Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

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Version of record first published: 03 Aug 2012.

To cite this article: M.A. Nakano , R.M. Feitosa , C.O. Moraes , L.D.C. Adriano , E.P. Hengles , E.L. Longui & M.S.C. Morini (2012): Assembly of Myrmelachista Roger (Formicidae: Formicinae) in twigs fallen on the leaf litter of Brazilian Atlantic Forest, Journal of Natural History, 46:33-34, 2103-2115

To link to this article: http://dx.doi.org/10.1080/00222933.2012.707247

Journal of Natural History
Vol. 46, Nos. 33–34, September 2012, 2103–2115

Assembly of *Myrmelachista* Roger (Formicidae: Formicinae) in twigs fallen on the leaf litter of Brazilian Atlantic Forest

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(*Received 30 November 2011; final version received 25 June 2012; printed 13 September 2012*)

The nests of *Myrmelachista* are found in tree trunk cavities and branches. The biology of these arboreal ants is still relatively unknown. We investigated the nesting behaviour of this genus in fallen dry twigs in the Atlantic rainforest of southeastern Brazil. Physical characteristics of the nests, colony demographics, presence of breeders and ant worker sizes were recorded. Samples were collected weekly for 12 months, along open, sunny and undisturbed trails within forest remnants. In all, 202 nests were collected and six species were recorded. *Myrmelachista ruszkii* had the highest population of immatures and the greatest number of nests found. *Myrmelachista nodigera* had the smallest workers, was the least populous and the colony was housed in the finest branches. These results expand the current knowledge about the diversity and biology of *Myrmelachista* in the Brazilian Atlantic forest, and describe polydomic nests and competitive behaviour of *M. ruszkii.*

Keywords: arboreal ants; wood density; nesting; polydomic; dry twigs

Introduction

Arboreal ants are an important part of animal biomass and they interact with numerous plants and animals for food and shelter (Carroll and Janzen 1973; Haber et al. 1981; Hölldobler and Wilson 1990; Rico-Gray and Oliveira 2007). *Myrmelachista* Roger is considered an exclusively arboreal genus (Longino 2006) that is restricted to the Neotropical region (Kempf 1972; Fernández and Sendoya 2004), where most of the species of this genus nest in tree trunk cavities and in the branches of living trees (Stout 1979; Brown 2000; Longino 2006; Edwards et al. 2009). Few workers have been observed foraging on the surface of live-stem nesters (Longino 2006). These ants are believed to consume animal protein (Torres 1984; Amalin et al. 2001; McNett et al. 2010) and can be associated with species of Coccoidea and Pseudococcidae (Kusnezov 1951; Stout 1979; Ketterl et al. 2003; Longino 2006; McNett et al. 2010).

Data on the ecology and behaviour of species from this genus have been reported by Morawetz et al. (1992), Renner and Ricklefs (1998), Frederickson (2005, 2006), Fredrickson and Gordon (2009), Edwards et al. (2009) and McNett et al. (2010). Longino (2006) reviewed the biology of some of the species, specifically those found in Costa Rica. Species of *Myrmelachista* can be found in crops (Amalin and Pena

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ISSN 0022-2933 print/ISSN 1464-5262 online

http://dx.doi.org/10.1080/00222933.2012.707247
http://www.tandfonline.com

1999; Amalin et al. 2001; Philpott et al. 2006; Armbrecht and Gallego 2007), in several tree families (Frederickson 2005; Morini et al. 2006; Goitía and Jaffé 2009; McNett et al. 2010), or on bromeliad epiphytes (Bromeliaceae) (Rosumek et al. 2008). However, some species have been reported in the leaf litter of well-preserved forest areas (Lutinski et al. 2008; Pacheco et al. 2009; Suguituru et al. 2011) and urban parks (Morini et al. 2007) or inside small, dry fallen twigs among the leaf litter (Ketterl et al. 2003).

Detailed information on the reproductive biology and breeding strategies of *Myrmelachista*, as for most Neotropical ants (Del-Claro and Torezan-Silingardi 2009), is still scarce in the literature. The goal of this study was to investigate the presence of species from this genus in small fallen dry twigs in the leaf litter of the Brazilian Atlantic forest, regarding the structure of the nest and colony.

