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Inventory of color polymorphism in populations of *Dendrobates galactonotus* (Anura: Dendrobatidae), a poison frog endemic to Brazil

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Abstract

Inventory of color polymorphism in populations of *Dendrobates galactonotus* (Anura: Dendrobatidae), a poison frog endemic to Brazil. We studied the various color morphs of *Dendrobates galactonotus* that occur in its range between the Amazon and Tapajós rivers, in the Brazilian states of Pará, Maranhão, northern Mato Grosso, and northern Tocantins. Dorsal coloration ranges from black to light blue and from red via orange to yellow, cream and white, with or without black spots or vermiculations. Most specimens are uniformly black below, but in some populations the color of the back has invaded the ventral surface and the black has been reduced to small areas on the seat patch and under the thighs. We could not locate any completely white populations, a color variant present in captivity and known as "Moonshine." No regularity in the distribution of color pattern could be distinguished; the majority of localities has orange colored populations, but other color morphs are sprinkled between them. Populations are uniform, only showing one color, although the amount of black elements on the back may vary. Threats to this species are deforestation, fragmentation of habitat, hydroelectric projects (already functioning, under construction, or projected), gold mining, and possibly illegal international trade. Although this species is widely distributed in terrariums in Europe, the United States, and Japan, all these specimens stem from illegal exports. Genetic research to try to establish a connection between color pattern and genetic make-up of populations is in progress.

Keywords: Amazonian forest, coloration, habitat, pet trade, threats, zoogeography.

Resumo

Inventário do polimorfismo cromático em populações de *Dendrobates galactonotus* (Anura: Dendrobatidae), um anuro venenoso endêmico do Brasil. Estudamos os diferentes padrões de coloração em *Dendrobates galactonotus* encontrados em sua área de distribuição entre os rios Amazonas e Tapajós, nos estados brasileiros do Pará, Maranhão, norte de Mato Grosso e norte de

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Tocantins. A coloração do dorso varia de preto a azul claro e de vermelho, via laranja, a amarelo, creme e branco, com ou sem manchas pretas ou vermiculações. A maioria dos espécimes apresenta o ventre negro uniforme, mas em algumas populações a cor do dorso estende-se ventralmente e o preto fica limitado a pequenas áreas na região posterior e sob as coxas. Não localizamos nenhuma população com indivíduos completamente brancos, um variante presente em cativeiro e conhecido como "Moonshine". Nenhuma regularidade na distribuição dos padrões de cor foi percebida; populações de cor laranja predominam, mas formam um mosaico com populações de outras cores. Populações são uniformes quanto à cor dos indivíduos, embora a quantidade de preto no dorso possa variar. Entre as ameaças a essa espécie estão o desmatamento, a fragmentação de habitat, usinas hidrelétricas (já construídas, em construção ou projetadas), mineração de ouro e possivelmente o tráfico ilegal internacional. Embora a espécie seja amplamente distribuída em terrários na Europa, Estados Unidos e Japão, todos esses exemplares derivam de exportações ilegais. Estudos moleculares buscando correlacionar os padrões de coloração com a variação gênica das populações estão em andamento.

Palavras-chave: ameaças, coloração, Floresta Amazônica, habitat, tráfico de animais, zoogeografia.

Introduction

The genus *Dendrobates* and several other dendrobatid frogs, distributed in northern South America and lower Central America, are well known for their large variation in color and color pattern, especially in *D. tinctorius* (Cuvier 1797) from the Guiana area (Hoogmoed 1971a, b, Silverstone 1975, Noonan and Gaucher 2006, Wollenberg *et al.* 2006, 2008, Wagner 2008, Born *et al.* 2010), *Oophaga pumilio* (Schmidt 1857) (Myers and Daly 1983, Rudh *et al.* 2007), *Ranitomeya* (Brown *et al.* 2011), and to a lesser extent in *Ameerega trivittata* (Spix 1824) (Hoogmoed 1971a, b). *D. galactonotus* Steindachner, 1864 from eastern Amazonian Brazil is known to exhibit color polymorphism, but nothing is known about the distribution of the morphs in nature.

Steindachner (1864) described *Dendrobates galactonotus* in the synonymy of *Dendrobates tinctorius,* based on a specimen from "Rio do Muria bei Sitio do S. Pedro Gurção, nördlich von Vigia zur Freguezia" (= Rio [do] Muria near the small property of Mister Pedro Gurção, north of Vigia direction of Freguezia), where it had been collected on February 17, 1835. The collector was not mentioned but it may have been Natterer (see below). In the list of synonyms Steindachner (1864) mentions "*Dendrobates galactonotus* Fitz. Tschudi, Mus. Vind.", the first time this name was used in a publication. Silverstone (1975) interpreted this as Steindachner (1864) attributing the name to Fitzinger. Frost (2011) followed Silverstone (1975) in this interpretation. However, in our opinion, Steindachner (1864) listed only those persons who had previously used the name *Dendrobates galactonotus.* In this case apparently both Fitzinger and Tschudi used this name (Fitzinger [1843] and Tschudi [1838] did not mention the name, but perhaps they mentioned it only on the label accompanying the specimen) but because they apparently did not provide a published description, the name used by them is not valid and is a *nomen nudum.*

In our opinion Steindachner (1864) implied that the name had been coined by Johann Natterer, by stating that the largest Brazilian specimen in the Vienna museum was labeled as *Dendrobates galactonotus* and that Joh. Natterer left short color notes on it. Therefore, Steindachner, not Natterer, is responsible for publishing the name and the description and according to the Rules of ICZN Steindachner, 1864 is author of this name.

Boulenger (1913) described *Dendrobates paraensis* on the basis of eight specimens from "Para," which may mean they were from Belém, shipped from Belém, or from the province of Pará. Bokermann (1962) was of the opinion that the type locality probably was Belém (the city). The character distinguishing *D. paraensis* from *D. tinctorius* according to Boulenger, apart from the tarsal tubercle, would be the much larger discs of the fingers, a sexually dimorphic character we know now is a trait of males in both *D. tinctorius* and *D. galactonotus.* Some specimens were described as being black with the upper parts (except forelimbs and feet) uniform grayish or yellowish white (yellow in life?), in others the black predominated, with the white restricted to the upper surfaces of the head and to more or less confluent blotches on the back, while the remaining specimens were said to be intermediate between the two extremes (Boulenger 1913). Three of these specimens were reported by Boulenger (1882) as Var. B of *Dendrobates tinctorius.* The name was synonymized with *D. galactonotus* by Silverstone (1975).

