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Geographical variation in the reproduction and sexual dimorphism of the Boddaert's tropical racer, *Mastigodryas boddaerti* (Serpentes: Colubridae)

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ABSTRACT. We obtained data on time of sexual maturity, dimorphism, fecundity and on the reproductive cycle of *Mastigodryas boddaerti* (Sentzen, 1796) through the examination of 321 preserved specimens, of which 221 were collected in the Brazilian Amazon region and 100 in the Cerrado savannas of Central Brazil. The degree of sexual size dimorphism (snout-vent length, SVL) was significantly greater in the specimens from the Cerrado in comparison with those from the Amazon. Females had a significantly larger number of ventral scales, on average, whereas males had more sub-caudal scales. However, there was no intersexual difference in tail length or head width, although the heads of the males were significantly longer, which may reflect dietary differences. Breeding females from the Amazon region contained between one and six eggs (N = 12, mean = 3.0), whereas two females from the Cerrado had four to six eggs (N = 10, mean = 5.0). No relationship was found between the SVL of the Amazonian females and the number of eggs or vitellogenic follicles they contained (Cerrado females were not analyzed here due to small sample size). Males are smaller than their female counterpart when they reach sexual maturity. Even though females from the Amazon reproduce throughout the year, females from the Cerrado breed seasonality.

KEY WORDS. Amazonia; ecology; Cerrado; morphology; population.

Reproduction is a main component of the life history of an organism (Begon *et al*. 1990), and is the most common element in studies of species ecology that focus on reproductive cycles, body size at sexual maturity, sexual dimorphism, and fecundity (Pizzatto & Marques 2002, Balestrin & Di-Bernardo 2005). Snakes have a great diversity of reproductive traits. This diversity is in part due to adaptations to local stimuli, because reproductive traits are responsive to the environment or ecology and the morphology of the species (Shine 2003, Pizzato *et al*. 2008).

The details of the life history of a number of Squamata species, in particular lizards, are relatively well known (Ballinger 1979, Dunham 1982, Tinkle & Dunham 1986). However, for most species, few data are available on geographic variations in diet, reproduction, and morphology (King 1993). For instance, the reproductive cycle and fecundity of some Neotropical snakes, such as the widely-distributed *Tantilla melanocephala* (Linnaeus, 1758) and *Erytrolamprus miliaris* (Linnaeus, 1758) are known to be affected by environmental factors (Pizzatto & Marques 2006, Santos-Costa *et al*. 2006).

The Neotropical *Mastigodryas* Amaral, 1934 belongs to Colubridae (*sensu* Zaher *et al*. 2009), which is composed by 12 species found in the New World between Mexico and northern Argentina (Stuart 1941, Peters & Orejas Miranda 1970, Tipton 2005, Montingelli & Zaher 2011). Among these species, *Mastigodryas boddaerti* (Sentzen, 1796) has one of the most widespread distribution, occurring on areas of western South America, from Bolivia, Peru, and Colombian and Brazilian Amazonia to the eastern portion of Venezuela (Montingelli *et al*. 2011). The species may be found in habitats ranging from primary forests to open areas, including secondary forests, plantations, and grasslands (Cunha & Nascimento 1978, Nascimento *et al*. 1988, Murphy 1997, Martins & Oliveira 1998).

The reproductive biology of *M. boddaerti* is poorly known, except for some data on fecundity, e.g., a female captured in eastern Pará, Brazil, which contained six eggs, and a neonate observed in the region of Manaus, in the central Amazon basin, in the month of April (Martins & Oliveira 1998). The present study analyzes the sexual maturity, fecundity, and reproductive cycle of *M. boddaerti* populations from the Brazilian Amazon and the Cerrado Savannas of central Brazil to describe patterns of sexual dimorphism between regions.

MATERIAL AND METHODS

A total of 321 specimens of *M. boddaerti* were examined, 221 of which were collected in the Brazilian Amazon, in the states of Amazonas, Rondônia, Roraima, Pará, Amapá, Amazonas, Mato Grosso, and Maranhão, while the other 100 specimens were obtained from the Cerrado domain, including localities in the Brazilian states of Mato Grosso, Mato Grosso do Sul, Tocantins, Maranhão, Goiás, and Distrito Federal. The specimens were obtained from the following institutions: Museu Paraense Emílio Goeldi (MPEG), Instituto Nacional de Pesquisas da Amazônia (INPA), Instituto Butantan (IBSP), Museu de Zoologia da Universidade de São Paulo (MZUSP), Universidade Federal do Mato Grosso (UFMT), Universidade de Brasília (CHUNB), and Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP-PUCRS) (Appendix 1).