Materials and methods

Study area and sampling

The colonies were collected from three areas of the Brazilian Atlantic forest, located within the Alto Tietê hydrographic basin, São Paulo State (Brazil): Francisco Affonso de Mello Municipal Natural Park (23°31′22″ S, 46°11′16″ W; 807–1140 m altitude; in the municipality of Mogi das Cruzes); Barragem de Ponte Nova (23°31′85″ S, 45°50′77″ W, 783 m altitude; in the municipality of Salesópolis); and Nascentes do Tietê State Park (23°34′19″ S, 45°44′10″ W; 1027 m altitude, in the municipality of Salesópolis) (Figure 1).

The ants were collected weekly for 12 months from random areas in the sampling sites, but always along open, sunny and undisturbed trails. The vegetation at the sampling sites consisted of 2–20-m tall trees with trunks with diameters of $\leq$ 20 cm at breast height (Tomasulo and Cordeiro 2000). The collection effort remained constant throughout the sampling period with respect to the number of field expeditions, length of stay ($\geq$ 4 hours), and number of collectors ($n = 3$). The collection was manual, and all of the 10–30-cm long dry twigs with ants that were found on the leaf litter surface were individually placed in plastic bags for later identification.

The small twigs with *Myrmelachista* nests were counted. The species of *Myrmelachista* were identified by comparison with specimens deposited in the reference collection of the Museum of Zoology, University of São Paulo (MZUSP). Vouchers were deposited in the collection of the Myrmecology Laboratory at the University of Mogi das Cruzes and the MZUSP.

Characterization and demographics of the nests

Using a digital caliper we measured the external and central cavity diameters of the twigs containing colonies of the most abundant species identified. Within the same nests, the immature ants (eggs, larvae and pupae) and workers were counted. The head capsule of the workers was measured using a micrometer ruler coupled to a stereoscopic microscope.

The apparent density of the wood was calculated using the hydrostatic balance method (Silveira et al. 1999; Longui et al. 2009) and the following equation:

$$\rho_{ap} = P_u / V_u$$

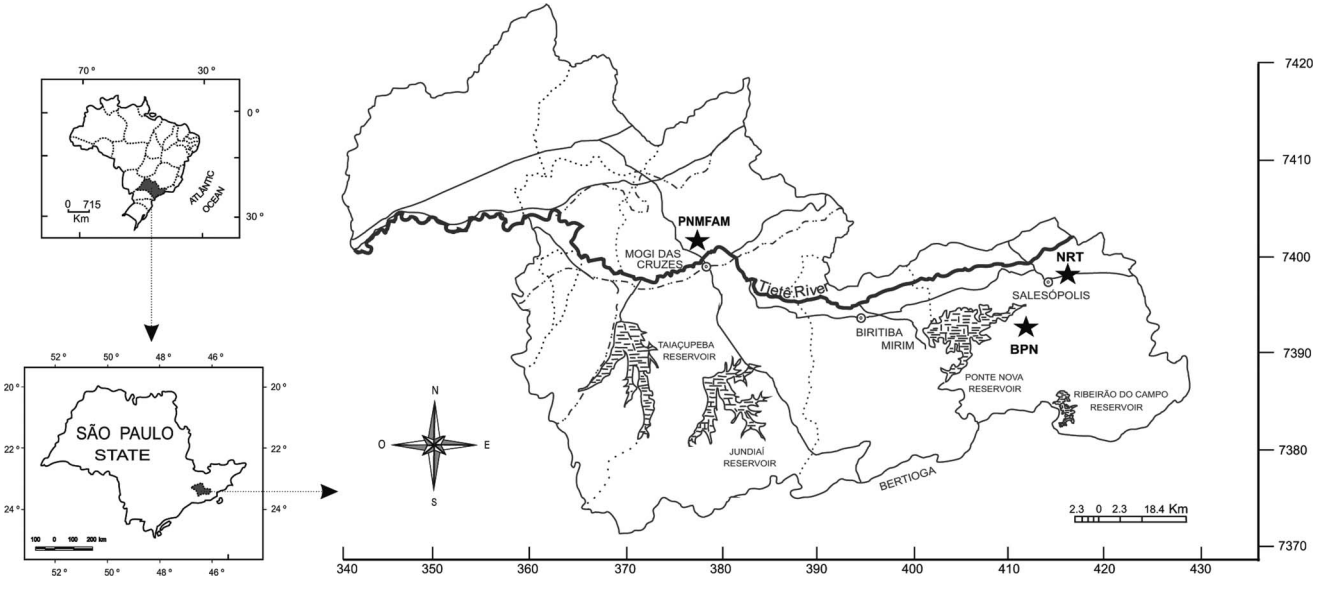

Figure 1. Sampling sites. The fragments of the Atlantic rainforest, where the study was conducted, are highlighted. PNMFAM: Francisco Affonso de Mello Natural Municipal Park; BPN: Barragem de Ponte Nova; NRT: Nascentes do Tietê State Park.

where ρ_{ap} is the bulk density (g/cm^3), P_u is the sample mass at a 15% moisture content (g), and V_u is the volume displaced by the sample, at a 15% moisture content (cm^3).

Data analysis

The total number of immature ants, workers and the mean head size were correlated with the diameters of the twig and the cavity where the colony was found using a Spearman correlation test. All analyses were preceded by the Lilliefors test to verify the data normality. Tests for differences in nest characteristics (the apparent density, twig diameter and diameter of the cavity where the colony was found) among the ant species were carried out using a Kruskal–Wallis and analysis of variance (ANOVA) test; the latter being performed when the distributions were normal. Means were compared by the Tukey test. The BIOESTAT 5.0 software (Ayres et al. 2007) was used for both of the tests, with a 5% significance level.

Results

Six species of *Myrmelachista* were recorded (Figure 2) in a total of 202 nests inside small dry, fallen twigs in the leaf litter. *Myrmelachista ruszkii* Forel (Figures 2, 3A,B) and *Myrmelachista catharinae* Mayr (Figures 2, 3C,D) had the most nests, followed by *Myrmelachista nodigera* Mayr (Figures 2, 3E,F). Only a single queen was in the nests of *M. ruszkii*, *M. catharinae* and *M. nodigera.* Winged ants were only observed in the *M. catharinae* and *M. ruszkii* nests, between February and September (Table 1, Figure 4A,B).

Colonies of *M. catharinae* are composed of between 13 and 1218 workers; *M. ruszkii* colonies comprise 6 to 519 workers and those of *M. nodigera* comprise 3 to 107 workers. *Myrmelachista ruszkii* had the highest average population of immature ants and, colonies of *M. nodigera* did not contain immature ants (Table 2. The total number of workers and immature ants was not correlated with the external and central cavity diameters of the twigs where the colony resided ($P > 0.05$), except in the case of *M. catharinae* (total number of workers × cavity diameter; rs = 0.47; $P < 0.05$).

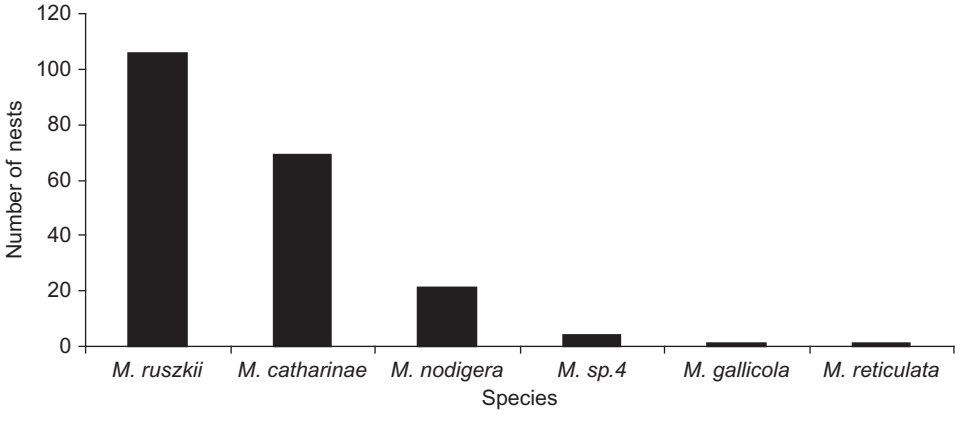

Figure 2. Total number of nests of each of the *Myrmelachista* species recorded in small fallen twigs in the leaf litter of the Atlantic Rainforest.

Table 1. Presence of *Myrmelachista* reproducers in small twigs, according to the months of the year.