Because this species is variable and the holotype (NMW 19189) is in deplorable condition, it seems useful to repeat the original description and provide an English translation of it: " 31''' lang,……..; es war im Leben schwarz mit theilweise gummigutgelbem Scheitel, Hals, und Rücken. Dieser grosse gelbe Rückenfleck wird durch eine schmale schwarze, stellenweise unterbrochene und am Rande ausgezackte Längslinie, welche hie und da auch quere Seitenäste aussendet (nämlich auf der Stirne und am Rücken, zwischen den Wurzeln der Vorderbeine) in 2 ziemlich gleiche seitliche Hälften getheilt, und ist wenigstens am Spiritus-Exemplar mit sehr feinen schwarzen Punktchen übersäet. Dieses Exemplar hat einige Aehnlichkeit mit der von D. Bibr. abgebildeten Var. *Cocteani,* doch fehlen die weissen Flecken an den Seiten des Körpers und an den Waden; die Schnauze ist vorne quer abgestuetzt, die hintere Extremität ist 1 1/3 mal so lang als der Körper" [= "31''' long……; in life it was black with a partly rubber-yellow top of head, neck, and back. This large yellow dorsal spot is divided into 2 nearly equal parts on each side by a narrow black longitudinal line, interrupted in some places and with lateral lines (on the head and on the back between the forelimbs), and, at least in the alcohol-preserved specimen, with many small black points. This specimen is more or less similar to the Var. *Cocteani* that was shown by D. Bibr., but the white spots on the flanks and on the calf of the leg are absent; the snout is transversely truncate in front, the hindlimb is 1/3 longer than the body"]. Silverstone (1975) reproduced only the first part of this detailed description, but he provided a detailed drawing of the pattern on the back of the holotype that agrees well with Natterer's description (above) in Steindachner (1864). Unfortunately, when the senior author examined the holotype in Vienna in 2006 this dorsal pattern was no longer recognizable. Natterer in Steindachner (1864) did not provide any data on the color of the underside of the holotype, but in 2006 the belly was black with some lighter areas, although it was not clear whether they were color marks or abraded areas caused by the length of time in preservative.

Lutz & Kloss (1952) erroneously used the name *Dendrobates galactonotus* for specimens of *D. tinctorius* from Suriname and Guyana. They based use of this name on identification of the material by E. R. Dunn; thus, these records should not be considered further.

Vences *et al.* (2003) found molecular differences between *D. galactonotus* and other large species of *Dendrobates,* and found that genetically it was closer to some small Amazonian poison frogs like *D. castaneoticus* Caldwell and Myers, 1990 (Lötters 2003), but these authors took a prudent position about this surprising find ("it should be interpreted cautiously until more sequence data for this species become available"), and did not make any nomenclatural changes. Grant *et al.* (2006), based on molecular data only, erected the genus

Adelphobates for *D. galactonotus,* the sympatric, much smaller *D. castaneoticus,* and two other small species, although from several comments it is clear they realized the discrepancy between the results of molecular and morphological character data ("…the occurrence of *galactonotus* in this clade is unexpected, as its morphology shares little with the diminutive *castaneoticus* and *quinquevittatus*") within this new genus. Poelman (2006) provided a well-founded critique on the splitting of *Dendrobates* into four genera that only can be separated on the basis of molecular data. Santos *et al.* (2009) did not accept the split of *Dendrobates* as proposed by Grant *et al.* (2006) and again considered *Adelphobates* (and other genera proposed by Grant *et al.* [2006]) part of *Dendrobates.* Rodrigues *et al.* (2011) described the chromosomes of five species of Brazilian poison frogs, among which was *D. galactonotus* from an unknown locality. Karyotypes of *Adelphobates* and *Dendrobates* are highly similar (2n = 18), and the chromosome morphology also is very similar. Thus, chromosome number does not separate *Adelphobates* and *Dendrobates* either. No acceptable morphological diagnosis enables recognition of members of the proposed genus *Adelphobates.* Because we are not convinced that *Adelphobates* is a natural entity, we prefer, on the basis of external morphology, to continue treating *D. galactonotus* as a member of the genus *Dendrobates* (Santos *et al.* 2009). *D. galactonotus* agrees in many characters with species of the *D. tinctorius* group (large size, habitus, sexual dimorphism [males with larger discs on fingers of hand than females], reproduction [males carrying maximally two tadpoles on back, no parental feeding of tadpoles], smooth skin).

In the present paper we provide a detailed description of the range of *Dendrobates galactonotus* and its known color morphs, describe the color morphs known in nature, provide information about its habitat and deal with the potential threats to the species.

Material and Methods

Material was collected in the field during several expeditions to areas in Pará, Brazil, walking trails in terra firme forest, disturbed areas, cerrado and agricultural fields. Fieldwork by us that yielded data on *Dendrobates galactonotus* was executed in Caxiuanã in five periods (22-X/19-XI-1992, 14/19-I-1993, 8/29-VII-1993, 4/10-XI-1995 and 9/23-II-2012), in Paragominas (30-VI/15-VII-1994), in São Felix do Xingu (21-I/7-III-1999), in Barcarena (8-XII-2002 and 28/29-I-2012), in Serra das Andorinhas (21-X/4-XI-2011), and in the region of Vigia (10/11-III-2012).

We further used data from material collected by others present mostly in the collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG), but also in the Coleção de Herpetologia da Universidade Federal de Maranhão, Brazil (HUFMA), in Museu de Zoologia "Prof. Adão José Cardoso" da Universidade Estadual de Campinas, São Paulo, Brazil (ZUEC), and in the collection of Célio F. B. Haddad, UNESP [Universidade Estadual Paulista], Rio Claro, São Paulo, Brazil (CFBH). Finally we obtained from the literature data about distribution and color morphs known.

The color of specimens collected by us was described before euthanasia using the color codes (names and numbers) provided by Smithe (1975). Specimens were photographed in a standard way before tissue collection and preservation, to show the pattern of the dorsum and legs and more recently, also the ventral parts. Specimens collected by us were deposited in the herpetological collection of MPEG. The color of the dorsum in life of preserved specimens cannot reliably be decided and it is only possible to indicate for preserved material whether the back is light or dark, and with or without black spots in the lighter part of the back.

Photographs of specimens (collected or not) provided by colleagues were also used and color descriptions were made using photographs observed on computer. In some cases we used

published photographs if accompanied by locality data. However, description of color using slides and color photographs should be done with care, because color may differ based on lighting conditions, type of flash used, type of camera used, and printing process. In one instance an orange specimen (MPEG 34620) photographed at the same time by different cameras appeared orange in pictures made by one camera and mostly yellow in those of the other camera. Another specimen (MPEG 23771) in one series of photographs came out as having a cream back, whereas in some photographs taken 10 minutes later with the same camera it appeared light blue.

The maps showing the distribution of color patterns were made using the program ArcMap. All localities used for making the distribution map are georeferenced. For obvious reasons (danger of illegal collecting of specimens) we do not publish the coordinates of localities. Only four localities for material in the MPEG collection (without indication of color in life) could not be georeferenced and were not used. However, they are located in areas where other material could be georeferenced, so the lack of this information does not change the overall distribution pattern. We used one locality that was not georeferenced, based on slides of live animals and noted this as "approximate." The Appendix I with material studied has been separated into three parts: one part with specimens studied, one part with localities from the literature and internet, and a final part with localities based on color photographs and personal communications. Asterisks in material studied indicate populations for which color photographs or descriptions were available. Asterisks accompanying references indicate that the references show color photographs.

Results

Distribution

Dendrobates galactonotus is an endemic species of Amazonian Brazil, only known to occur south of the Amazon River, mainly in Pará between the Tapajós River (Santarém and Itaituba) and Teles Pires River in the west and the Atlantic coast in the east, south to extreme northern Mato Grosso and northern Tocantins, and east to São Luis in Maranhão (Barreto *et al.* 2011), at altitudes between sea level (Belém, Vigia, São Luis) and 355 m (Serra das Andorinhas) and to about 600 m in Serra de Carajás (Figure 1). Its distribution falls completely in the Belém, Xingu, and Tapajós areas of endemism (Silva *et al.* 2005). The maps provided by Silverstone (1975), Noonan and Wray (2006), and Rodrigues *et al.* (2010) are incomplete and lack western, southern, and eastern portions of the presently known range. The map provided by Roberts *et al.* (2006) is more complete in the southern part, but also lacks the eastern portion of the range. The brief description of the range by Frost (2011) does not portray the correct range. Our map with known points of occurrence clearly shows that the distribution is relatively continuous in the area indicated and that areas that seem to lack localities have been under-collected because of difficult access. In the south the distribution abuts the Cerrado and in the extreme east (São Luis, Maranhão) the Caatinga.

