

Reproductive biology and food habits of the swamp racer *Mastigodryas bifossatus* from southeastern South America

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The swamp racer *Mastigodryas bifossatus* is a large colubrid snake distributed mainly in open areas in South America. Dissection of 242 specimens provided data on body sizes, sexual size dimorphism, reproductive cycles and food habits of this species. Adult *M. bifossatus* average approximately 1100 mm in snout–vent length, with males and females attaining similar sizes. Reproductive cycles in females seem to be continuous, although oviductal eggs occur mainly from the beginning to the middle of the rainy season with peak recruitment at the end of the rainy season. Clutch size ranges from four to 24 and each newborn individual is about 300 mm SVL. *Mastigodryas bifossatus* is euryphagic, feeding mainly on frogs (44%) and mammals (32%). Lizards (16%), birds (4%) and snakes (4%) form the remaining prey. Relatively small prey (0.05–0.019) are ingested by adults, and juveniles eat mammals, which suggests that there is no ontogenetic shift in the diet of this snake. Swamp racers forage by day on the ground in open areas but may use arboreal substrates for sleeping or basking.

Key words: Brazil, Colubrinae, diet, reproductive cycles, sexual dimorphism

INTRODUCTION

The snakes of the subfamily Colubrinae are widely distributed over all landmasses of the world, but are most dominant and diverse in the northern hemisphere (Greene, 1997). At least 20 genera of colubrines occur in the neotropical region, occupying several habitats. The neotropical colubrine snakes are usually large and diurnal (Ferrarezzi, 1994; Greene, 1997), but detailed natural history data are unavailable for most species. The swamp racer *Mastigodryas bifossatus* is a neotropical colubrine, widely distributed from northern South America in Venezuela and Colombia to northern Argentina (Peters & Orejas Miranda, 1970). This species lives mainly in open areas of the Brazilian cerrado, Pantanal and grasslands in southern Brazil, but also occurs in low abundance in the Amazonian and Atlantic forests (Hoogmoed, 1979; Strüssmann & Sazima, 1993; Lema, 2002; Argôlo, 2004; Marques et al., 2004). Apart from anecdotal reports (e.g. Amaral, 1978; Strüssmann & Sazima, 1993; Marques et al., 2004) nothing has been published on the ecology of this snake, although specimens from central and southeastern Brazil are relatively common in herpetological collections. The present study provides information on sexual size dimorphism, reproductive cycles, fecundity and food habits of *M. bifossatus* (Fig. 1) from southeastern South America.

MATERIALS AND METHODS

A total of 242 specimens were examined from the collection of the Instituto Butantan (IB) and Museu de História Natural da Universidade Estadual de Campinas (ZUEC), in São Paulo, Brazil. The sample included only specimens from southeastern South America (20–30°S and 45–55°W; see Appendix I). This region has a climate

characterized by two distinct seasons: a dry season from April to August, with less rainfall and lower temperatures, and a rainy one from September to March, with higher rainfall and temperatures (Nimer, 1989). The following data were taken from each specimen: 1) snout–vent length (SVL); 2) sex; 3) reproductive maturity or immaturity: males were considered mature if they had enlarged testes and opaque deferent ducts (Shine, 1982), females if they had either ovarian follicles in vitellogenesis or oviductal eggs (Shine, 1980); 4) diameter of the largest ovarian follicles, diameter of the largest egg, number of ovarian follicles in vitellogenesis (>10 mm) and number of oviductal eggs; 5) stomach and/or intestine contents. When only insects were found in the hindgut they were interpreted as secondary prey items having been first ingested by a frog (cf. Martins & Gordo, 1993; Martins et al., 2002). All food items in the stomach were removed, identified to the lowest possible taxonomic level, and measured.

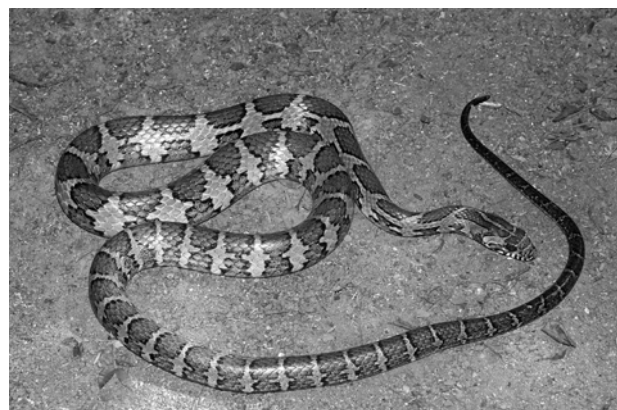


Fig. 1. The swamp racer *Mastigodryas bifossatus* (female, SVL=1180 mm, mutilate tail=326 mm, mass=465 g, IB73758), from Garruchos, RS.