Month	*Myrmelachista ruszkii*		*Myrmelachista catharinae*	
	Female	Male	Female	Male
January		x		x
February		x		x
March				
April				
May				
June				
July				
August				
September	x	x		
October	x	x		
November	x	x	x	x
December	x	x	x	x

Cephalic capsules were measured for 6548 workers (from 58 nests) of *M. ruszkii*, 4649 (from 25 nests) of *M. catharinae* and 237 (from four nests) of *M. nodigera* and measurements were 0.30–0.72 mm, 0.39–0.71 mm and 0.35–0.48 mm, respectively. The mean head sizes of *M. ruszkii*, *M. catharinae* and *M. nodigera* (Figure 5) were not correlated ($P > 0.05$) with the diameters of the twig and the cavity where the colony resided.

The diameters of the twigs inhabited by *Myrmelachista* differed among the three species (Kruskal–Wallis = 14.12, df = 2; $P < 0.05$). The twigs where *M. nodigera* were found were smaller than those inhabited by *M. ruszkii* ($Z = 3.37$; $P < 0.05$) and *M. catharinae* ($Z = 3.63$; $P < 0.5$). The diameter of the cavity where the colony resided also differed among the species (one-way ANOVA, $F_{2,93} = 3.2792$; $P < 0.05$), but only between *M. catharinae* and *M. nodigera* (Tukey = 3.2792; $P < 0.05$).

The density of the wood where the nest was formed did not differ among the ant species (one-way ANOVA, $F_{2,77} = 0.7265$; $P > 0.05$). The highest variation of the apparent density of the wood was observed in the twigs inhabited by *M. ruszkii* (Table 3).

Discussion

Myrmelachista is reported to be predominantly arboreal (Longino 2006) and specialized (Silvestre et al. 2003). External nests, as observed in *Azteca* (Fowler et al. 1996; Farias et al. 2010) and *Crematogaster torosa* Mayr, 1870 (Lanan et al. 2011), are possible though, because nests with immatures, workers, a queen and winged ants can be found inside small, dry twigs scattered among the leaf litter.

This microhabitat probably originated from trees near the site where the colonies resided that fell, bringing the eggs, larvae and adults to the ground. This hypothesis is corroborated by Ketterl et al. (2003), who noted the presence of three species

Figure 3. *Myrmelachista* nests in small twigs. (A, B) *Myrmelachista ruszkii*; (C, D) *Myrmelachista catharinae*; (E, F) *Myrmelachista nodigera*. (B, D, E) queens. Scale bar: 5 mm.

of *Myrmelachista* in *Araucaria angustifolia* (Bertol.) Kuntze in trees and fallen branches close by. In some species, such as silk-nesting *Camponotus*, the fall of an entire colony is frequent, especially during the rainy season (Santos and Del-Claro 2002).

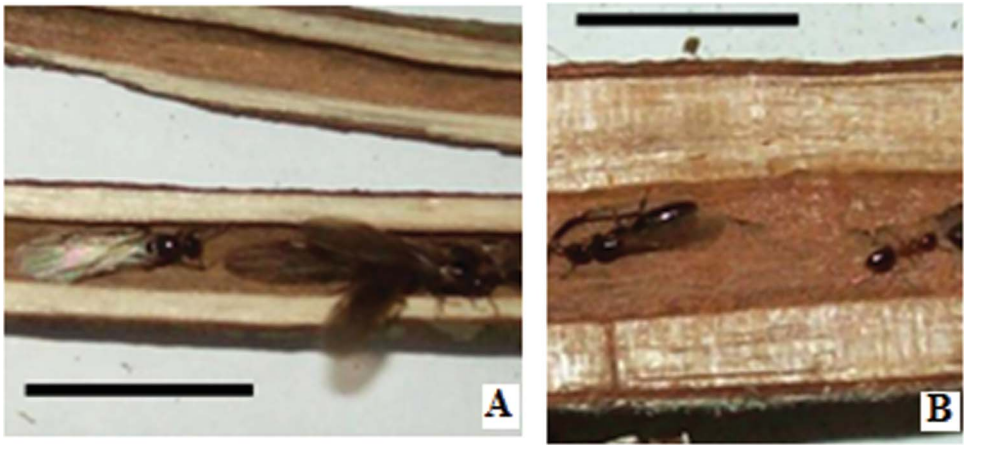

Figure 4. Breeding flight of *Myrmelachista*. (A) *Myrmelachista catharinae* male; (B) *Myrmelachista ruszkii* female. Scale bar: 1 cm.