Confusion about the distribution of *D. galactonotus* was caused because an early version of the IUCN distribution map included an area north of the Amazon. This error possibly resulted from a large shipment of *D. tinctorius* and *D. galactonotus* confiscated at Guarulhos Airport in São Paulo, in 1999, that was presumably from the "Alto Rio Trombetas, PA" (Pistoni and Toledo 2010). Although *D. tinctorius* occurs in that area (Avila-Pires *et al.* 2010), *D. galactonotus* has never been found north of the Amazon River. Lötters *et al.* (2007) and Overkamp (2009) copied this erroneous IUCN map, suggesting that *D. galactonotus* would be restricted to five isolated areas and would occur north of the Amazon as well. This erroneous IUCN map in the meantime has been replaced by a map that correctly excludes areas north of the Amazon and gives a better, but still

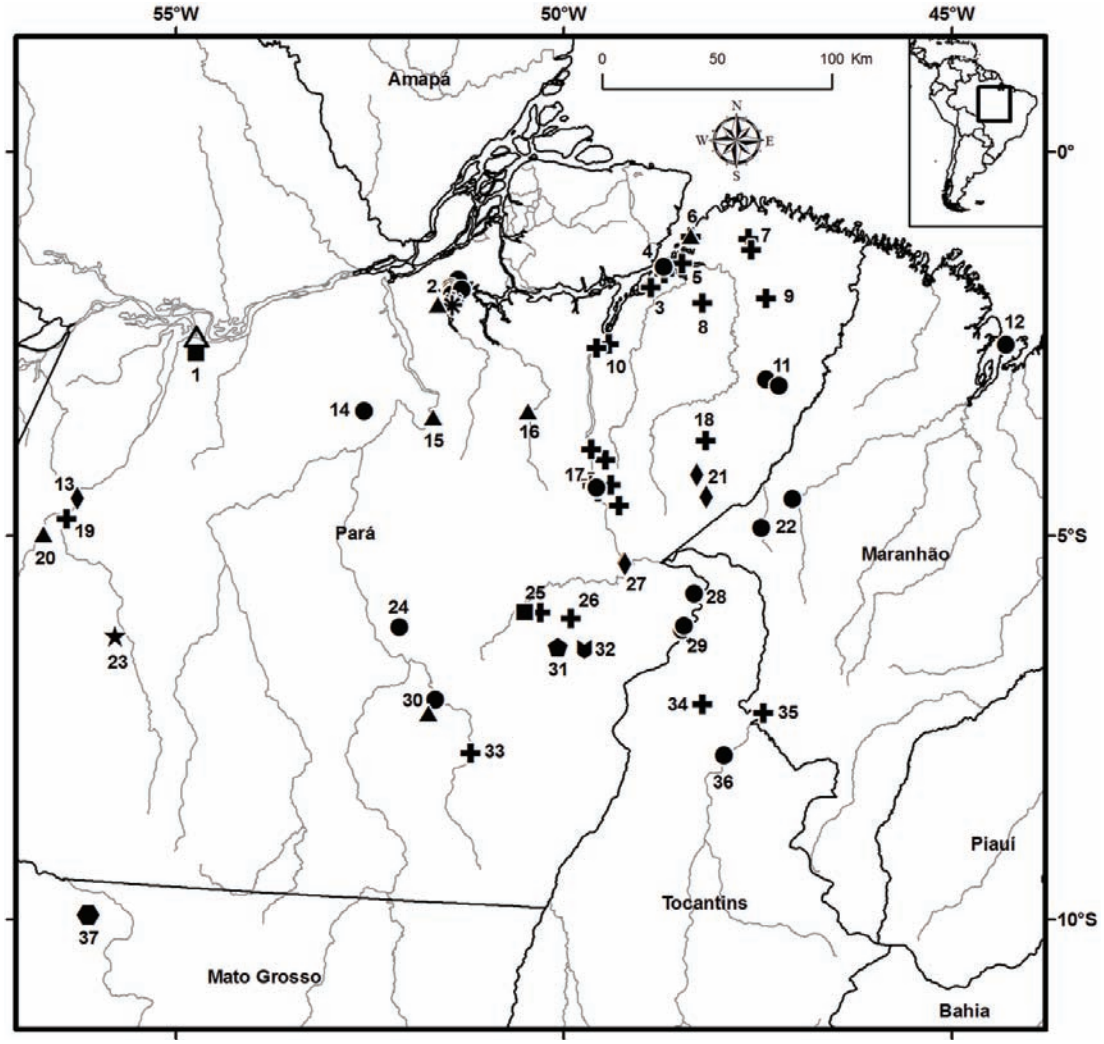

Figure 1. Map of Pará and surroundings showing the distribution of color morphs of *Dendrobates galactonotus*. Black dots: orange; triangles: yellow; hexagon: yellow with black vermiculations; diamonds: red; asterisk: light blue; irregular hexagon pointing down: black with cream; squares: black; star: black with bluish to greenish vermiculations; pentagon: black with extensive white spots; crosses: color unknown; black square with open triangle on top: black and unknown. Localities without indication of state are in Pará. Sometimes one number indicates more than one locality in the same general area. (1) Santarém; (2) Baía do Caxiuanã (see detailed map in Figure 4); (3) Abaetetuba; (4) Barcarena; (5) Belém; (6) Vigia type locality); (7) BR Belém-Brasilia, km 75/Igarapé-Açu; (8) Acará; (9) BR Belém-Brasilia, km 163; (10) Rio Tocantins, Mazagão/Mocajuba; (11) Paragominas, Fazenda Vitória and Agrosete; (12) São Luis, Maranhão; (13) Itaituba, Boa Fé; (14) Brasil Novo; (15) Anapu; (16) Portel, Fazenda Riacho Monte Verde; (17) Tucuruí (several localities); (18) Paragominas, Fazenda Cauaxi; (19) Cachoeira Caí, Jamanxim River; (20) West of Rio Jamanxim (approximate); (21) Rondon do Pará (two localities); (22) Açailândia (two localities), Maranhão; (23) Mina do Palito; (24) São Félix do Xingu, Fazenda Cascatinha; (25) Canaã de Carajás; (26) Parauapebas, Serra de Carajás; (27) Marabá, Estrada Velha; (28) Palestina do Pará; (29) Serra das Andorinhas (two localities); (30) São Félix do Xingu, Rio Riachuelo and Aldeia Kikretum; (31) Canaã dos Carajás; (32) Curionópolis; (33) São Félix do Xingu, Gorotire; (34) Araguaína, Tocantins; (35) Carolina, Maranhão; (36) Palmeirante, Tocantins; (37) Alta Floresta, Cristalino River, Mato Grosso.

incomplete, picture of the distribution (Rodrigues *et al.* 2010).

Hermann (2006) stated that *D. galactonotus* only occurs along the Tapajós River to its junction with the Amazon River. This distribution is greatly underestimated and probably resulted from an incorrect translation of the area indicated by Silverstone (1975).