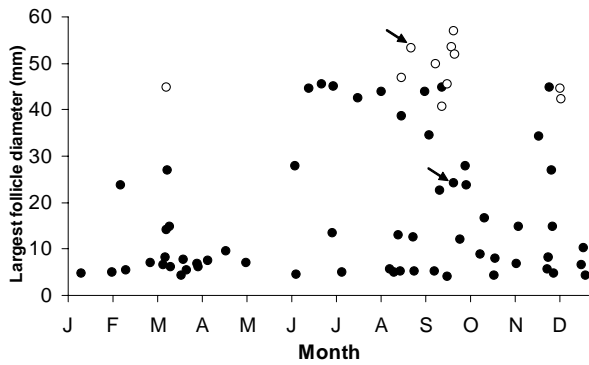


Fig. 2. Seasonal variation in the diameter of the largest follicle in adult female *Mastigodryas bifossatus*. Solid circles represent ovarian follicles; open circles represent oviductal eggs. Arrows represent follicles and eggs in the same individual.

Sexual size dimorphism index was calculated as follows: (mean SVL of the largest sex)/(mean SVL of the smallest sex) – 1. This index is expressed as positive if females are the larger sex and negative if males are the larger (cf. Shine, 1994a).

RESULTS

Body size and sexual dimorphism

Mature males averaged 1101 mm SVL (SD=162, $n=79$, range 700–1455 mm), and mature females averaged 1078 mm SVL (SD=22.1, $n=100$, range 625–1630 mm). This difference is not significant ($t=-0.8198$, $df=176$, $P=0.2070$). The degree of sexual dimorphism (SSD) was -0.021 (cf. Shine, 1994a).

Female reproductive cycle

Females with ovarian follicles in vitellogenesis (>10 mm) were found throughout the year, except in January, April and May (Fig. 2). Eggs were recorded in March, August, September and December (Fig. 2). A female (IB 25995) with 16 ovarian follicles in secondary vitellogenesis (largest follicle = 24.3 mm) and four oviductal eggs was recorded in September (Fig. 2).

Thirty-eight (54%) of 71 females were at the reproductive stage (27 females had vitellogenic follicles and 11 females had oviductal eggs).

Fecundity

Clutch size averaged 13 eggs ($s=3.0$, range 4–24). Clutch size was positively and significantly related to maternal SVL ($r^2=0.1698$; $F=7.1350$; $n=31$; $df=30$; $P=0.0122$) or marginally significant for log-transformed data ($r^2=0.1244$; $F=4.123$; $P=0.0515$) (Fig. 3).

Growth rates

The smallest field-collected snake measured 275 mm SVL. Newborn snakes (SVL approximately 300 mm) were collected mostly between January and May (Fig. 4). Thus, recruitment may occur mainly from January to May. From seasonal distributions of SVLs (Fig. 4), it is possible to infer that *M. bifossatus* almost doubles its body size during the first year, and males and females attain sexual

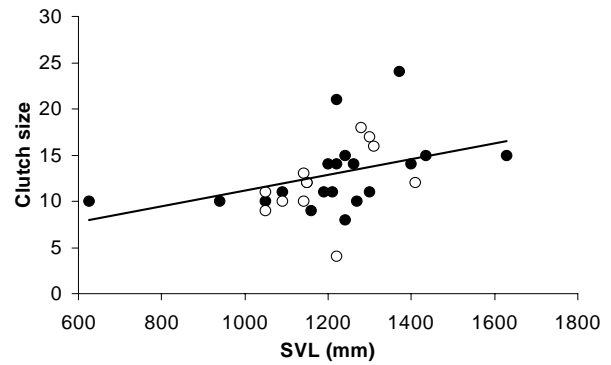


Fig. 3. Relationship between female snout-vent length and clutch size in *Mastigodryas bifossatus* (see text). Solid circles represent vitellogenic follicles; open circles represent oviductal eggs.

maturity at about 24 months. However, growth trajectories need to be interpreted with caution as this snake produces offspring over an extended period of time.

