

# An overview of cytogenetics of the tribe Meliponini (Hymenoptera: Apidae)

Mara Garcia Tavares<sup>1</sup> · Denilce Meneses Lopes<sup>1</sup> · L. A. O. Campos<sup>1</sup>

Received: 24 October 2016 / Accepted: 1 March 2017 / Published online: 18 March 2017  
© Springer International Publishing Switzerland 2017

**Abstract** The present study provides a comprehensive review of cytogenetic data on Meliponini and their chromosomal evolution. The compiled data show that only 104 species of stingless bees, representing 32 of the 54 living genera have been studied cytogenetically and that among these species, it is possible to recognize three main groups with  $n=9$ , 15 and 17, respectively. The first group comprises the species of the genus *Melipona*, whereas karyotypes with  $n=15$  and  $n=17$  have been detected in species from different genera. Karyotypes with  $n=17$  are the most common among the Meliponini studied to date. Cytogenetic information on Meliponini also shows that although chromosome number, in general, is conserved among species of a certain genus, other aspects, such as chromosome morphology, quantity, distribution and composition of heterochromatin, may vary between them. This reinforces the fact that the variations observed in the karyotypes of different Meliponini groups cannot be explained by a single theory or a single type of structural change. In addition, we present a discussion about how these karyotype variations are related to the phylogenetic relationships among the different genera of this tribe.

**Keywords** Stingless bees · Chromosome number · Karyotype · Phylogeny · Evolution · Molecular cytogenetics

**Electronic supplementary material** The online version of this article (doi:10.1007/s10709-017-9961-2) contains supplementary material, which is available to authorized users.

✉ Mara Garcia Tavares  
mtavares@ufv.br

<sup>1</sup> Departamento de Biologia Geral, Universidade Federal de Viçosa, CEP: 36.570-000 Viçosa, Minas Gerais, Brazil

## Introduction

Stingless bees are important pollinators of native plants in tropical and subtropical regions of the world (Heard 1999). The number of stingless bees found in the Neotropics is high; 418 species have been described to date (Camargo and Pedro 2013; Pedro 2014). These species are grouped into 34 genera (including one that is extinct) (Camargo and Pedro 2013; Melo 2016). There are also 89 valid species grouped into 15 genera in the Indo-Malayan/Australasian region (Rasmussen 2008) and 19 species belonging to six genera in Africa (Eardley 2004). In Brazil, 244 species are found, distributed among 29 genera with valid names (Camargo and Pedro 2013; Pedro 2014).

Cytogenetic analysis can contribute greatly to the understanding of the types of chromosome changes that might have occurred during the differentiation of these species and how chromosome evolution occurred in the different taxa of this group. Cytogenetics also helps to solve questions related to systematics and the existence of morphologically cryptic species and species complexes in several groups of organisms (Crossa et al. 2002; Van Daele et al. 2004; Ravaoarimanana et al. 2004; Vicari et al. 2005; Rossi et al. 2005; Tinni et al. 2007; Maurício et al. 2012).

The first cytogenetic study on Meliponini was published by Kerr (1948), and since then, more than 100 species have been karyotyped. The first analyses were restricted to the description of chromosome numbers, but with the emergence of new techniques, it was possible to describe and compare the patterns of heterochromatin constitution (Rocha et al. 2002), distribution and localization of genes or regions (e.g., 18S rRNA, 5S rRNA) (Fernandes et al. 2011; Martins et al. 2013; Lopes et al. 2014) and whole chromosomes (Martins et al. 2013).

Some studies have pointed to some possible mechanisms generating karyotype changes within Meliponini. Kerr and Silveira (1972) proposed that polyploidy would be the main mechanism responsible for the karyotypic evolution of Meliponini, followed by subsequent changes in the chromosome number, such as Robertsonian rearrangements. In contrast, data published by Pompolo (1992), Rocha et al. (2003a, b) and Brito et al. (2005) suggested that the karyotype evolution of Meliponini follows the same cycle of changes proposed by the Minimum Interaction Theory (Imai et al. 1988; Imai 1991; Hoshiba and Imai 1993). According to this theory, karyotype evolution involved an increase in chromosome number by centric fission, resulting in a reduction of chromosome size and an increase of heterochromatic regions to stabilize the telomeres. This process would reduce the occurrence of deleterious chromosomal translocations (for details, see Imai 1991; Imai et al. 2001). In some species of the genus *Melipona*, however, there seems to have been an increase in heterochromatin content without fission having occurred (Rocha and Pompolo 1998; Rocha et al. 2007). This shows that despite the Minimum Interaction Theory being widely used to explain karyotype evolution in Meliponini, different mechanisms are probably involved in this process, which requires a more detailed analysis of the information available.