Silverstone (1975) mentioned the locality Araguaina (incorrectly as "Araguainago") in northern Goiás, but in 1989 the northern part of Goiás became the new state of Tocantins and as a consequence of this political change, the species no longer occurs in the present-day state of Goiás. Baas and Peper (2010) erroneously mentioned Goiás as part of the distribution of *D. galactonotus,* but this error was most likely based on the old literature records.

Duellman (1999) considered this species as one of five frogs endemic to the eastern part of his Amazonia–Guiana region.

Caldwell and Araujo (2005) provided thorough inventories of the anurofauna of two localities (Curuá-Una and (lower) Xingu Rivers, both in Pará) south of the Amazon River within the range of *Dendrobates galactonotus.* They did not find this species, although they did encounter a population of *Adelphobates castaneoticus* (Caldwell and Myers 1990). The species may be absent in those localities, although it is known to occur close to their (lower) Rio Xingu locality (in Brasil Novo, and in the Belo Monte area, municipality Anapu) (Lima 2009; MPEG 25194–8). Alternatively the frogs may not have been active during their expeditions.

Color Polymorphism

Dendrobates galactonotus is a vividly colored large poison frog up to 42 mm in snout-vent length. Color of the dorsum of various populations ranges from yellow via orange to red, from white to light blue, with varying amounts of black on the dorsum to even completely black, and to black with blue to greenish dots.

The first color photograph of this species was published by Martins and Sazima (1989), who depicted an orange specimen from Tucuruí, Pará, and mentioned that specimens from Serra de Carajás, Pará, were black. Avila-Pires and Hoogmoed (1997) provided photographs and pointed out that in the area of the Estação Científica Ferreira Penna (ECFP), Pará specimens had an orange back with a varying number of black dots and spots, whereas specimens from Posto IBAMA (= Sede da FLONA Caxiuanã) had uniformly orange backs without any black spots. These localities are only 7 km apart, but separated by the relatively small Caxiuanã River. Lisboa and Ferraz (1999) re-published one of the photographs shown in Avila-Pires and Hoogmoed (1997) and repeated the remarks about local variation. Bartlett and Bartlett (2003), Henkel and Schmidt (2011), Herrmann (2006), Keller and Schneider (2005), Lötters (2003), Poelman (2006), Overkamp (2009), Schmidt and Henkel (2004), and Starosta and Moncuit (2006) all provided excellent photos of one or more white (= Moonshine), yellow, orange, or red specimens, without mentioning localities from where they came. Galatti *et al.* (2007) published a photograph of the species in an article about the amphibian fauna of Belém, but the specimen depicted was from Tucuruí, Pará (pers. comm. U. Galatti). Lötters *et al.* (2007) provided photographs of red (Pará), pale orange (Pará), yellow (Pará), yellow with black spots (Mato Grosso), white (Pará), and black (Pará) color morphs from two Brazilian states without further locality details. They are the only ones to provide a "locality" (Pará) for the white Moonshine colormorph. Brasileiro *et al.* (2008) published a photograph of an orange specimen from Açailandia, Maranhão. Neckel-Oliveira and Galatti (2008) reported the species from São Felix do Xingu, Pará, but the orange specimen they depicted is from the Tucuruí area in Pará (pers. comm. U. Galatti). Vitt and Caldwell (2009) reproduced a photo of the yellow with black vermiculations color morph from the lower Cristalino River, Alta Floresta, northern Mato Grosso, which was previously

published on their websites and in Lötters *et al.* (2007).

Since 1992 we have been collecting data on color in life of this species from as many localities and sources (fieldwork, publications, slides of colleagues) as possible, and we have made a map showing the distribution of color morphs (Figure 1). For many localities we still do not have color information, and it is impossible to determine color of preserved specimens. Preserved specimens without color notes only can serve to indicate the extent of color on the body and limbs. Most publications on this species state that specimens have a black belly, but this is not generally true, as will be shown below. Silverstone (1975) mentioned that one specimen examined by him (no museum or field number given) had small light spots on the throat and ventral surface of the calves.

At present we are aware of the following color morphs in nature: orange, red (including black with a few tiny red spots, and black with some large peach colored areas), yellow, yellow with black vermiculations, light blue, dark grayish blue to black, black with blue to green spots, black with white spots and lines, and black with a varied cream pattern. Most populations are uniform, showing the same general pattern with slight individual variations, but two populations (Curianópolis and Canãa de Carajás) show a larger range in pattern. We have not been able to localize the white Moonshine color morph, known in the terrarium hobby, in nature.

Generally *Dendrobates galactonotus* is a black frog that is differently colored with a large area of orange, red, yellow, light blue, or white on the dorsum, which may extend to the flanks and even onto the belly, sometimes nearly covering it. One population has small blue to greenish spots on the back. Some populations may have colored (same color as back) spots on the belly, or the entire belly may be yellow like the back, with the black reduced to the seat patch and the underside of the thighs. The legs may be black, spotted with color, or even be completely colored, only leaving the hands (including the fingers) and the toes black.

Orange morphs.—Orange morphs show considerable variation, from nearly completely orange to orange on the back with many small black spots or lines. The orange color may vary from Orange Yellow (Color 18), via Spectrum Orange (17) to Chrome Orange (16). Most populations have black undersides, but one population in the Caxiuanã area has orange spots on the underside. Specimens from Barcarena, Pará, have a wide dorsolateral band extending onto the flanks that is distinctly lighter (Orange Yellow [18]) than the Chrome Orange (16) in the middle of the back (Figure 2A). The pattern of Tucuruí specimens is similar, although the dorsolateral band is less distinct. In most other areas no dorsolateral band is recognizable. Orange populations are known from many localities throughout the distribution of the species: Tapajós, west of the Jamanxim River (uniform Spectrum Orange (17) dorsum to Spectrum Orange dorsum with a sprinkle of small black spots) (Figure 2B), Brasil Novo (many small black spots on Orange Yellow (18) back) (Figure 2C); São Felix do Xingu, Aldeia Kikretum and Fazenda Cascatinha (black spots on orange back) (Figure 2D), Caxiuanã area (see above and below), Barcarena (see above), Tucuruí (see above), Palestina do Pará (dorsum uniform orange) (Figure 2E) and Paragominas (black spots on Orange Yellow back), all in Pará; São Luis (back uniform orange) (Figure 2F) and Açailândia (rather narrow uniform orange spot on the back, flanks black) (Brasileiro *et al.* 2008) (Figure 2G) in Maranhão; Palmeirante in Tocantins (back uniform orange) (Marchezini 2010).

Red morph.—The distinction of the red (= Flame Scarlet [15]) morph from the orange ones displays a gliding scale from red to orange (Chrome Orange ([16]). Red morphs are known only from Itaituba (the part of the municipality on the right bank of the Tapajos river only, north of the Jamanxim River) (black spots on red back) (Figure 2H), Rondon do Pará (MPEG

Figure 2. *Dendrobates galactonotus* color morphs. (**A**) MPEG 33758 Barcarena, Pará. Photo MSH; (**B**) west of Rio Jamanxim, Pará. Photo L. F. Storti; (**C**) Brasil Novo, left bank Xingu River, Pará. Photo E. A. Oliveira; (**D**) São Felix do Xingu, Aldeia Kikretum, Pará. Photo A. Jerozolimski; (**E**) Palestina do Pará, Pará. Photo P. L. V. Peloso; (**F**) HUFMA 890, São Luis, Maranhão. Photo G. V. Andrade; (**G**) Açailandia, Maranhão. Photo A. L. Silveira; (**H**) MPEG 34471, Itaituba, north of Rio Jamanxim. Photo P. L. V. Peloso; (**I**) MPEG 34627, Rondon do Pará, Pará. Photo A. C. M. Dourado; (**J**) MPEG 34500, Marabá, Pará. Photo A. O. Maciel; (**K**) MPEG 31706, Marabá, Pará. Photo A. O. Maciel; (**L**) MPEG 34499, Marabá, Pará. Photo A. O. Maciel.