Food habits

Thirty-five snakes contained prey. Ten of these snakes contained two prey items and two specimens had at least three prey items in the gut. A wide variety of vertebrate prey was consumed (Table 1). Anuran amphibians were the most common prey of *M. bifossatus* (44%). At least one snake had eaten eggs and tadpoles. It was not possible to accurately identify most amphibians (because we found vestiges of anuran bodies, or insects, the latter secondary prey), and *Leptodactylus* was the only genus identified. Reptiles represented 20% of the total prey with lizards being the most frequent reptile consumed (Table 1). Two colubrid opisthoglyphous snakes were found, at least one of them (*Tantilla melanocephala*) swallowed head first. This snake was practically intact (total prey length = 310 mm, mass = 5.9 g; SVL of snake = 1090 mm; relative prey mass = 0.014). The other snake (*Philodryas patagoniensis*) was identified by its scalation pattern. Sixteen mammals (32%) were recorded, all of them rodents, but most were in an advanced stage of digestion and only two were relatively intact (4.5 g and 8.5 g, relative prey mass = 0.05 and 0.019; genus *Oryzomys* sp.). Two specimens of *M. bifossatus* that contained rodents in their digestive tracts had preyed on birds (4%), as inferred by the presence of feathers. Three prey items (two rodents and one amphibian) were recorded from digestive tracts of three young *M. bifossatus* (SVL < 600 mm). Seasonal or sexual differences in diet were not detected.

DISCUSSION

The approximate equivalence of adult body size in male and female *M. bifossatus* is not surprising: females are larger than males in most neotropical colubrids (e.g. dipsadines and xenodontines; see Fowler & Salomão, 1994; Marques, 1996; Pizzatto & Marques, 2002; Martins & Oliveira, 1998, Oliveira, 2001; Balestrin, 2004), but this is not true for colubrine snakes (see Shine, 1994a). The lack of body size dimorphism and the extreme negative SSD

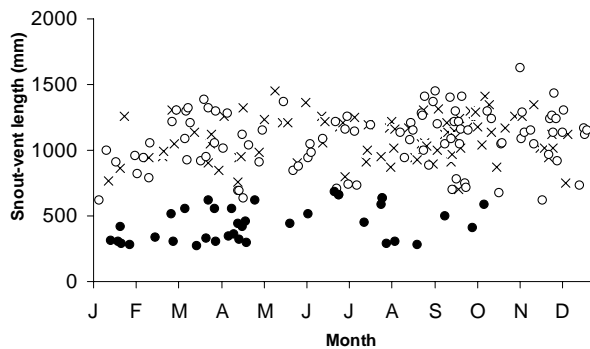


Fig. 4. Seasonal distribution of body sizes in *Mastigodryas bifossatus*. Solid dots show juveniles (immature individuals), circles show mature females, and crosses show mature males.

value (-0.21 , see Shine, 1994a) suggest the presence of male combat in *M. bifossatus*. Male combat may be widespread among colubrine snakes, including South American species such as *Chironius* spp. and *Spilotes pullatus* (Almeida-Santos & Marques, 2002; Pizzatto et al., in press). However, more observational records for South American snakes are clearly required in order for extent and distribution of this behavior to be ascertained.

Females of *M. bifossatus* appear to reproduce throughout the year. The continuous cycle of *M. bifossatus* is similar to those reported for some other neotropical snakes (e.g. Fitch, 1970, 1982; Marques, 1996; Marques & Sazima, 2004; Pizzatto & Marques, 2002), including other colubrines (e.g. *Senticolis triaspis*; Censky & McCoy, 1988). However, data from preserved specimens suggested that oviposition occurs mainly during the beginning to middle part of the rainy season (only one female with oviductal eggs was not collected during this period). The peak of newborn snakes confirms this seasonality and indicates that recruitment occurs mainly at the end of the rainy season and beginning of the dry season. Peak recruitment of newborn snakes during this period is verified in several other snakes from southeastern Brazil (Pizzatto & Marques, 2002; Marques & Sazima, 2004; Sawaya, 2004). A seasonal cycle, but apparently not continuous, was also described for *M. melanolomus* from Central America (Censky & McCoy, 1988).