The last review on cytogenetic data in Meliponini was performed by Rocha et al. (2003a), and this has been used as reference in several works. However, since its publication, several species have been analysed cytogenetically, and studies on phylogenetic relationships in Meliponini in general (Rasmussen and Cameron 2010) and some genera in particular (Ramirez et al. 2010; Rasmussen and Cameron 2007) have been published, allowing a new evaluation and the development of hypotheses about the evolution of the karyotype of Meliponini. Thus, we see the need to re-evaluate the available cytogenetic data, focusing mainly on the chromosome number variation and its distribution in this tribe.

## Materials and methods

Information on the chromosome number of different species of stingless bees presented in this review was obtained by consulting the papers published in specialized journals, theses and/or dissertations and abstracts presented at scientific events (Table 1). Thus, all described karyotypes, even those presenting different chromosome numbers were included. It is noteworthy, however, that when the same data were presented at any event and subsequently published in specialized magazines, sometimes we chose to include only the published work, especially when the

summary did not carry information about the geographical location of the samples analysed.

The nomenclature used for the species was based on the proposals of Camargo and Pedro (2013) for the Brazilian species, Rasmussen (2008) for the Indo-Malayan/Australasian species and Eardley (2004) for the African species. Thus, we present a synonymy table (Table S1) to allow comparisons with the original work and make information more clear and accurate.

It is noteworthy that many of the data described in Table 1 were obtained from studies conducted in the 1950s, 1960s and 1970s, using the squashing cytogenetic technique available at the time. This may explain the discrepancies observed when comparing such results with the most current data, when some of these species were reanalysed using more refined techniques for the preparation of slides (Rocha et al. 2003a; Oliveira et al. 2013). In such cases, in the present study discussion (when there was no evidence that the differences were due to the study of different populations, the occurrence of B chromosomes or chromosome polymorphisms), we considered the chromosome number obtained in the most recent work due to better definition of the number and morphology of chromosomes provided by the techniques used. Additionally, when the published work only provided the species haploid or diploid number, double or half were assumed, respectively, as the complementary values, in the discussion.

We also stress that many times, in older works, the authors only made reference to previous analyses, without reanalysing the species and therefore, only the original work was considered. In addition, species cited as *sp.*, i.e., without species-specific identification, were not included in Table 1, except for one *Trigonisca* species, which was the only species of this genus analysed cytogenetically until now. When a species with a doubtful identification presented a different chromosome number of other species of its genus (as in the case of one *Trigona* with 32 chromosomes), it was only reported in the text.

On the other hand, it must be considered that there are specific names that are possibly being used for a group of sibling species, such as *Frieseomelitta varia*, *Scaptotrigona postica* and *Tetragonisca angustula* (Camargo and Pedro 2013). This can also occur with other widely distributed groups, such as *Plebeia droryana*.

## Results and discussion

### Karyotype diversity in Meliponini

The compiled data show that only 104 species of stingless bees (19.77% of the species described to date), representing 32 of the 54 living genera (59.26%) have been studied