Figure 3. *Dendrobates galactonotus* different color morphs. (**A**) locality unknown, confiscated. Photo L. F. Toledo; (**B**) MPEG 25197, Anapu, right bank Xingu River, Pará. Photo P. L. V. Peloso; (**C**) juv., São Felix do Xingu, Rio Riozinho, Pará. Photo A. Jerozolimski. (**D**) Alta Floresta, Cristalino River, Mato Grosso. Photo J. P. Caldwell; (**E**) ZUEC 9036, Parauapebas, Serra de Carajás, N1, Pará. Photo M. R. C. Martins; (**F**) Parauapebas, Serra de Carajás, Pará. Photo M. Gordo; (**G**) MPEG 33790, Itaituba, Mina de Palito, Pará. Photo A. d'Angiolella; (**H**) MPEG 34502, Itaituba, Mina de Palito, Pará. Photo A. O. Maciel; (**I**) MPEG 16264, Canãa de Carajás, Pará. Photo V. B. Assis; (**J**) MPEG 23772, Curionópolis, Pará. Photo V. B. Assis; (**K**) MPEG 23771, Curionópolis, Pará. Photo V. B. Assis; (**L**) MPEG 34619, Melgaço, FLONA Caxiuanã, Santa Cruz, Pará. Photo MSH.

34627, with few large black blotches in the red) (Figure 2I) and from Marabá, Pará, where specimens may have a uniform red dorsum (MPEG 28118, 34500–1) (Figure 2J) or show some black vermiculations on the red dorsum (MPEG 31796–7) (Figure 2K). One specimen from Marabá (MPEG 34499) is black above, below, and on the flanks, with minute red dots on the posterior upper part of the flanks and tympanic area, one small red spot on the shoulders and one above the cloaca (Figure 2L). Hermann (2007) provided a photo of a specimen with a Pratt's Ruby (210) dorsum, and Staroska and Moncuit (2006) depicted a specimen with a Scarlet (14) back. However, it is unknown how much these colors have been influenced by the printing process. Overkamp (2009) mentions that red specimens in the terrarium are bright red when metamorphosing, but with increasing age they steadily become darker to "stone red" or reddish brown. A specimen of unknown provenance (confiscated by IBAMA) has a few large Peach Red (94) blotches on a black back (Figure 3A). All red specimens have uniform black undersides.

Yellow morphs.—Yellow morphs vary from Spectrum Yellow (55) to Sulphur Yellow (157) but are uniform within populations. The back may be uniformly Spectrum Yellow (Portel: Riacho Verde and Caxiuanã Plot PPBio; Anapu) (Figures 3B, 5C, I), or may show an extensive black pattern of spots and lines on a Sulphur Yellow back (São Felix do Xingu: Riacho Riozinho (Figure 3C) and Vigia [see Silverstone 1975, Figure 11F]).

Yellow with black vermiculations morph.—Although the population of Alta Floresta, Cristalino River, in Mato Grosso has a predominantly bright yellow back and limbs with black lines and spots, with a black belly, we have indicated this population as a separate color morph on the map (Figure 1) because of its strikingly different appearance (Figure 3D) from any other population. Roberts *et al.* (2006) mentioned this color morph (described as having "a yellow-orange dorsum and legs mottled by irregular, barbell- to kidney-shaped blotchy spots and a black venter") as "*Dendrobates* sp. Mato Grosso" and considered it a (undescribed) species different ("sister taxon") from *D. galactonotus.* This same color morph was depicted in Lötters *et al.* (2007), Vitt and Caldwell (2009), and Baas and Peper (2010). In the meantime the DNA of this color morph, suspected to be a new species, was 99–100% identical to that of *D. galactonotus* (F. Toledo, pers. comm.). Thus, this morph is not an undescribed species as still mentioned by Baas and Peper (2010).

Black morphs.—Silverstone (1975) mentioned one entirely black specimen from Santarém, but stated that this color might be an artifact of preservation. Another preserved specimen from Santarém was said to have a partly light back with irregular black areas. Specimens from the top of Serra de Carajás in life are uniformly black (Lötters *et al.* 2007) (Figure 3E) to grayish blue (Neckel-Oliveira *et al.* 2012) (Figure 3F). We did not include in this black morph the specimen from Marabá (MPEG 34499) that is black with red spots on the flanks (Figure 2L), and which we consider to belong to the red morph that is present in Marabá.

Morph with bluish to greenish vermiculations.—In western Pará the population of Mina de Palito is black with numerous Robin´s Egg Blue (93) (MPEG 33790) (Figure 3G) or Opalin Green (162D) (MPEG 34502) (Figure 3H) irregular small spots and vermiculate broad lines on head and back, and with black flanks, legs, and venter, sometimes with a few light spots on the knee. The belly is black.

White-spotted morph.—Some specimens from Canaã de Carajás, Pará, are black with a reticulum of white spots and vermiculations on the back, and white spots on the hind limbs (Figure 3I). Other specimens in life are "dark," or bluish grey (V. B. Assis, pers. com. and photographs). It is not certain they are from the same population as the white-spotted specimens because collections were made over a large area. The color of the venter is not known, but could very well have been black.

Morph with cream pattern.—From Curionópolis, we have two specimens with data on color in life (MPEG 23771–2). In contrast to all other specimens studied by us, MPEG 23772 has a black back and the lighter pattern (cream to milky white) is restricted to the sides of the head (canthal bands), the flanks, and the limbs (Figure 3J). MPEG 23771 (Figure 3K) has a cream to bluish white dorsum. In some photos the same specimen appears light blue, but we assume (based on pers. comm. V. B. Assis) that the light blue color may have been caused by special lighting conditions and we have considered specimens from this municipality as cream colored.

Morphs from Caxiuanã area, Pará.—We recently (February 2012) sampled FLONA de Caxiuanã more extensively (Figure 4) and can confirm the differences mentioned by Avila-Pires and Hoogmoed (1997) (above), adding that specimens from ECFP have black arms, hands, black legs with variably sized orange spots, black feet and a black belly, and those from the Sede da FLONA also have black arms and hands, a black belly, but largely orange legs with black feet. In February 2012 we collected on both sides of the Baía de Caxiuanã along a northeast–southwest axis. The northernmost locality on the western side of the bay is ECFP, of which the color pattern of specimens was described above. A specimen from Santa Cruz (MSH 11623) slightly further south, at the northwestern bank of the confluence of the Rio Caxiuanã and Igarapé Curuá, has the same color pattern as specimens from ECFP (Figure 3L). The color pattern of specimens from the Sede da FLONA was described above. South of the Sede da FLONA, specimens from Muju generally agree with those from the Sede da FLONA, although one specimen (MPEG 34584) has a few small black spots and narrow lines on the back. Their bellies are black. Further south a specimen from Sítio Manguinho was bright orange (between Chrome Orange [Color 16] and Spectrum Orange [Color 17]) with completely orange arms and legs and only black hands and feet. The black belly showed several large spots of orange (Figure 5A, B). Even further south, in the plot of PPBio (Programma de Pesquisa em Biodiversidade) adult specimens are nearly completely yellow dorsally and ventrally, with only the seat patch and the underside of the thighs with interconnected black areas, with a narrow black ring around the insertion of the forelimbs, a small black spot in the groin, a small black spot on the lower part of the tympanum, black spots around the nostrils, and often with a narrow black line on the lips (Figure 5C). The limbs are completely yellow above and below, with the exception of the underside of the thighs. Five juveniles (MPEG 24579, 24599, 24600, 26995, 26998) from this locality nicely show the ontogenetic color changes reported for captive bred specimens (Overkamp 2009): the smallest specimen is nearly completely dark grey, the larger specimens have a light (yellow in life) back and varyingly sized lighter spots on the ventral surface that are greater in number and larger in size with increasing snout-vent length. Thus, on the west side of Caxiuanã bay we observed a cline from north to south with specimens having increasingly less black and more lighter (orange or yellow) coloration.

