2b), whereas that of procurvoides consists of 1-4 A notes, 2-9 B notes, and 4-23 C notes (N = 21, Figs. 1 and 2a,b). Furthermore, the dominant frequency values of the notes in gyldenstolpei loudsongs vary little, whereas in both sanus and procurvoides, the loudsongs increase significantly in frequency, with C type notes having higher frequencies compared to notes A and B (Figs. 1 and 2a,b).

Phylogenetic relationships.— DNA sequence data for the mitochondrial genes cytochrome b (cyt b, 1,076 base pairs) and NADH subunit 2 (ND2, 1,041 base pairs) were obtained for 41 individuals (see Table 4 in the SI file for a list of specimens sequenced) of all species in the genus Campylorhamphus, including all taxa currently grouped under the polytypic C. procurvoides (sensu Marantz et al. 2003; i.e., multostriatus, probatus, procurvoides, and sanus; Fig. 4). Trees were rooted in Lepidocolaptes fuscicapillus, which belongs with one of the sister genera to Campylorhamphus (Derryberry et al. 2011). The phylogeny estimated by Bayesian inference strongly supports that C. procurvoides, as currently defined, represents a polyphyletic species, with taxa currently classified as its subspecies found in three separate clades with disparate phylogenetic affinities (Fig. 3). The three highly supported and reciprocally monophyletic clades group taxa currently classified as subspecies of the polyphyletic \hat{C} . procurvoides as follows: (1) birds occurring south of the Amazon and east of the Xingu River in the Xingu center of endemism (Silva et al. 2005; corresponding to the taxon multostriatus, whose type locality lies in this area of endemism; Fig. 4); (2) birds found south of the Amazon and west of the Madeira River (in the Inambari center of endemism, corresponding to the new taxon described herein, i.e. gyldenstolpei) and birds distributed north of the Amazon, which correspond to the taxa sanus (found in the Napo and Imeri areas of endemism) and procurvoides (corresponding to the Guiana area of endemism; Fig. 4); and (3) birds found south of the Amazon and between the Madeira and Xingu rivers, corresponding to the taxon probatus (distributed in the Madeira center of endemism; Fig. 4) and to the taxon formerly known as multostriatus but which in fact represent an unnamed taxon described by Portes et al. (2013) in this volume (endemic to the Tapajós area of endemism; Fig. 4). The fact that the Bayesian phylogeny recovered gyldenstolpei, procurvoides, and sanus as reciprocally monophyletic taxa with strong statistical support (Fig. 3) in conjunction with morphological and vocal diagnoses of these taxa, supports their recognition as valid species level taxa (De Queiroz 2007). Thus, we recommend the recognition of three species and vernacular names in the C. procurvoides complex, henceforth defined as consisting of only three taxa (gyldenstolpei, procurvoides, and sanus): Tupana Scythebill (C. gyldenstolpei; distributed west of the Madeira and south of the Solimões rivers in Amazonian Brazil; Fig. 4); Curve-billed Scythebill (C. procurvoides; distributed on the Guianan shield north of the Amazon and east of the Negro - Branco rivers in Venezuela, Brazil, Guyana, Suriname, and French Guiana); and Zimmer's Scythebill (C. sanus; distributed west of the Branco - Negro rivers in Amazonian Brazil and Venezuela westward towards the base of the Andes in Colombia, Ecuador, and Peru north of the Amazon / Solimões rivers).

Conservation. — Campylorhamphus gyldenstolpei is a low-density species in its preferred habitat. Because it is endemic to one of the least disturbed parts of Amazonia (the Inambari area of endemism), it is not currently threatened by anthropogenic alteration of its habitat. Of particular concern in the long term is the recent advancement of soybean plantations in parts of the range of C. gyldenstolpei such as around Lábrea, in the southern part of Amazonas, Brazil. If the advancement of agro-business at the core of C. gyldenstolpei's range becomes more widespread, it could imperil this and many other endemic terra-firme species of the Inambari region in the long run.

Acknowledgments.— We thank the curators and curatorial assistants of the following collections for allowing us to use skins, tissues, and vocal recordings under their care: AMNH, ANSP, BLNS, CM, COP, FMNH, INPA, LSUMZ, MCZ, MLS, MN,

Figure 4. Geographic distribution of specimens, vocalizations, and tissues of Campylorhamphus procurvoides taxa analyzed in this study. Asterisks = C. gyldenstolpei; dots = C. multostriatus; crosses = unnamed taxon described by Portes et al. (2013) in this volume; triangles = C. procurvoides; squares = C. probatus; and pentagons = C. sanus. Type localities for each taxon are shown as red symbols. Letters next to a symbol represent material available for that given *locality: "P" = photographs* only; "S" = skins only; "V" = tape-recordings only; "T" tissues only; "S,V" = skins and vocalizations only; "S,T" = skins and tissues only; "C" = tape-recordings, skins, and tissues. Dashed lines delimit main lineages recovered by a molecular phylogeny and interpreted as natural populations as follows: A = multostriatus. B = unnamedtaxon described by Portes et al. (2013) in this volume. C =probatus, D = gyldenstolpei, E= sanus, and F = procurvoides. The question mark denotes an area between the Branco and Negro rivers where the taxonomic identity of any taxa of C. procurvoides is unknown.

MZUSP, NHMW, NR, UMMZ, USNM, and ZMB. M. A. Raposo (through CNPq grant# 479049/2006-8) kindly sent us high resolution digital pictures of the type specimen of nominate procurvoides deposited at the MCZ. S. Dantas and B. M. Whitney generously allowed us to analyze recordings from their personal archives. M. Ferreira and L. J. dos Anjos provided assistance in designing some figures presented in this paper. Field and laboratory work related to this study was funded through the following agencies and institutions: CI-Brazil, WWF-Brazil, MMA, CNPg (#476212/2007-3, 490387/2007-1, "INCT em Biodiversidade e Uso da Terra da Amazônia" # 574008/2008-0, "Evolução da Fauna de Vertebrados Terrestres Brasileiros do Cretáceo ao Presente: Paleontologia e Filogenia" # 565046/2010-1, and 471342/2011-4), FMNH Marshall Funds, and NSF (DEB-0515672, DEB-0543562, and DEB-01120054). AA is supported by a productivity fellowship from CNPq. DNA sequencing for this project was carried out in part at the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution, operated with support of the Pritzker Foundation. Hilary Burn painted the illustration.

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