**Table 1** Overview of the karyotypic data described for Meliponini species

Species	Origin	n, 2n	References
<i>Austrolebeia australis</i> <sup>b</sup> (Friese, 1898)	Sydney (Australia)	2n = 36	Travanzoli et al. (2015)
<i>Camargoia nordestina</i> Camargo, 1996	Brejo da Conceição (PI)	2n = 34	Rocha et al. (2003a)
<i>Celetrigona longicornis</i> (Friese, 1903)	Barra do Garças (MT)	n = 15	Silveira (1971)
	Nova Xavantina (MT)	n = 15	Tarelho (1973)
<i>Cephalotrigona capitata</i> (Smith, 1854)	Piranga (MG)	2n = 30	Maurício et al. (2012)
<i>Cephalotrigona femorata</i> (Smith, 1854)	Urbano Santos (MA)	2n = 34	Rocha et al. (2003a)
<i>Cleptotrigona cubiceps</i> <sup>a</sup> (Friese, 1912)	Zango and Luanda (Angola)	2n = 34	Miranda et al. (2013)
<i>Dactylurina staudingeri</i> <sup>a</sup> (Gribodo, 1893)	Ilonga (Tanzania)	n = 18	Kerr and Araújo (1957)
<i>Duckeola ghilianii</i> (Spinola, 1853)		n = 17	Kerr (1969, 1972)
	Manaus (AM)	n = 15	Kerr (1969)
<i>Friesella schrottkyi</i> (Friese, 1900)	Ribeirão Preto (SP)	n = 15	Kerr (1972)
		n = 18	Tarelho (1973)
		2n = 34	Pompolo (1992)
		n = 17	Mampumbu (2002)
<i>Friesoemelitta dispar</i> (Moure, 1950)	Viçosa, Paula Candido, Guaraciaba (MG) and Anchieta (ES)	2n = 34	
	Ilhéus (BA)	n = 15	Carvalho and Costa (2011)
		2n = 30	
<i>Friesoemelitta doederleini</i> (Friese, 1900)	Jequié (BA)	2n = 30	Rodrigues et al. (2012)
	Três Lagoas (MT)	n = 15	Tarelho (1973)
	Santana do Seridó (RN)	2n = 30	Rocha et al. (2003a)
	Sudoeste Bahia (BA)	2n = 30	Waldschmidt et al. (2005)
	Urbano Santos (MA)	n = 15	Elizeu et al. (2013)
		2n = 30	
<i>Friesoemelitta francoi</i> (Moure, 1946)	Cairu (BA)	n = 15	Carvalho and Costa (2011)
		2n = 30	
<i>Friesoemelitta languida</i> Moure, 1990	Jequié (BA)	2n = 30	Rodrigues et al. (2012)
<i>Friesoemelitta trichoceratta</i> Moure, 1990	Divinópolis (MG)	2n = 30	Rocha et al. (2003a)
<i>Friesoemelitta varia</i> (Lepelletier, 1836)	Tangará da Serra (MT)	2n = 30	Nascimento (2005)
	Ribeirão Preto (SP)	n = 15	Kerr (1969)
	Divinópolis (MG)	n = 15	Tarelho (1973)
<i>Geotrigona mombuca</i> (Smith, 1863)	Ribeirão Preto (SP)	2n = 30	Rocha et al. (2003a)
	Ribeirão Preto (SP)	2n = 30	Pompolo (1992)
	Ribeirão Preto (SP)	n = 15	Rocha et al. (2003a)
<i>Geotrigona subterranea</i> (Friese, 1901)		n = 17	Kerr and Silveira (1972) <sup>c</sup>
<i>Hypotrigona gribodoi</i> <sup>a</sup> (Magretti, 1884)	Massinga (Moçambique) and Luanda (Angola)	n = 13 to 15	Kerr (1969)
		n = 14	Kerr (1972)
		n = 14 or 15	Kerr and Silveira (1972)

Table 1 (continued)

Species	Origin	n, 2n	References
<i>Lestrimelitta limao</i> (Smith, 1863)	Aragarças (GO) Divinópolis (MG)	n = 14 n = 14 2n = 28	Silveira (1971) Tarelho (1973) Rocha et al. (2003a)
<i>Leurotrigona muelleri</i> (Friese, 1900)	Araxá (MG)	n = 8 n = 8	Kerr (1969) Tarelho (1973)
	Senador Mourão (MG), Cajuru (SP) and Itacajá (TO)	2n = 16 n = 8 2n = 16	Pompolo (1992, 1994) Pompolo and Campos (1995)
<i>Leurotrigona pusilla</i> Moure and Camargo, 1988 in Moure et al. 1988	Manaus (AM)	2n = 30 2n = 30	Pompolo (1992, 1994) Pompolo and Campos (1995)
<i>Melipona (Eomelipona) asilvai</i> Moure, 1971	Manaus (AM)	2n = 30	Pompolo (1992)
	Pedra de Maria da Cruz (MG)	2n = 18	Rocha and Pompolo (1998)
	Santana do Seridó (RN) and Pedra de Maria da Cruz (MG)	n = 9 2n = 18	Rocha et al. (2002)
	Sudoeste da Bahia (BA)	2n = 18	Waldschmidt et al. (2005)
<i>Melipona (Eomelipona) bicolor bicolor</i> (Lepeletier, 1836)	Viçosa (MG)	2n = 18	Pompolo (1992)
	Caeté (MG) and Cunha (SP)	n = 9 2n = 18	Rocha and Pompolo (1998)
<i>Melipona (Eomelipona) bicolor schencki</i> Gribodo, 1893		n = 9 2n = 18	Rocha et al. (2002) Kerr (1948)
<i>Melipona (Eomelipona) marginata marginata</i> Lepeletier, 1836		2n = 18 n = 9	Kerr (1948) Kerr (1969)
	Caeté (MG)	2n = 18	Pompolo (1992)
	Caeté (MG)	2n = 18	Rocha and Pompolo (1998)
	Altamira (PA)	n = 9 2n = 18	Rocha et al. (2002)
<i>Melipona (Eomelipona) puncticolis</i> Friese, 1902		2n = 18	Silva et al. (2013a, b)
<i>Melipona (Melikerria) fasciculata</i> Smith, 1854	São Luiz (MA)	2n = 18	Kerr (1952)
	Urbano Santos (MA)	n = 9 n = 9 2n = 18	Kerr (1969) Rocha et al. (2002)
	Manaus (AM)	n = 9 2n = 18	Lopes et al. (2011b)
<i>Melipona (Melikerria) interrupta</i> Latreille, 1811		n = 9	Kerr (1969)
		n = 9	Kerr (1972)