On the east side of Caxiuanã bay we sampled three localities. In the northernmost locality (São Benedito) specimens had uniform Spectrum Orange (Color 17) backs without black spots, undersides, arms and hands black, black feet and black legs with varyingly sized orange spots (MPEG 34617–8) (Figure 5D). In Brabo specimens had Light Sky Blue (Color 168D) backs, legs, and arms, but with black creeping up from the underside in the axillary and inguinal areas, with black nostrils, hands, and toes (Figure 5E, F) (MPEG 34582–4, 34586–7). Specimens from Rio Mujuá had the same Light Sky Blue color as specimens from Brabo, but with arms and legs completely blue in dorsal view and with extensive blue areas on the entire underside, including tibiae and tarsi as well (Figure 5G, H) (MPEG 34588–95, 34599). Thus, to a certain degree, the north–south trend observed west of

Caxiuanã bay of increasingly less black and more lighter color elements is paralleled east of the bay as well, but with the "anomaly" of having a northern orange population that suddenly gives way to light blue populations that tend to lose black color elements the further south they are located. No intermediate populations with a mixture of colors are known.

Another locality in the municipality of Portel, southeast of the group of localities along the Baia de Caxiuanã sampled in February 2012, is Riacho Monte Verde. In this locality specimens

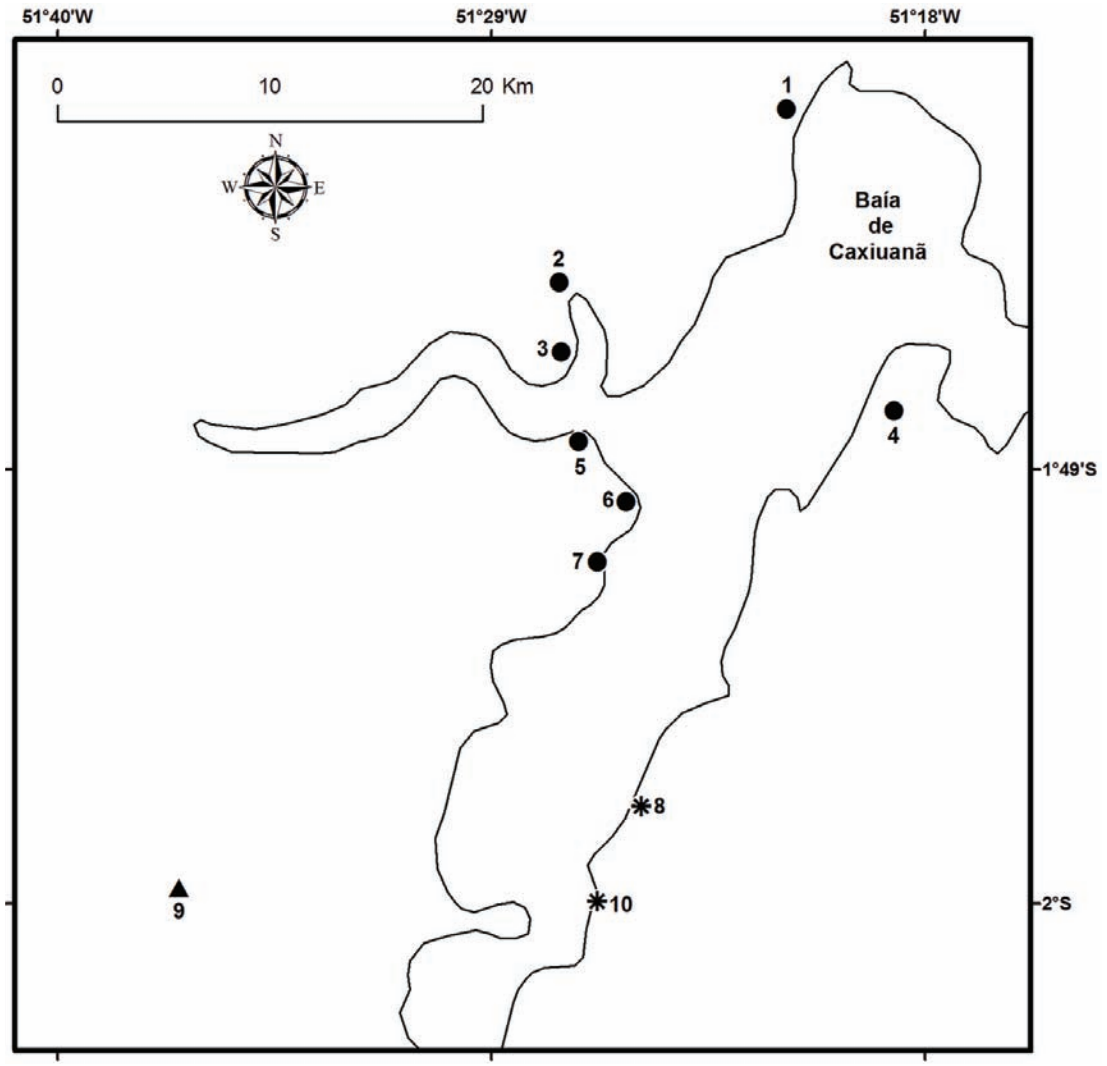

Figure 4. Map of the Caxiuanã area, Pará, showing distribution and color morphs of sampled populations of *Dendrobates galactonotus*. Dots: orange populations; asterisks: light blue populations; triangle: yellow population. (1) Melgaço, Laranjal; (2) Melgaço, ECFP; (3) Melgaço, Santa Cruz; (4) Portel, Comunidade São Benedito; (5) Portel , Sede da FLONA Caxiuanã; (6) Portel, Praia do Castanhal; (7) Portel, Sitio do Mandioquinha; (8) Portel, Brabo; (9) Portel, Plot PPBio; (10) Portel, Rio Mojuá.

Figure 5. *Dendrobates galactonotus* different color morphs. (**A**, **B**) MPEG 34608, Portel, FLONA Caxiuanã, Sitio Manguinho, Pará. Photos MSH; (**C**) MPEG 24581, with Acari infection on flank, Portel, FLONA Caxiuanã, Plot PPBio, Pará. Photo M. A. Ribeiro Jr; (**D**) MPEG 34618, Portel, FLONA Caxiuanã, São Benedito, Pará. Photo MSH; (**E**, **F**) MPEG 34587, Portel, FLONA Caxiuanã, Brabo, Pará. Photos MSH; (**G**) MPEG 34894, Portel, FLONA Caxiuanã, Rio Mojuá, Pará. Photo G. F. Maschio; (**H**) MPEG 34591, Portel, FLONA Caxiuanã, Rio Mojuá, Pará, ventral aspect. Photo MSH; (**I**) male with tadpole, Portel, Riacho Monte Verde, Pará. Photo J. O. Gomes; (**J**) male MPEG 34603 with two tadpoles in water-filled Brazil-nut pod, Pará, Portel, Sede da FLONA Caxiuanã, Pará. Photo MSH; (**K**) Habitat of blue morph in Portel, FLONA Caxiuanã, Brabo, Pará, recently burned vegetation in stand of *Bertholletia excelsa*. Photo MSH.

also are bright yellow like in the PPBio plot, but the underside is either uniform black or has one or more yellow spots, and thighs, groins, and axils have large black areas (Figure 5I).