The Amazon basin encompasses a variety of vegetation types, although the vast majority of the region is covered by *terra firme* rainforest, which is composed by relatively tall trees with overlapping crowns that shade the ground permanently (Leitão-Filho 1987). The region's climate is hot and humid, with mean temperatures between 24°C and 26°C (Fisch *et al.* 1998), corresponding to Köppen's humid tropical A category, with mean annual temperatures above 18°C and oscillations of less than 5°C (Müller 2006). The mean annual precipitation is approximately 2,300 mm, with a rainy season typically occurring between October and March, and a dry season between April and September (Fisch *et al*. 1998).

The Brazilian Cerrado savannas encompass a mosaic of grassland and woodland vegetation, with gallery forest along rivers (Silva & Bates 2002). The predominant climate is seasonal tropical with dry winters, and annual temperatures of 22-23°C, but with minimum temperatures close to or even below zero during May, June, and July, and maximum of 40°C. The mean annual precipitation is between 1,200 mm and 1,800 mm, most of which is concentrated between October and March (Coutinho 2002).

The following data were recorded for each specimen of *M. boddaerti* (linear measurements in mm) studied: date of collection, locality, sex, sexual maturity, snout-vent length (SVL), tail length (TL), head length (HL) and head width (HW), and the number of ventral (VS) and sub-caudal scales (SS). The specimens were weighed (in grams) after draining excess liquid and remove gut contents, if present, through an abdominal incision. Sexual maturity was evaluated based on the examination of the deferent ducts and oviducts. The diameter of the final portion of the deferent duct was measured, as were the length, width, and height of the eggs and testicles. The number of eggs and follicles was also counted, and the length of the largest follicle measured. Females were considered sexually mature when containing eggs or flaccid oviducts (Shine 1977a, Siqueira *et al.* 2012), whereas males were considered mature when they presented opaque and convoluted deferent ducts, which indicates the presence of sperm (Shine 1977b). Individuals with an umbilical scar were considered to be newborns (Santos-Costa *et al*. 2006).

The sexual size dimorphism index (SSD) for each population was calculated according to Shine (1994): mean body size of the largest sex divided by mean body size of the smallest sex, minus one. By convention, positive values represent that females are the larger sex and negative values represent that males are the larger sex (Shine 1994). This analysis included only mature specimens. Similar variation in patterns of robustness, based on male and female weights, was tested using an analysis of covariance (ANCOVA) for each population separately. The SVL was used as covariate to remove the effects of the body size.

The significance of the differences between the sexes in SVL, and the number of ventral and subcaudal scales were evaluated using the Student's *t* test. Sexual dimorphism in TL, HL, and HW was assessed using a one-way ANCOVA with SVL as covariate. To evaluate geographical differences in sexual dimorphism, we employed a factorial ANOVA analysis, in which SVL was considered as the dependent variable, and sex and region as the factors (Pizzatto & Marques 2006). Specimens with an injured belly and/or tail were not included in the meristic analyses of sexual dimorphism (VS and SS). Specimens that showed deformation in head shape were also excluded from analyzes of sexual dimorphism in length and width of the head. To analyze sexual dimorphism in *M. boddaerti*, we used specimens from both the Cerrado and the Amazon, as a whole. However, to analyze the degree of sexual dimorphism and robustness, the specimens were separated by populations.

A simple linear regression was used to evaluate the relationship between SVL and the number of follicles and eggs carried by the females.

RESULTS

On average, mature *M. boddaerti* females (N = 102) were significantly larger (SVL) than mature males (N = 99) (t = 7.734, p < 0,001) (Table I). The degree of size dimorphism was significantly greater (two-way ANOVA: F = 4.586, p < 0.05) in the sample from the Cerrado savanna (females = 27, males = 41), where SSD = 0.184, in comparison with that from the Amazon rainforest (females = 75, males = 58), where SSD = 0.102 (Fig. 1). No difference was found in the robustness of the two sexes, either in the Sample from the Amazon (ANCOVA: $F_{1,126}$ = 0.00009, p = 0.756, males = 58, females = 70) or in that from the Cerrado (ANCOVA: $F_{1,58}$ = 0.660, p = 0.420, males = 40, females = 21), indicating a lack of dimorphism.