Table 1 (continued)

Species	Origin	n, 2n	References
<i>Melipona (Melikerrria) quinquefasciata</i> Lepelletier, 1836	Cristalina (GO)	n = 18 n = 18 2n = 20 n = 9 + Bs 2n = 18 + Bs 2n = 18 + Bs	Kerr (1969) Kerr (1972) Pompolo (1992) Rocha (2002)
<i>Melipona (Melipona) favosa</i> (Fabricius, 1798)	Brasília (DF), Luizânia (GO) Bicas and Januária (MG) Suriname (referred as Surinum)	n = 9 2n = 18 n = 9 2n = 18 n = 9 2n = 18	Silva et al. (2013a, b) Hoshiba (1988) Hoshiba and Imai (1993)
<i>Melipona (Melipona) mandacaiia</i> Smith, 1863	Irecê (BA)	n = 9 2n = 18	Rocha et al. (2003b)
<i>Melipona (Melipona) orbigny</i> (Guérin, 1844)		n = 9 2n = 18	Rocha et al. (2007)
<i>Melipona (Melipona) quadrifasciata anthidioides</i> Lepelletier, 1836	Santana de Parnaíba (SP) Bocaina (MG) Pocinhos do Rio Verde (MG) Viçosa (MG)	n = 9 n = 9 2n = 18 n = 9 2n = 18	Kerr (1948) Kerr (1972) Tarelho (1973) Tambasco et al. (1979) Pompolo (1992) Rocha and Pompolo (1998)
<i>Melipona (Melipona) subnitida</i> Ducke, 1910	Caeté and Viçosa (MG) Brejo Grande (SE) Mossoró (RN) Santana do Seridó (RN)	n = 9 2n = 18 n = 9 2n = 18 n = 9 2n = 18	Rocha et al. (2002) Silva et al. (2012) Silveira (1971) Kerr (1972) and Tarelho (1973) Rocha et al. (2002)
<i>Melipona (Michmelia) capixaba</i> Moure and Camargo, 1994	Venda Nova do Imigrante (ES)	n = 9 2n = 18 n = 9 2n = 18	Rocha and Pompolo (1998) Rocha et al. (2002)
<i>Melipona (Michmelia) capiosa</i> Moure, 1962	Venda Nova do Imigrante (ES)	2n = 18	Rocha and Pompolo (1998)
<i>Melipona (Michmelia) crinita</i> Moure and Kerr, 1950	Rio Branco (AC) Rio Branco (AC)	n = 9 2n = 18	Rocha et al. (2002)
<i>Melipona (Michmelia) flavolineata</i> Friese, 1900	Urbano Santos (MA) Maranhão (MA)	n = 9 2n = 18 n = 9 2n = 18	Lopes et al. (2011b) Silva et al. (2007)

Table 1 (continued)