Habitat

Dendrobates galactonotus is known to occur in terra firme forest (Estupiñan and Galatti 1999), where it is present on the forest floor among leaf litter. The frogs seem to have a preference for areas with stands of Brazil nut trees (*Bertholletia excelsa*), where the animals congregate [but not in large numbers as stated by Overkamp (2009)] between piles of opened Brazil nut pods, many of which contain water and which presumably are used for depositing tadpoles (Figure 5J). *Adelphobates castaneoticus* (Caldwell and Myers 1990) and *Bufo castaneoticus* Caldwell, 1991 overlap part of the distribution of *D. galactonotus* and share the same habitat, and are also known to use Brazil nut pods for reproduction. We encountered specimens in several localities on the right margin of Caxiuanã bay in recently cleared and burnt areas beneath Brazil nut trees near forest edges (Figure 5K), in the burnt open margin between forest and cassava plantations, and even in the midst of a cassava plantation. Several localities from where this species is known (Açailândia and Carolina, both in Maranhão; Araguaina and Palmeirante, in Tocantins; Serra das Andorinhas, in southeastern Pará) are in the transition zone between Cerrado and Amazonian forest where these vegetation types form a patchy mosaic. A similar situation is found in Paragominas and São Felix do Xingu, where forest has been severely fragmented and is surrounded by pastures. Generally specimens are restricted to the Amazonian forest, but one specimen in Serra das Andorinhas was found in daytime (during rain, after a few rainy days) in Cerrado, but near a forest edge. Silveira (pers. comm.) and Brasileira *et al.* (2008) found the species in Açailândia, Maranhão, in isolated stands of secondary terra firme forest surrounded by pasture and *Eucalyptus* forest and considered the species rare in the area.

Considering our observations in the field (see above), we do not agree with Estupiñan and Galatti (1999) that *Dendrobates galactonotus* is characteristic in areas with little human disturbance and could be used as an indicator of that habitat type. The species seems to be tolerant of disturbance, although it is not known whether it can endure adverse conditions for any length of time. Several popular references (Schmidt and Henkel [2004]; Overkamp [2009]) stated that this species is numerous near fallen trees, but, although we have found single specimens near fallen trees, they were not more numerous in those areas than in the rest of the forest. Lötters *et al.* (2007) stated that these frogs "congregate in sun-exposed clearings," but we have never observed that behavior, although specimens do enter open places in the forest. In general we can state that the species is nowhere very abundant (also see Baas and Peper 2010; A. L. Silveira, pers. comm.), independent of the time of the year, although in some localities several specimens were encountered in one day. In one locality near the Tapajós River L. F. Storti (pers. comm.) observed about 12 specimens close to each other. M. J. Sturaro collected five specimens in one day in Itaituba and considered the species common.

Discussion

Our data provide an overview of the distribution of *Dendrobates galactonotus,* although a number of localities indicated on the map (Figure 1) may no longer support populations, as most certainly is the case with Belém (Estupiñan and Galatti 1999), the area around Vigia and the area now flooded by the Tucuruí lake. We have not been able to detect any regularity in the distribution pattern of color morphs throughout the range of the species, although it is clear that the majority of known populations are orange in one form or another (21), followed by yellow, uniform or spotted with black (five), red (three),

light blue and black (two each), and finally bright yellow with black vermiculations, black with bluish to greenish spots, black with large white spots, black with cream pattern on back or flanks (one each). The color in life is unknown for another 26 localities. In FLONA Caxiuanã and surrounding areas, an area with mostly orange or yellow populations, at least two populations are light blue. At the southwestern edge of the distribution, two populations have aberrant, unique patterns, *viz.,* bright yellow with black vermiculations in Alta Floresta (3D), and black with small bluish to greenish dots in Mina de Palito (Figure 3G, H). All populations (except the one from Mina de Palito) have the same color pattern, which may vary in extent, but no population has more than one color pattern. The red Marabá population shows extreme variation among specimens, from black with a red back to completely black with only a few small red dots (found in only one adult specimen). In Canãa de Carajás specimens vary from black to black with a reticulum of white spots and vermiculations, although these specimens may have been collected in widely separated localities (V. B. Assis, pers. comm.). According to Silverstone (1975) one specimen from Santarém was black and another had a partly light (color in life not known) dorsum, which may either indicate an artifact of preservation (Silverstone 1975), or that the population shows extreme variation like the Marabá and Canãa de Carajás populations. The Curionópolis population has specimens with a cream back and specimens with the cream color located on the sides. These cases are the only ones known to us where variation is that extreme. In most other populations the variation is within narrow limits, although in orange, red, and yellow populations with black spotting, the amount of spotting is variable. From our data it is clear that the description of color pattern by Silverstone (1975) was based on only a few preserved specimens and thus could not document the extent of the variability of the color in life.

We have not been able to locate the origin of two known morphs: one with large black and red areas on the back that is only known from a confiscation by IBAMA (Figure 3A) possibly from Pará, and the completely white "Moonshine" morph that is only known from the pet trade (Overkamp 2009), but which was reported from "Pará" without further details by Lotters *et al.* (2007).

The southern and eastern parts of the range of *Dendrobates galactonotus* coincide with the "Arco do Desmatamento" (= Arc of deforestation), an area in western Maranhão, northern Tocantins, southern and eastern Pará and northern Mato Grosso where deforestation has been extensive and much of the land has been converted to pasture or agriculture (Figure 1). Although deforestation rates seem to be diminishing slightly, the area certainly is not free from deforestation, which continues at a lower rate and less visibly. But Pará and Mato Grosso continue to be extensively deforested, and four municipalities (Altamira, Anapu, São Felix do Xingu, and Itaituba) where *D. galactonotus* occurs are among the 10 with the most deforestation (INPE [Instituto Nacional de Pesquisas Espaciais] 2012). Primary rainforest, the habitat of *D. galactonotus* in the Arco do Desmatamento (and beyond), has been and is continuing to be reduced to small (partly degraded) patches surrounded by agricultural land, *Eucalyptus* forest, and pasture. Although we observed some tolerance of *D. galactonotus* to slash and burn agriculture in the Caxiuanã area, we doubt whether populations can sustain such attacks on their habitat for prolonged periods, especially when remaining forest isolates are far from larger forested areas.