Mature females (N = 100) also have a significantly larger number of ventral scales, on average, than mature males, N = 99 (t = 23.156, p < 0.001), whereas males (N = 60) have significantly more sub-caudal scales than females (N = 62),

Table I. Sexual dimorphism in SVL, tail length (TL), head length (HL), head width (HW), ventral scales (VS) and subcaudal scales (SS) for adult *Mastigodryas boddaerti* from Amazon and Cerrado populations. Means ± sd. Sexual differences in SLV, VS and SS were tested using Student t test and sexual differences in TL, HL and HW were tested using ANCOVA.

Sex	SLV (mm)	TL (mm)	HL (mm)	HW (mm)	VS	SS
Males	727.85 ± 94.23	271.12 ± 3.63	29.40 ± 0.37	13.89 ± 0.25	184.46 ± 2.63	104.32 ± 3.74
N	99	75	90	89	99	60
Females	822.15 ± 78.11	293.78 ± 3.02	31.69 ± 0.28	15.74 ± 0.26	193.23 ± 2.71	101.98 ± 3.18
N	102	67	93	89	100	62
Statistical test	t-value = 7.734	$F_{(1,139)} = 0.097$	$F_{(1,180)} = 9.323$	$F_{(1,175)} = 0.037$	t-value = 23.156	t-value = -3.716
p	$p < 0.001$	$p = 0.756$	$p < 0.01$	$p = 0.848$	$p < 0.001$	$p < 0.001$

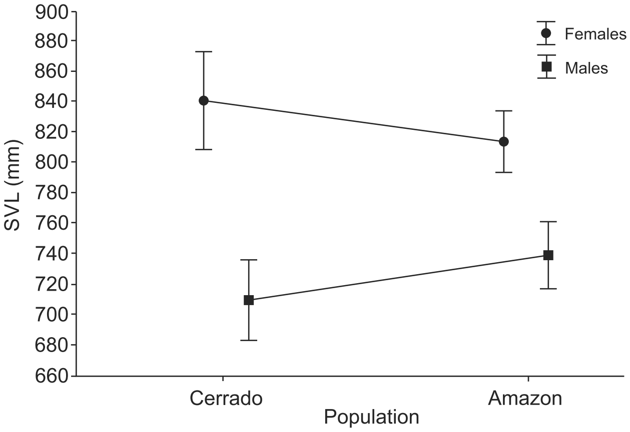

Figure 1. Variation in the degree of sexual size dimorphism (SVL) between the Amazonian and Cerrado populations of *Mastigodryas boddaerti.*

on average (t = -3.716, $p < 0.001$). No significant difference was found between the sexes (females = 67, males = 75) in tail length (ANCOVA: $F_{1,139} = 0.097$, $p = 0.756$), and there was no dimorphism in head width between males (N = 89) and females, N = 89 (ANCOVA: $F_{1,175} = 0.037$, $p = 0.848$). However, the heads of the males (N = 90) were significantly longer than those of the females, N = 93 (ANCOVA: $F_{1,180} = 9.323$, $p < 0.01$) (Table I).

Considering the sample from the Amazon, the smallest mature female had a SVL of 671 mm, while the smallest mature male was 521 mm in length. In the sample from the cerrado, the smallest mature female was 723 mm, and the smallest male was 536 mm. Therefore, in both populations, males are smaller than their female counterparts when they reach sexual maturity.

Amazonian females of *M. boddaerti* contained one to nine secondary follicles, with a mean of 5.2 (N = 41). Among this sample we encountered four gravid females carrying one to six eggs, with a mean of 3.0. Two pregnant snakes also had secondary follicles in the ovaries. In the sample from the cerrado, the number of secondary follicles (N = 4) varied from four to 11 (mean = 6.4), and two females had four and six eggs, respectively. No relationship was found between the number of secondary follicles or eggs and the size (SVL) of the females collected in the Amazon region ($r^2 = 0.007$, $p = 0.588$, N = 40). It was not possible to analyze the Cerrado group due to the small number of pregnant females in this sample.

In the sample from the Amazon, gravid females were observed in March (N = 2), April (N = 1), and May (N = 1), while vitellogenic follicles and newborns with an umbilical scar were observed throughout the year, which indicates a lack of breeding seasonality in this population. Two specimens had both vitellogenic follicles (11.90 mm and 17.49 mm) and eggs in the oviduct. In the sample from the cerrado, the only two pregnant females were recorded in January, and the three females with vitellogenic follicles were observed in January, February, and June. Newborns were recorded in January (N = 1), April (N = 4), June (N = 1), and December (N = 2).