Species	Origin	n, 2n	References
<i>Melipona (Michmelia) fuliginosa</i> Lepeletier, 1836	Urbano Santos (MA)	n=9 2n=18	Lopes et al. (2011b)
<i>Melipona (Michmelia) fuscopilosa</i> Moure and Kerr, 1950	Rio Branco (AC)	n=9 2n=18	Rocha and Pompolo (1998) Rocha et al. (2002)
<i>Melipona (Michmelia) mondury</i> Smith 1863	Diogo Vasconcelos, Rio Vermelho, Itamarandiba (MG) and Rio Bonito (RJ)	n=9 2n=18	Lopes et al. (2008)
<i>Melipona (Michmelia) paraensis</i> Ducke, 1916	Altamira (PA)	2n=18	Cassinela et al. (2013)
<i>Melipona (Michmelia) rufiventris</i> Lepeletier, 1836	Cajuru (SP) Guimarães (MG)	n=9 n=9 2n=18+B	Kerr (1948) Tarelho (1973) Lopes et al. (2008)
<i>Melipona (Michmelia) scutellaris</i> Latreille, 1811	Lençóis (BA) Lençóis (BA)	n=9 2n=18	Almeida (1981) Pompolo (1994)
<i>Melipona (Michmelia) seminigra merrillae</i> Cockrell, 1919	Manaus (AM)	2n=18	Rocha and Pompolo (1998)
<i>Melipona (Michmelia) seminigra pernigra</i> Moure and Kerr, 1950	Altamira (PA)	n=9 2n=18	Rocha et al. (2002)
<i>Meliponula (Axestotrigona) ferruginea</i> (Lepeletier, 1836)	Zango and Luanda (Angola)	n=11 2n=22	Francini et al. (2011)
<i>Meliponula<sup>a</sup> (Meliplebeia) becarii</i> (Gribodo, 1879)	Massinga (Moçambique)	2n=22	Silva et al. (2014)
<i>Meliponula (Meliponula) bocandei</i> (Spinola, 1851)	Dande (Angola)	n=18	Kerr and Araújo (1957)
<i>Moureia caerulea</i> (Friese, 1900)	Canguçú (RS)	n=17	Kerr (1969)
<i>Nannotrigona punctata</i> (Smith, 1854)	Altamira (PA)	n=17	Kerr (1972)
<i>Nannotrigona testaceicornis</i> (Lepeletier, 1836)	Ribeirão Preto (SP)	n=18	Kerr and Araújo (1957)
		2n=34	Rocha et al. (2003a)
		2n=34	Godoy et al. (2014)
		n=18	Kerr (1969)
		n=17	Tarelho (1973)
		2n=34	Pompolo (1992)
		2n=34	Hoshiba and Imai (1993)
		2n=34	Rocha et al. (2003a)
		2n=34	Krinski et al. (2010)
<i>Oxytrigona cf. flaveola</i> (Friese, 1900)		n=17	Kerr (1969)
<i>Oxytrigona tataira</i> (Smith, 1836)	Presidente Venceslau (SP) Napo (Equador) Pichincha (Equador)	n=17 n=17 2n=32	Kerr (1972) Bravo and Arcos (1991) Bravo and Arcos (1991)
<i>Parapatamona brevopilosa</i> (Schwarz, 1948)		n=16	
<i>Parapatamona zonata</i> (Smith, 1854)		2n=32	

Table 1 (continued)

Species	Origin	n, 2n	References
<i>Paratrigona incerta</i> Camargo and Moure, 1994		2n = 34	Duarte et al. (2005)
<i>Paratrigona subnuda</i> Moure, 1947	Curitiba (PR)	n = 18	Kerr (1969)
		n = 18	Kerr (1972)
		2n = 34	Pompolo (1992)
	Ribeirão Preto (SP)	2n = 34	Rocha et al. (2003a)
	Aragarças (GO)	n = 17	Tarelho (1973)
<i>Partamona ailyae</i> Camargo, 1980	Nova Xavantina (MT)	n = 17	Brito-Ribon et al. (1999)
		2n = 34	
<i>Partamona chapadicola</i> Pedro and Camargo, 2003	Urbano Santos (MA)	n = 17	Lopes et al. (2011a)
		2n = 34	Miranda (2012)
	Urbano Santos (MA)	2n = 34	Fernandes et al. (2012)
<i>Partamona cupira</i> (Smith, 1863)	Guimarânia (MG)	2n = 34 + B	Marthe et al. (2010)
<i>Partamona helleri</i> (Friese, 1900)	Ribeirão Preto (SP)	n = 17	Tarelho (1973)
	Viçosa (MG)	2n = 34 + Bs	Pompolo (1992)
		2n = 34 + Bs	Pompolo (1994)
	Viçosa, São Miguel do Anta and Guaraciaba (MG)	n = 17 + B	Costa et al. (1992)
		2n = 34 + Bs	
	Viçosa, São Miguel do Anta, Guaraciaba and Juiz de Fora (MG)	n = 17	Brito et al. (1997)
		2n = 34 + Bs	
	Viçosa, São Miguel do Anta, Argirita and Porto Firme (MG)	2n = 34 + Bs	Brito (1998) Brito et al. (2005)
	Porto Firme and Viçosa (MG)	2n = 34 + Bs	Tosta et al. (2004)
	Pedra do Anta and São Miguel do Anta (MG)	2n = 34 + Bs	Tosta et al. (2014)
	Camaçari, Salvador, Valença, Cravolândia, Cruz das Almas e Itacaré (BA); Viçosa (MG); Ribeirão Preto and Rio Claro (SP)	n = 17 + Bs	Martins (2008)
	Cravolândia and Jequié (BA)	2n = 34 + Bs	
		n = 17 + B	Martins et al. (2009)
		2n = 34 + B	
	Viçosa (MG)	2n = 34 + B	Martins et al. (2013)
	Cruz das Almas and Itacaré (BA); Santa Tereza (ES)	n = 17 + Bs	Martins et al. (2014)
		2n = 34 + Bs	
<i>Partamona mulata</i> Moure, 1980 in Camargo, 1980	Cuiabá (MT)	n = 17	Brito-Ribon et al. (1999)
		2n = 34	
<i>Partamona nhambiquara</i> Pedro and Camargo, 2003	Nova Xavantina (MT)	n = 17	Brito-Ribon et al. (1999)
		2n = 34	
	Tangará da Serra (MT)	n = 17	Lopes et al. (2011a)
		2n = 34	Miranda (2012)
<i>Partamona peckoliti</i> (Friese, 1901)	Cotopaxi (Equador)	2n = 34	Brito et al. (2003)