Other problems confronting *Dendrobates galactonotus* are that part of its former habitat has been inundated by Tucuruí lake, originated because of the construction of a hydroelectric project in the Tocantins River (2,875 km^2: Petesse and Petrere 2012). The species survived for some time on tiny islets isolated by the rising waters of the lake, but probably most of those mini-populations now have become extinct. A new threat to this species is the construction of the hydroelectric project Belo Monte in the

Xingu River, which will cause the flooding of about 500 km^2, much of which is primary forest and potential *D. galactonotus* habitat. Hydroelectric plants are also planned (and partly already under construction) along the Tapajós, Jamanxim, and Teles Pires Rivers, which may negatively influence areas where the species occurs. Because of the rise in the price of gold, gold mining (both by individual "garimpeiros" and by companies) recently has increased considerably in the upper Tapajós and Teles Pires Rivers, and a new large gold mining project is supposed to begin soon in the Volta Grande area of the Xingu River (Borges 2012), on the right bank of the river, close to the hydroelectric project in the same region. It is envisaged that this project will yield 4600 kg of gold per year starting in 2015. Apart from directly destroying *D. galactonotus* habitat for mining and for the construction of repository lakes for poisonous waste, these mining operations cause silting of streams and rivers and significant poisoning of surface water with chemicals, including mercury and cyanide, causing deleterious effects for all amphibians in the region.

Eastern Pará (east of Belém to the Atlantic Coast and southeast to the border with Maranhão) since the beginning of the 19th century has been subject to intense urbanization, colonization, and accompanying conversion of primary forest to agricultural and pastoral use, and as a consequence primary forest is de facto absent from the area, although there is some secondary forest. Thus, suitable habitat for *Dendrobates galactonotus* has become scarce in eastern Pará, although the species has been recently reported in Abaetetuba (Galatti *et al.* 2007), a highly urbanized area close to Belém. Galatti *et al.* (2007) reported that specimens from the Parque Zoobotanico do Museu Paraense Emílio Goeldi in Belém, now completely surrounded by city housing, were collected there in 1910. The species is no longer encountered in the the Parque Zoobotanico do Museu Paraense Emílio Goeldi. On March 11 and 12, 2012, we tried to obtain topotypical material in the area north of Vigia. The Rio (do) Murio (type locality) was not known to anyone living in the area, and we were unsuccessful in finding potentially good habitat (primary forest) for this species. We located some areas of secondary forest, but we did not encounter any specimens. Probably the species has disappeared from this area because of extensive deforestation. On the other hand, the species (still?) does occur in some disturbed and fragmented forests close to villages, like in Barcarena, c. 25 km (airline) southwest of Belém.

Dendrobates galactonotus is a species widely kept in terrariums in Europe, U.S.A. and Japan (Overkamp 2009). All these specimens stem from illegal exports (Nijman and Shepherd 2010, Saurian Enterprises Inc. 2012). One attempt to illegally export this species from Brazil is known (Pistoni and Toledo 2010). According to the CITES Trade Database no legal exports of live *D. galactonotus* were ever reported from Brazil. Although the species is commonly bred in captivity, it remains interesting for the pettrade to obtain wild-caught specimens (cf. examples in Brown *et al.* 2011 for species of *Ranitomeya*) and Brazilian authorities should remain vigilant for attempts to smuggle this species out of the country.

A positive bit of information about *Dendrobates galactonotus* is that this species, in contrast to *D. tinctorius,* apparently is not susceptible to *Batrachochytrium dendrobatidis* in captivity (Fioravanti 2012). The reason for this apparent immunity is unknown.

Poison frogs have lipophilic alkaloids in their skins, and the brighter or more boldly colored dendrobatids are, the most toxic they are (Vitt and Caldwell 2009). A problem that confronts us here is that variation in color throughout a relatively large, but homogeneous area (eastern Amazonian tropical lowland rainforest), has taken off in several directions, but it is difficult to envisage a mechanism that could have caused this variability. Also it is not known how, and whether, the different colors relate to differences in toxicity. In cooperation with several colleagues

a project to study the relationship between the colors of different morphs and the genetic make-up of populations has been started.

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Appendix I. Material Examined (*indicates that color in life of the specimens is known) (all specimens are from Brazil).

PARÁ: Itaituba: MPEG 33790*, 34502–3*, 34467–75*; Anapu: MPEG 25194–8*; Melgaço: MPEG 5772, 5807, 5656–7, 5772*, 5807*, 5856–7*, 5860*, 5864*, 5872–3*, 5902–4, 5912*, 5915, 5919, 6597*, 6645*, 6687–9, 6705–6, 6711–3, 6715, 6718, 6723, 8116, 8120, 8125–6, 8135–6, 8148, 8170–2, 8184–8, 8200–3, 8205, 8232, 8243–4, 8370, 9150, 11200, 14672, 15214–8, 15303–7, 15361, 15418, 15518, 15562–3, 15585, 15745, 15747, 15758, 15791, 15826, 15828, 17306, 17418, 34596–7*, 34600*, 34612–16*, 34619–21*; Portel: MPEG 5749*, 5878*, 5893*, 6604*, 6620*, 7621, 15518, 22702–41*, 24578–601*, 26992–27005*, 32034–36, 32037*, 32093–97, 32098–100*, 34582–7*, 34588–95*, 34598–99*, 34601–11*, 34617–8*; 34892–3, 34894–5*; Mocajuba: MPEG 530–31; Barcarena: MPEG 18373, 28984, 33757–8*; Vigia: NMW 19189* (holotype); Belém: MPEG 471–3; Acará: MPEG 1678; Road Belém–Brasília, km 75: MPEG 365; Paragominas: MPEG 713–4, 7184*, 14672; Tucuruí: MPEG 2906–8, 2912, 2920–4, 2930–1, 2940–1, 2970, 3027–30, 3347–9, 3753, 3755–9, 17746–8, 19543–5, 19921–6, 21122–3, 21164–5; Rondon do Pará: MPEG 34627–8*; Marabá: MPEG 2858*, 28118*, 31796–7*, 34499–501*; Parauapebas: MPEG 27748; Curionópolis: MPEG 23771–2*; Canaã dos Carajás: MPEG 16264*, 16269,16271*, 21169–70, ZUEC 9036*; São Geraldo do Araguaia, Serra das Andorinhas: MPEG 34622–3*; São Félix do Xingu: MPEG 3190, 3191, 3195, 5993, 9379*.
MARANHÃO: Açailândia: MPEG 3861; São Luis: HUFMA 890*.
TOCANTINS: Araguaína: MPEG 693–4.

Localities mentioned in literature and internet (*indicates that color in life of the specimens is known):

Pará: Ananindeua (Galatti *et al.* 2007); Igarapé-Açu (Silverstone 1975); Mazagão and Breu Branco, Rio Tocantins (Silverstone 1975); Santarém (Silverstone 1975); Piratuba, 18 km SE Abaeté (Silverstone 1975); Cachoeira Cahy (= Caí), Rio Jamanxim (Silverstone 1975); Tucurui (*Martins and Sazima 1989); Carajás (*Neckel-Oliveira *et al.* 2012).
Maranhão: Açailândia (*Brasileiro *et al.* 2008 [CFBH 15625*]): Carolina (Silverstone 1975).
Tocantins: Palmeirante (*Marchezini, 2010).
Mato Grosso: Alta Floresta (*Baas and Peper 2010, *Lötters *et al.* 2007, *Vitt and Caldwell 2009).

Localities based on color photographs or on pers. comm.:

Pará: Brasil Novo (E. Oliveira); Tucurui (M. Martins); Canaã de Carajás (A.B. de Assis, L. Ferreira): São Felix do Xingu, TI Kayapo (A. Jerozolimski); Palestina do Pará (P. L. V. Peloso); L. F. Storti (west of Jamanxim River, Rio Tapajós).
Maranhão: Açailândia (A. Silveira); UTE Itaqui, São Luis (D. Pavan).