DISCUSSION

The pattern of sexual dimorphism observed in *M. boddaerti*, in which females are generally larger than males, is typical for many snakes (Orofino *et al.* 2010, Pizzatto & Marques 2002, Marques *et al.* 2006, Pizzatto *et al.* 2008, Scartozzoni *et al.* 2009, Zanella & Cechin 2010). Sexual dimorphism in which males are larger than females is normally restricted to species in which males compete directly for access to breeding females (Shine 1993), as within *Chironius* Fitzinger, 1826, in which the males of most species attain larger sizes than females and are likely to display male-male combat (Almeida-Santos & Marques 2002, Marques *et al.* 2009). A larger body size may have different consequences for males and females. For instance, larger females have more internal space for the development of eggs or embryos, as well as for the storage of the energy reserves necessary for the reproductive process (Bonnet *et al.* 1998). For the males, on the other hand, a smaller body may provide greater agility during the search for breeding females, as well as reduce the costs of locomotion and general metabolism (Rivas & Burghardt 2001).

Leite *et al.* (2009) also observed relatively large *Mastigodryas bifossatus* (Raddi, 1820) females in the subtropical region of southern Brazil. In southeastern Brazil, however, Marques & Muriel (2007) found no sexual size dimorphism in *M. bifossatus*. In snakes, deviations of this type in the degree of sexual size dimorphism may occur as a result of distinct growth rates in different populations, related to the consumption of prey with varying nutritional value, associated with selective pressures which favor differences in body size between the sexes (Madsen & Shine 1993, Krause *et al.* 2003).

The lack of sexual dimorphism in tail length contrasts with the pattern observed in most other snakes, in which males usually have longer tails than females (King 1989, Shine *et al.* 1999). A larger tail provides the male with additional internal space for the storage of the hemipenis and retractor muscles (King 1989). An absence of sexual dimorphism in tail size may be related to ecological factors, such as foraging strategies and defense mechanisms (Zanella & Cechin 2010). The fact that 23% of the specimens (of both sexes) from both the Amazon (N = 51) and the Cerrado (N = 23) had broken tails suggests that *M. boddaerti* may use its tail for defense. This behavior has been suggested for *M. bifossatus* (Ferreira & Outeiral 1998, Leite *et al.* 2009, Dourado *et al.* 2013), and has been observed in species of other genera, such as *Coniophanes fissidens* (Günther, 1858) (Zug *et al.* 1979), *Dendrophidion dendrophis* (Schlegel, 1837) (Prudente *et al.* 2007) and *Echinanthera cyanopleura* (Cope, 1885) (Zanella & Cechin 2010). The difference in the length of the heads of males and females of *M. boddaerti* may be related to the exploitation of different resources, which may contribute to reduce intraspecific competition (Shine 1993, Vincent *et al.* 2004) between the sexes, since males feed on larger prey (Siqueira *et al.* 2012).

In both populations, males are smaller than their female counterparts at sexual maturity. A similar pattern was observed for *Mastigodryas melanolomus* (Cope, 1868) from Costa Rica (Goldberg 2006). This may reflect the relatively lower costs of reproduction for males, which are able to participate in more reproductive events by maturing early, whereas females that mature at a larger size may be able to produce a larger number of relatively large eggs (Seigel & Ford 1987, Bonnet *et al.* 1998). Madsen & Shine (1994) have suggested that fecundity is directly related to body size in most snake species. In the present study, however, the number of eggs or vitellogenic follicles was not related to the size of the female. The clutch sizes recorded in the present study are consistent with the observation of Martins & Oliveira (1998), who recorded a female with six eggs in eastern Amazon, and indicate the production of relatively small clutches in comparison with *M. bifossatus*, which produces clutches of up to 22 eggs in the subtropical region of southern Brazil (Leite *et al.* 2009). Clutch size in *M. boddaerti* is nevertheless similar to that recorded in Costa Rica for *M. melanolomus* (four to six eggs) by Goldberg (2006). The reduced fecundity of *M. boddaerti* is probably related to the small size of the adults.