Table 1 (continued)

Species	Origin	n, 2n	References
<i>Partamona rustica</i> Pedro and Camargo, 2003	Itaberaba and Iaçú (BA)	n = 17 2n = 34	Martins (2008)
	Lontra (MG)	n = 17 2n = 34	Miranda (2012) Lopes et al. (2012)
<i>Partamona seridoensis</i> (Pedro e Camargo, 2003)	Januária and Lontra (MG) Sant'Ana do Seridó (RN)	2n = 34 + Bs n = 17 2n = 34	Tosta et al. (2014) Brito (1998) Brito et al. (2005)
<i>Partamona vicina</i> Camargo, 1980	Nova Xavantina (MT)	n = 17 2n = 34	Brito-Ribon et al. (1999)
<i>Partamona testacea</i> (Klug, 1807)	Santana de Parnaíba (SP)	n = 18	Kerr (1969)
<i>Plebeia droryana</i> (Friese, 1900)	Ribeirão Preto (SP)	n = 9 n = 18 n = 18 n = 18	Kerr (1952) Kerr (1969) Kerr (1972)
	Brasil	n = 18 2n = 34	Tarelho (1973) Pompolo (1992)
	Ribeirão Preto (SP)	n = 17 2n = 34	Hoshiba and Imai (1993)
	Viçosa (MG), Anchieta (ES) and Porto Seguro (BA)	n = 17 2n = 34	Caixeiro (1996) Caixeiro (1999)
<i>Plebeia emerina</i> (Friese, 1900)	Curitiba (PR)	n = 18	Kerr (1969)
<i>Plebeia juliani</i> Moure, 1962	Ribeirão Preto (SP)	n = 18 n = 17 2n = 34	Kerr (1972) Caixeiro (1996)
<i>Plebeia lucii</i> Moure, 2004	Viçosa (MG)	n = 17 2n = 34	Caixeiro (1996)
<i>Plebeia phrynostoma</i> Moure, 2004	Viçosa (MG) Espírito Santo (ES)	2n = 34 2n = 34	Godoy et al. (2013) Ferreira et al. (2012)
<i>Plebeia remota</i> (Holmberg, 1903)	Curitiba (PR) Coimbra (MG) Curitiba (PR)	n = 18 n = 18 2n = 34 2n = 34	Godoy et al. (2013) Kerr (1969) Kerr (1972) Caixeiro (1996) Caixeiro (1999)
<i>Plebeina hildebrandti</i> <sup>a</sup> (Friese, 1903)	Moamba (Moçambique)	n = 18	Kerr (1969)
<i>Ptilotrigona lurida</i> (Smith, 1854)	Manaus (AM)	n = 18	Kerr (1972)
<i>Scaptotrigona barrocoloradensis</i> (Schwarz, 1951)	Brasil <sup>d</sup>	n = 11	Rocha et al. (2003a)
<i>Scaptotrigona bipunctata</i> (Lepelletier, 1836)	Altamira (PA)	2n = 34 2n = 34	Hoshiba and Imai (1993) Godoy et al. (2014)