The continuous and seasonal reproductive pattern observed in *M. bifossatus* has been reported in a number of the other species that occur in southeastern Brazil (see Marques, 1996; Pizzatto & Marques, 2002). Apparently, climatic variation in this region (see Nimer, 1989) may impose a certain amount of seasonal variation in species with continuous reproduction (Pizzatto & Marques, 2006). Extended reproductive cycles could be interpreted at the individual level, due to multiple clutches, or at the population level, due to asynchronous reproduction (Licht, 1984; Seigel & Ford, 1987). The simultaneous presence of oviductal eggs and vitellogenic follicles in one female suggests that *M. bifossatus* may produce multiple annual clutches, as reported for several tropical snakes including colubrines (Vitt, 1983; Tryon, 1984; Jordão &

Table I. Prey items from gut contents of *Mastigodryas bifossatus* from southeastern South America.

| Prey type | <i>n</i> | % |
|---------------------------------|----------|----|
| Amphibia | | 44 |
| <i>Leptodactylus</i> sp. | 1 | |
| Unidentified | 21* | |
| Snakes | | 4 |
| <i>Philodryas patagoniensis</i> | 1 | |
| <i>Tantilla melanocephala</i> | 1 | |
| Lizards | | 16 |
| <i>Ameiva ameiva</i> | 1 | |
| <i>Cnemidophorus</i> sp. | 1 | |
| <i>Kentropyx</i> sp. | 1 | |
| <i>Mabuya</i> sp. | 4 | |
| Unidentified | 1 | |
| Mammals | | 32 |
| <i>Oryzomys</i> sp. | 1 | |
| Unidentified | 15 | |
| Aves | | 4 |
| Unidentified | 2 | |

*Includes eggs and tadpoles found in one individual.

Bizerra, 1996; Marques, 1996; Stafford, 2003). Clutch size in *M. bifossatus* is higher than *M. melanolomus*, the latter a smaller species with low fecundity (see Censky & McCoy, 1988). However, clutch size in *M. bifossatus* is relatively low as well considering the females' body size. Other smaller colubrid snakes from southeastern Brazil, in particular *Oxyrhopus guibei*, *Tomodon dorsatus* and *Waglerophis merremii*, produce clutches with a similar number of eggs (Jordão, 1996; Pizzatto & Marques, 2002; Bizerra et al., 2005). The body size of newborn individuals in most neotropical snakes is around 200 mm (Marques et al., 2004). Thus, relatively small clutches in *M. bifossatus* may be a consequence of the large size of their newborn offspring (SVL approximately 300 mm).

The broad diet recorded for *M. bifossatus* is consistent with previous information published on the ecology of this species (Amaral, 1978; Cunha & Nascimento, 1978; Strüßmann & Sazima, 1993). However, some of these accounts indicated that mammals are a minor item (see Amaral, 1978; Strüßmann & Sazima, 1993). The data obtained here from preserved specimens show that anurans comprise the major part of the diet, with mammals representing approximately a third. Two other species from the genus, *M. melanolomus* and *M. boddaerti*, feed primarily on lizards (Seib, 1984; Martins & Oliveira, 1998), whereas lizards seem to be a minor dietary item in *M. bifossatus*. Snakes are only occasionally eaten by *M. bifossatus*, and *M. melanolomus* is also known to prey on them (see Seib, 1984). Snakes are an uncommon prey among neotropical colubrines but many species that eat lizards occasionally capture snakes (e.g. Sazima & Argôlo, 1994; Martins & Oliveira, 1998; Hartmann & Marques, 2005).

The presence of mammals in the gut of juvenile *M. bifossatus* indicates the absence of an ontogenetic diet shift in this snake. Snakes with ontogenetic diet shifts usually drop ectothermic prey from their diets and incorporate endothermic prey (see Andrade & Silvano, 1996;

Marques & Sazima, 2004; Hartmann & Marques, 2005). Mammals are generally larger prey than anurans and lizards and ontogenetic shifts in the diet of snakes may be largely a consequence of changing body size (Shine, 1994b). Thus, size constraints may prevent the consumption of mammals by small juvenile snakes. Nevertheless, newborn individuals of *M. bifossatus* have a relatively large body, and this trait may allow the consumption of mammals by juveniles. A sample size of three prey items for juveniles is not sufficient to address the question of ontogenetic variation in prey utilization. However, the fact that *M. bifossatus* eats small prey reinforces the supposition of the absence of an ontogenetic shift in this snake. Another species of the genus, *M. melanolomus*, also feeds on small prey and the larger specimens continue to consume small items (Seib, 1984). The tendency to eat small prey and the absence of ontogenetic variation may be a common trait in colubrine snakes (see Marques & Sazima, 2004).