Table 2. Demographic data for nests constructed in fallen twig in the leaf litter, according to species of *Myrmelachista*.

Taxon	Total no. of nests with workers	No. of workers		Total no. of nests with immature	No. of immature	
		Variation	Mean ± SD		Variation	Mean ± SD
M. ruszkii	58	6–519	111.53 ± 99.69	41	1–276	76.88 ± 71.23
M. catharinae	25	13–1218	263.08 ± 300.27	14	1–187	43.71 ± 47.49
M. nodigera	4	3–107	45.25 ± 44.75	–	–	–

Heavy rains in the region during early September (Minuzzi et al. 2007) may lead to increased tree falls and the death of entire colonies inhabiting the extremities of dry twigs (Nakano, personal observation). Because the increased rainfall is also an important stimulus for the synchronized release of winged ants (Torres et al. 2001; Santos and Del Claro 2009), it is possible that upon falling in the leaf litter, the colony already contains breeders as well as workers and immature ants. Hence, in the early spring, a colony is able to release breeders that will colonize other environments, increasing the dispersal of the colony.

The presence of arboreal ant colonies inside small twigs has also been reported by Carvalho and Vasconcelos (2002). However, the colony has a short residence time in this new habitat, ranging between 35 and 146 days, after which the colony moves, possibly because of a lack of resources or the wood decomposition (Byrne 1994).

Hence, for many arboreal ant species, small, fallen tree twigs in the leaf litter represent ephemeral homes or satellite nests containing workers and immature ants, as observed for *Crematogaster brasiliensis* Mayr (Carvalho and Vasconcelos 2002). The existence of satellite nests increases the chances of defending a given territory, protects the host plant, and increases the survival of the colony itself, which when concentrated in one place is at the greatest risk of predation (Hölldobler and Wilson 1990; Delabie

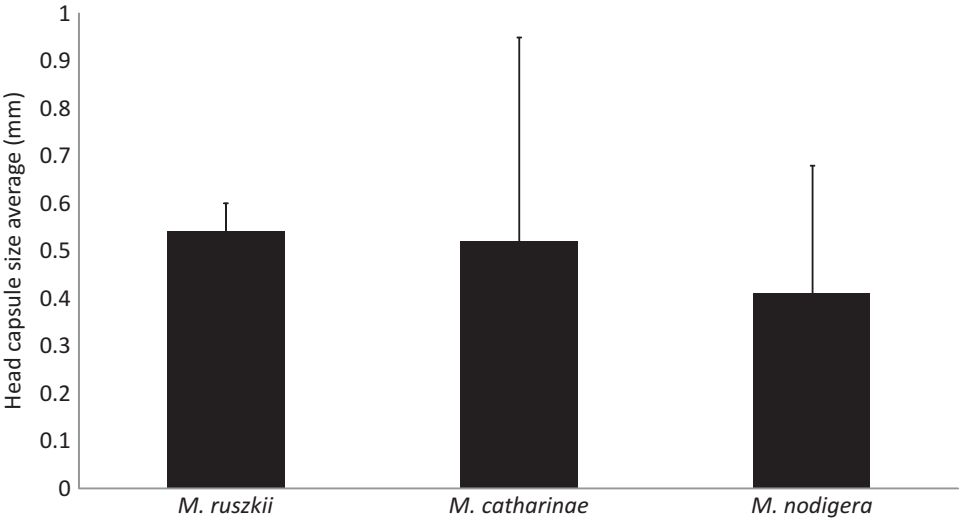

Figure 5. Head capsule size average (mm) of *Myrmelachista* workers found in dry twigs. Vertical bars represent standard deviations.

et al. 1991; Krebs and Davies 1993; Santos and Del-Claro 2002, 2009). This temporary nesting does not seem to be the case for *Myrmelachista* because one queen was recorded in the nests of *M. ruszkii*, *M. catharinae* and *M. nodigera* inside fallen twigs. Perhaps it was not possible to find the queen in other species because of difficulties in accessing the queen's location within the nest (Carvalho and Vasconcelos 2002).