**Table 1** (continued)

Species	Origin	n, 2n	References
<i>Scaptotrigona depilis</i> (Moure, 1942)	Ribeirão Preto (SP)	n = 17	Tarelho (1973)
	Ribeirão Preto (SP)	2n = 34	Rocha et al. (2003a)
<i>Scaptotrigona postica</i> (Latreille, 1807)	Aragarças (GO) and Piracicaba (SP)	n = 17	Tarelho (1973)
	Ribeirão Preto (SP)	2n = 34	Rocha et al. (2003a)
<i>Scaptotrigona tubiba</i> (Smith, 1863)	Sudoeste da Bahia (BA)	2n = 34	Duarte et al. (2005)
<i>Scaptotrigona xanthotricha</i> Moure, 1950	Piranga (MG)	2n = 34	Rocha et al. (2003a)
	Sudoeste Bahia (BA)	2n = 34	Waldschmidt et al. (2005)
	Valença and Camacan (BA), Viçosa (MG)	n = 17	Duarte et al. (2009)
		2n = 34	
<i>Scaura atlantica</i> Melo, 2004	Ilhéus (BA)	n = 17	Domingues et al. (2004)
		2n = 34	Domingues (2005)
<i>Scaura latitarsis</i> (Friese, 1900)	Ribeirão Preto (SP)	n = 17	Silveira (1972)
	Ribeirão Preto (SP)	n = 17	Tarelho (1973)
	Ribeirão Preto (SP)	2n = 34	Rocha et al. (2003a)
		n = 17	Domingues (2005)
		2n = 34	
<i>Scaura longula</i> (Lepeletier, 1836)	Luiziana (GO)	2n = 34	Domingues (2005)
<i>Schwarziana quadripunctata</i> (Lepeletier, 1836)	Pocinhos do Rio Verde (MG)	n = 16	Tarelho (1973)
		2n = 34	Pompolo (1992)
<i>Tetragona elongata</i> (Fabricius, 1804)	Viçosa (MG)	2n = 34	Rocha et al. (2003a)
	Cosmópolis (SP)	n = 17	Tarelho (1973)
	Viçosa (MG)	2n = 34	Rocha et al. (2003a)
<i>Tetragona dorsalis</i> (Smith, 1854)		n = 18	Kerr (1969)
	Altamira (PA)	2n = 34	Oliveira et al. (2013)
<i>Tetragona quadrangula</i> (Lepeletier, 1836)		n = 17	Silveira (1971)
	Aragarças (GO) and Pitangueiras (SP)	n = 17	Tarelho (1973)
<i>Tetragona truncata</i> Moure, 1971	Aragarças (GO)	n = 17	Tarelho (1973)
<i>Tetragonisca angustula</i> (Latreille, 1811)	Ribeirão Preto (SP)	n = 17	Tarelho (1973)
		2n = 34	Pompolo (1992)
	Brasil	2n = 34	Hoshiba and Imai (1993)
	Viçosa (MG)	2n = 34	Rocha et al. (2003a)
	Redenção (PA)	2n = 34	Fernandes et al. (2011)
	Tangará da Serra (MT)	n = 17	Barth et al. (2011)
		2n = 34	
<i>Tetragonisca fiebrigi</i> (Schwarz, 1938)	Tangará da Serra (MT)	n = 17 + B	Barth et al. (2011)
<i>Tetragonula minangkabai</i> <sup>b</sup> (Sakagami and Inoue, 1985)	Brasil <sup>d</sup>	2n = 34 + Bs	Hoshiba and Imai (1993)
		n = 20	
		2n = 40	

Table 1 (continued)

Species	Origin	n, 2n	References
<i>Trigona branneri</i> Cockerell, 1912	Cuiabá (MT)	n = 17 2n = 34	Costa et al. (2004)
<i>Trigona chanchamayoensis</i> (Schwarz, 1948)	Cuiabá (MT)	n = 17 2n = 34	Costa et al. (2004)
<i>Trigona cilipes</i> (Fabricius, 1804)		n = 17 2n = 34	Barth et al. (2005)
<i>Trigona fuscipennis</i> (Friese, 1900)	Ribeirão Preto (SP)	n = 18	Kerr (1969)
<i>Trigona hyalinata</i> (Lepeletier, 1836)	Sudoeste Bahia (BA) Cuiabá (MT)	n = 17 2n = 34	Tarelho (1973) Waldschmidt et al. (2005) Costa et al. (2004)
<i>Trigona hypogea</i> Silvestri, 1902	Altamira (PA)	2n = 34	Ferreira (2015)
<i>Trigona pallens</i> (Fabricius, 1798)	Altamira (PA)	2n = 34	Ferreira (2015)
<i>Trigona recursa</i> Smith, 1863	Aragarças (GO) Luislândia (MG) Cuiabá (MT)	n = 17 n = 17 2n = 34 n = 17 2n = 34	Silveira (1972) Tarelho (1973) Rocha et al. (2003a) Costa et al. (2004)
<i>Trigona spinipes</i> (Fabricius, 1793)		n = 18 <sup>e</sup> n = 17	Kerr (1969) Tarelho (1973)
<i>Trigona truculenta</i> Almeida, 1984	Ribeirão Preto (SP) and Viçosa (MG)	2n = 34	Rocha et al. (2003a)
<i>Trigona williana</i> Friese, 1900	Altamira (PA)	2n = 34	Ferreira (2015)
<i>Trigonisca</i> sp. Moure, 1950	Urbano Santos (MA)	2n = 34	Ferreira (2015)
		2n = 30	Lopes (personal communication)

<sup>a</sup>Afrotropical species<sup>b</sup>Indo-Malayan/Australasian species<sup>c</sup>Kerr and Silveira (1972) mention that Silveira and Kerr (1971, unpublished) analyzed the karyotype of *Geotrigona subterranea*. However, the 1971 paper was not found in the literature<sup>d</sup>Although cited as “from Brazil”, these species does not exist in this Country<sup>e</sup>Cited as originally presented in the reference manuscript

cytogenetically. Despite this restriction, a detailed analysis of Table 1 shows that the haploid chromosome number of Meliponini ranges from  $n=8$  to  $n=20$ , and it is possible to recognize three main groups, with  $n=9$ , 15 and 17.