Several of the prey (lizards, snakes and frogs) live in open areas, indicating that *M. bifossatus* forages in this habitat (see Hartmann & Marques, 2005). Although one author described this snake as an arboreal species (Amaral, 1978), others mentioned that this species is terrestrial (Strüssmann & Sazima, 1993). The data presented here indicate that *M. bifossatus* forages on the ground, since all prey items are terrestrial. Probably, *M. bifossatus* uses arboreal substrates for sleeping or basking (see Argôlo, 2004; Marques et al., 2004) and forages by day on the ground for active (e.g. lizards) or inactive prey (e.g. frogs, rodents). Such prey may be subdued by bite and semi-constriction, as occurs with some colubrine snakes (see Marques & Sazima, 2004).

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APPENDIX: SPECIMENS EXAMINED

Mastigodryas bifossatus – IB 24492, 24491, 24454, 25095, Água Branca – São Domingos, ES; IB 20389, Agulhas Negras, RJ; IB 4536, Albuquerque Caraguatá, MT; IB 19023, Alegres, RJ; IB 20770, 20785, Aparecida do Norte, SP; IB 13868, 15683, 15684, Aquidauana, MT; ZUEC 1032, Araçatuba, SP; IB 30830, Assis, SP; IB 29696, Atibaia, SP; IB 14285, Agachi, MT; IB 16919, Aguapeí, SP; IB 22799, Agulhas Negras, RJ; IB 19921, 19922, Alberto Torres, RJ; IB 4630, Albuquerque Caraguatá, MT; IB 21619, Altinópolis, SP; IB 13864, 13867, Antônio Carlos, MG; IB 6222, 13856, 16735, 16988, 19394, 19593, Aquidauana, MT; IB 20470, 30112, 30223, Araguaia, ES; ZUEC 1676 Araraquara, SP; IB 5631, 12317, Arapuá, MT; IB 17717, Avelar, RJ; IB 22925, Baixo Grandeí, ES; IB 19466, 23217, Balsa Nova, PR; IB 27928, Barra da Tijuca, RJ; IB 9814, 13866, Barra Mansa, RJ; IB 54268, Barro Alto, GO; IB 16769, 18861, Bodoquena, MT; IB 22658, Botucatu, SP; ZUEC 1322, Bragança Paulista, SP; IB 28500, Cabo Frio, RJ; IB 19717, Cabeceira do Apá, MT; IB 22911, 22912, Caçapava, SP; IB 27280, Cáceres, MT; IB 21551, Cainá, SP; IB 27760, Camapuã, MT; IB 17321, 27763, ZUEC 535, Campinas, SP; ZUEC 100, 535, 1023, 1376, ZUEC 35, Campo Limpo-Jordanésia, SP; IB 25612, 25613, Campos, RJ; IB 26850, Cândido Mota, SP; IB 22790, Colatina, ES; IB 23688, 22985, Coronel Fabriciano, MG; IB 22789, Colatina, ES; IB 9791, Coluia, SP; IB 53855, Conceição do Castelo, ES; IB 22984, 23928, 23929, 23930, 23357, 23358, Coronel Fabriciano, MG; IB 7327, Correntes, MT; IB 7888, 8161, Corumbá, MT; IB 21606, Cotrin, MT; IB 27709, 27722, 27723, 27724, 27725, 27726, 28252, Cruzália, SP; IB 23809, Curitiba, PR; IB 13883, Demétrio Ribeiro, RJ; IB 27586, Dourado, MT; IB 53275, Dianópolis, TO; IB 50183, 50043, ES; ZUEC 99, Fazenda Rio das Pedras; IB 30831, Florínea, SP; IB 13862, Franco da Rocha, SP; IB 40007, Furnas; IB 9779, Galia, SP; IB 15419, Garça, SP; IB 15607, Garcia, MT; IB 50005, 50006, 50007, 50008, 50009, 50010, Guandú, ES; IB 30506, Guaragi (Palmeiras), PR; IB 14344, 25113, Guaicurus, MT; IB 11403, Guia Lopes, MT; IB 36485, 37806, 38115, Ilha Solteira, MT; IB 18305, Itajubá, MG; IB 21651, 22213, 22325, 22774, Jupiá (Três Lagoas), MT; ZUEC 130, Ilha da Sepultura – Rio Piracicaba, SP; IB