The *Myrmelachista* species can be polydomic, where the queen is not always recorded (Lanan et al. 2011). Polydomy is relatively common among ants, occurring in over 150 species (Debout et al. 2007); in the litter of tropical forests about one third of the species are polydomic (Kaspari 1996a). The occurrence of polydomy may be a *Myrmelachista* strategy related to the occupation of new areas (Delabie et al. 1991), for food storage (Lanan et al. 2011), or increased foraging area (Santos and Del Claro 2009; Schmolke 2009). The nest is not centralized; the foraging can be done by workers who are in the periphery. Hence, the ability to forage is increased and the distance to be travelled by food to the feed source is reduced (Holway and Case 2000). This is particularly important for those species that exploit stable resources such as extrafloral nectar and insect honeydew (Pfeiffer and Linsenmair 1998) such as *Myrmelachista* (Silvestre et al. 2003; McNett et al. 2010). Despite these reasons, the causes of polydomia in ants are still uncertain (Lanan et al. 2011). The polydomy is also observed in polygynous species as *Crematogaster pygmae* Forel, 1904 (Quinet et al. 2009) and *Myrmelachista schumanni* (Frederickson 2005; Frederickson and Gordon 2007).

Hence, the record of *Myrmelachista* when using techniques for collecting hypogaeic ants (Pacheco et al. 2009; Suguituru et al. 2011) and epigaeic ants (Morini et al. 2007; Souza et al. 2012) may be a relatively common phenomenon, differing from the discussion made by Delabie et al. (2000) for species of *Nylanderia*, *Crematogaster*, and *Camponotus*, which are also arboreal.

The population and the workers found inside dry branches and twigs scattered among the leaf litter are relatively small because the space is limited (Hölldobler and

Table 3. Metric characterization of nests according to species of *Myrmelachista* and bulk density of the wood.

Taxon	Total no. of nests	Twig diameter (mm)		Central cavity diameter (mm)		Bulk density(g/cm^3)	
		Variation	Mean ± SD	Variation	Mean ± SD	Variation	Mean ± SD
M. ruszkii	53	3.78–19.23	9.13 ± 3.18	1.14–3.59	2.26 ± 0.55	0.24–1.40	0.50 ± 0.16
M. catharinae	32	4.50–50.80	11.02 ± 7.91	1.48–4.99	2.43 ± 0.70	0.17–0.73	0.53 ± 0.13
M. nodigera	11	4.21–8.44	6.26 ± 1.33	1.42–2.72	1.90 ± 0.44	0.33–0.69	0.48 ± 0.14

Wilson 1990). However, the colonies observed here, especially those of *M. catharinae* and *M. ruszkii*, were well populated. Similarly, Ketterl et al. (2003) recorded colonies with more than 1000 workers for one unidentified *Myrmelachista* species.

The smallest populations were observed in *M. nodigera* and their colonies were recorded in the finest branches. Using head capsule size as an indicator of body size (Kaspari 1993, 1996b; Weiser and Kaspari 2006), *M. nodigera* is the smallest among the three species. Moreover, *M. ruzkii*, *M. catharinae* and *M. nodigera* are similar regarding the type of wood in which the colonies are housed, even if the morphological attributes are different, especially those of *M. nodigera*.

The record of species and the description of a population's demographic data and characteristics of *Myrmelachista* nests are important because they fill the gap on the diversity and natural history of this taxon in the Atlantic rainforest of southeastern Brazil. This work also helps to establish the evidence in the literature about the richness of genera (Longino 2006). Hence, the result is very important for studies on diversity because many works performed on branches and trunks of fallen leaf litter in tropical forests (Byrne 1994; Delabie et al. 1997; Carvalho and Vasconcelos 2002; Pereira et al. 2007) do not report on *Myrmelachista* species.

Acknowledgements

The authors would like to thank the CNPq for the scholarships granted to the first two authors (grants 132485/2008-7 and 121175/2009-0) and to MSC Morini (grant 301151/2009-1), Prof. Dr CRF Brandão and Prof. Dr JHC Delabie for valuable suggestions, FAPESP for aid to RM Feitosa (grant 07/01310-2), FAEP for financial support, and SS Suguituru for preparing the map.

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