The reproductive cycle of a species may vary according to the climatic conditions faced by different populations (Pizzatto *et al.* 2007), a pattern observed in widely-distributed snakes, for instance *M. bifossatus* (Marques & Muriel 2007, Leite *et al.* 2009) and *T. melanocephala* (Santos-Costa *et al.* 2006). The continuous reproductive cycle of *M. boddaerti* in the Amazon region is similar to that observed for other Neotropical snakes (Pizzatto & Marques 2002, Santos-Costa *et al.* 2006, Prudente *et al.* 2007, Orofino *et al.* 2010). In the Amazon region in particular, there is a strong tendency for a non-seasonal breeding pattern (Duellman 1978), which may be related to the relative climatic stability of the region, and ecological factors such as the sustained abundance and diversity of available prey (Seigel & Ford 1987). In the Cerrado, on the other hand, the absence of reproducing females between July and October suggests that seasonal breeding is a response to the region's relatively low temperatures, which may affect reproduction and activity patterns (Pizzatto *et al.* 2007). Additional factors such as prey availability may result in different encounter rates over the course of a year (Marques *et al.* 2000), and snakes tend to adjust their reproductive cycle to the period when prey are most abundant and temperatures are more adequate for incubation (Shine 2003), which is normally during the rainy season. However, the analysis of a much larger sample would be necessary to confirm this hypothesis.

In conclusion, this study provides a better understanding of the geographic variation in the reproductive biology of a widespread species in two distinct biomes. Our results demonstrate that the only difference found among the two populations is in the seasonality of the reproductive period.This is likely to be a response to temperature variations and prey availability. We also found a sexual dimorphism in size, expressed in the SVL. This dimorphism may be associated with the consumption of prey with varying nutritional values, which in turn is associated with selective pressures that favor differences in body size between the sexes. Other sexual attributes remained invariable throughout the geography, being apparently not affected by seasonality or geographic isolation. Certainly, the knowledge of these data together with studies from different biomes will contribute towards a better interpretation on the reproductive biology of this species.

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Appendix 1. Specimens examined.

Brasil, *Amapá*: without provenance (CHUNB 3639), Cajubim (MPEG 433), Macapá (CHUNB 13157, IBSP 24787), Mazagão (MPEG 23300), Oiapoque (IBSP 14681), Rio Tracajuba (IBSP 24819), Serra do Navio (MPEG 181); *Amazonas*: Fortaleza Paraná do Urariá (MZSP 5240), Humaitá (IBSP 40814), Icoatiara (IBSP 44174, 44422), Itapiranga (MZSP 5090), Km 95 da Br 156 (MPEG 16675), Manaus (MPEG 299, IBSP 1566, 1567, MZSP 7633, 7987), Parintins (MZSP 1290), Reservas INPA WWF (MZSP 9516, 9517), Tefé (MZSP 8371); *Goiás*: Minaçu/U.H.E. Serra da Mesa (MCP 82212, 8213, 8220, 8223, 8224, 8225, 8550); *Maranhão*:

Arari (MPEG 13548), Nova Vida (MPEG 15712), BR 222. Início da estrada do Rosário (MPEG 20253), Nova Vida (MPEG 15712), Paruá. Br 316 (MPEG 10268, 10269, 10270, 10271, 10827, 11166, 13639, 14224, 14356, 14357), Peri Mirim (IBSP 21773, 21774), São Luís (IBSP 44316, MZSP 8380); *Mato Grosso*: Alto Paraguai (UFMT 1716), APM Manso (UFMT 499, 500), Aripuanã (UFMT 7217, 7219, 6185, 6808, 7221), Barra do Tapirés (MZSP 3798, 4429), Barra dos Bugres (UFMT 1637), Canarana (IBSP 62872), Chapada dos Guimarães (UFMT 1968, 4583), Cláudia (UFMT 3659, 3661, 3663, 3687, 3690), Cuiabá (UFMT 1636, 3621, 3622, 5825, 6505, IBSP 34408), Nobres (UFMT 1635), Nova Ubiratã (UFMT 5446, 7634), Nova Bandeirantes (UFMT 4878), Nova Xavantina (UFMT 1976), Poconé (UFMT 5376), São Felix do Araguaia (IBSP 46289), São Luiz de Cáceres (MZSP 1390), Sapezal (UFMT 5899), Sinop (UFMT 8436), U.H.E Manso (MZSP 11971, 11972, 11973, 11974, 11975, 11976, 11978, 11979, 11997), Utiriatí (MZSP 4750), Vale de São Domingos (UFMT 1638); *Mato Grosso do Sul*: Corumbá (UFMT 1397, 1404, 1405, 1407, 1408, 1415, 1416, 1420), Serra do Urucum (MZSP 4434); *Pará*: Acará (MPEG 19382), Alter do Chão – Santarém (MCP 9713), Ananindeua (MPEG 2369, 21268), Augusto Corrêa (MPEG 1075, 1989, 6662, 9101), Belém (PAB 55, MPEG 220, 221, 4695, 18179, 18180, 18187, IBSP 3144, 14682,15043, 25441), Benevides (MPEG 6027), Bom Jesus do Tocantins (MPEG 9474, 9475), Bragança (MPEG 5052, 6339, 7840, 7877, 8330, 11193, 13038), Cametá (IBSP 2190, 2223), Capitão Poço (MPEG 2155, 3541, 6101, 8021, 8112, 8120, 8742, 14067), Curuçá (MPEG 2735, 4049, 4874, 4875, 7112, 7114, 7116, 7591, 7593, 7624), Dom Eliseu (MPEG 14961), Estrada do Acará (MPEG 14478), Faro (MPEG 18354), Inhangapi (MPEG 2730, 2731), Itaituba (MCP 4445, 4446, 4447, 4448, 7917, MPEG 21238), Itupiranga (IBSP 32812), Juruti (MPEG 22538, 22654, 22663), km 74 da estrada Altamira-Itaituba (MPEG 743), Marabá (MPEG 15204, 16549, 16669, 16947, CHUNB 30421), Maracanã (MPEG 2758, 3358, 3359, 3360, 3361) Melgaço (MPEG 20440, 22037, 22038, 22040, 22041, 22043, 22044, 22045, 22046, 22047, 22048), Novo Progresso (CHUNB 33923, 35063), Ourém (MPEG 1269, 4212, 4213), Ourilândia do Norte (MPEG 20661, 20663, 20790), Palestina do Pará (MPEG 11785, 12954), Parauapebas (CHUNB 6668, MPEG 22931), Peixe-boi (MPEG 1391), Portel (MPEG 18661, 20211), Porto Trombetas – Oriximiná (MPEG 21574), Primavera (MPEG 18743), Projeto Manganês do Azul (MPEG 21518), Santarém (MPEG 395, 401, 19042, MCP 7616, 7913, 8690, 8905, 10504, 11331), Santarém Novo (MPEG 3454), Santo Antônio do Tauá (MPEG 1137, 1436, 1439), São Domingos do Capim (MPEG 8071, 9388, 10966), São Geraldo do Araguaia (CHUNB 30420), Serra Norte – Carajás (MPEG 16582), Soure – Ilha do Marajó (IBSP 25466), Tailândia (CHUNB 56246), Tucuruí (MPEG 16768, 16769, IBSP 46409), Viseu (MPEG 4353, 4442, 5144, 5234, 5935, 7379, 7723, 7768, 8905, 14016, 14154, 15133, 16280, 16284, 16288, 16289); *Rondônia*: Alto Alegre dos Parecis (UFMT 6940, 7046, 7545), Costa Marques (MCP 6267), Guajará-Mirim (CHUNB 22055, 22056), Jaci-Paraná. Br 364 (MPEG 17066), Margem esquerda do Rio Jamari (MPEG 18760), Monte Negro (IBSP 73954, 73955, 73956, MZSP 12339), Mutum-Paraná (MZSP 3209), Porto Velho (MPEG 18005, MZSP 3203, 3204, 3205, 3206, 3207); *Roraima*: Apiaú (MZSP 10015, 10016), Boa Vista (MZSP 9856, 10479, 10890), Cachoeira do Cajubim-Rio Catrimani (MZSP 6392), Missão Catrimani (MZSP 10896); *Tocantins*: AHE Peixe Angelical (IBSP 74343), Lajeado (IBSP 64235, 65192, 65197, 65198, 66188, 66189, 66190, 66191, 66192, 66193, 66194, 66251, 66479), Palmas (IBSP 65177, 65178, 65256, 65294, 65404, 65406, 65407, 65408, 65585, 65986, 65987, 65990, 65991, 65992, 65994, 65405, 65989, 65995), Peixe (CHUNB 52565, 52566, 52567), Porto Nacional (IBSP 65697, 65851, 65852, 65853, 65854, 65855, 65856, 65967, 65968), São Salvador do Tocantins (IBSP), without provenance (UFMT 673).

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