27484, 27485, Itacuruça, RJ; IB 22942, Itapira, ES; IB 7781, Jaraguá, MT; IB 24283, Jacarezinho, PR; IB 23164, Jacareí, SP; ZUEC 727, Jaguariúna, SP; IB 20858, Joaquim Távora, PR; IB 23353, Juiz de Fora, MG; IB 22774, Jupiá (Três Lagoas), MT; IB 21509, Jupiá (Três Lagoas), MT; IB 17081, Lima Duarte, SP; ZUEC 133, Louveira, SP; IB 13863, Novo Horizonte, SP; IB 726, Manguinhos, RJ; IB 27266, 30832, Maracai, SP; IB 15997, 19835, Maracaju, MT; IB 37477, Marília, SP; IB 20802, Miguel Pereira, RJ; IB 8365, Minas de Brejaúba, MG; IB 6133, Miranda, MT; IB 22999, Morro Agudo, SP; IB 18780, Muzambinho, SP; IB 15425, 15736, Ouro Fino, MG; IB 19391, IB 27727, Palmital, SP; IB 26843, Paraguaçu Paulista, SP; IB 27265, Pavão, SP; IB 15349, Pedro II, MG; IB 53960, Pereira Barreto (UHE Três Irmãos), SP; IB 17854, 19391, Pindamonhangaba, SP; ZUEC 130, Piracicaba, SP; IB 36996, 36997, 36998, Porto Itamaraty, MT; IB 19832, Ponta Porã, MT; IB 8281, Porto Esperança, MT; IB 26804, Porto Novo, MG; IB 22185, 57361, Ponta Grossa, PR; IB 20746, 20767, Pindamonhangaba, SP; IB 16943, Presidente Venceslau, SP; IB 26844, 27268, 27263, Rancharia, SP; IB Rancharia, SP; IB 31272, Represa Billings, SP; IB 21547, 23139, Resende, RJ; IB 16599, Ribas do Rio Pardo, MT; IB 7740, Ribeirão Claro, MT; IB 28224, Ribeirão Preto, SP; IB 15731, 15450, RJ; IB 43086, 43087, Rubinéia, SP; IB 50049, Santa

Cruz do Rio Pardo, SP; IB 16088, Santo Amaro, SP; ZUEC 471, Santo Antônio da Posse; IB 50001, São Gabriel da Palha, ES; IB 31035, Santos Dumont, MG; IB 23102, São Carlos, SP; IB 23314, São Joaquim da Barra, SP; IB 23320, 24493, 24994, São Domingos, ES; ZUEC 611, São João da Boa Vista, SP; IB 23001, 23002, 23043, São José dos Campos, SP; ZUEC 966, São José do Rio Pardo, SP; IB 50000, 50002, 50003, 50004, São Gabriel da Palha, ES; IB 25096, 25094, 25995, 25996, 25999, 25998, São Domingos, ES; IB São Domingos, ES; IB 48672, São Mateus, ES; ZUEC 131, São Miguel Paulista, SP; IB 12429, Sereno, MG; IB 9816, Simplício, MG; IB, 23143, 52602, Sorocaba, SP; IB 122, ZUEC 122, Sumaré, SP; IB 20768, 23629, 23691, Sossego, MG; IB 52513, Taubaté, SP; IB 17583, Tesouro, MT; IB 18433, Taboas, RJ; IB 6489, 14289, Taunay, MT; IB 26850, 27264, Tepê, SP; IB 9069, Tereus, MT; IB 27006, Tombos, RJ; IB 5970, Três Lagoas, MT; ZUEC 1099, Ubatuba, SP; IB 23044, Uberlândia, MG; IB 17588, Vale do Paraíba, SP; IB 28298, 28426, Valença, RJ; IB 43058, Vazante, MG; IB 20889, Viçosa, MG; IB 258, 10077, Volta Redonda, RJ; IB 23360, Valença, RJ; IB 15499, Vassouras, RJ; IB 27009, Vila de Santo Antônio de Pádua, RJ; IB 7667, 7815, Vitorino, MT; IB 15499, IB 259, Vargem Alegre, RJ; IB 52538; Vargem Grande Paulista – SP; Volta Redonda – RJ.