The first group comprises the species of the genus *Melipona*. Among the 74 described species (Camargo and Pedro 2013), 23 were analysed cytogenetically. Of these, 22 species have the chromosome number of  $n=9$  ( $2n=18$ ), while the two subspecies of *Melipona seminigra* (*M. seminigra merrillae* and *M. seminigra pernigra*) have karyotypes consisting of 22 chromosomes in the normal complement (Francini et al. 2011; Silva et al. 2014). Other numerical chromosomal variations were found in *Melipona rufiventris* and *Melipona quinquefasciata*, but in these cases, the changes were due to the presence of B chromosomes (see below). It is also noteworthy that the chromosome number of  $n=9$  was not found in any of the other genera analysed to date.

Karyotypes with  $n=15$ , in turn, have been detected in 11 species belonging to the genera *Celetrigona* (01 species), *Duckeola* (01), *Frieseomelitta* (06), *Geotrigona* (one of the two species examined), *Leurotrigona* (one of the two species analysed) and *Trigonisca* (01). Considering these genera, *Celetrigona*, *Trigonisca* and *Leurotrigona* are species that belong to the same clade (*Trigonisca*) in the phylogeny proposed by Rasmussen and Cameron (2010). *Duckeola* and *Frieseomelitta* are also close to each other but phylogenetically distant from the *Trigonisca* clade (Rasmussen and Cameron 2010). *Geotrigona*, in turn, has no close phylogenetic relationships with any of the genera referred to above, which suggests that the chromosome number of  $n=15$  appeared several times, independently in the evolution of Meliponini. Worth noting are the case of two species of *Leurotrigona*, *Leurotrigona muelleri* and *Leurotrigona pusilla*, with  $n=8$  and 15 chromosomes, respectively, and that the two species of *Geotrigona* already karyotyped also have different chromosome numbers, being  $n=15$  (*Geotrigona mombuca*) and  $n=17$  (*Geotrigona subterranea*).

Moreover, karyotypes with  $n=17$  ( $2n=34$ ) have already been verified in species of *Camargoia*, *Cephalotrigona*, *Dactylurina*, *Friesella*, *Geotrigona*, *Meliponula* (one of the three species analysed), *Mourela*, *Nannotrigona*, *Oxytrigona*, *Paratrigona*, *Partamona*, *Plebeia*, *Scaptotrigona*, *Scaura*, *Schwarziana*, *Tetragona*, *Tetragonisca* and *Trigona*. In all, 54 species have this chromosome number which, as already observed by Rocha et al. (2003a), is the most common in the Meliponini studied to date.

Regarding chromosome number, three other genera, not phylogenetically related, should be highlighted, *Lestrimelitta* (Neotropical), *Hypotrigona* (Afrotropical) and *Tetragonula* (Indo-Malayan/Australasian). Whereas in *Lestrimelitta*, data indicate a haploid number of 14

chromosomes, the analyses conducted by Kerr (1969, 1972) and Kerr and Silveira (1972) in *Hypotrigona* are unclear, indicating a range between 13 and 15 chromosomes. So, if  $n=14$  is the chromosome number of *Hypotrigona*, this feature also appeared more than once in the evolution of Meliponini. The genus *Tetragonula*, in turn, deserves to be mentioned because it presents  $n=20$  chromosomes, the largest haploid chromosome number ever recorded between Meliponini.

Cytogenetic information on Meliponini (Table 1) also shows that, with few exceptions (previously mentioned), chromosome number is constant within a genus. For *Partamona*, for example, the 11 already karyotyped species have  $2n=34$  chromosomes and the same happens for 23 of the 24 *Melipona* species (as discussed above). Such a numerical constant has also been observed in *Frieseomelitta*, *Plebeia*, *Scaptotrigona*, *Scaura*, *Tetragona* and *Trigona*, all with at least three species analysed cytogenetically.

In this respect, numerical variations caused by the presence of B chromosomes in Meliponini has attracted attention (Costa et al. 1992; Brito et al. 1997; Brito 1998; Martins et al. 2009, 2014; Barth et al. 2011; Silva et al. 2013a, b) and for the study of these chromosomes, both classical and molecular cytogenetic techniques have been used (Costa et al. 1992; Tosta et al. 2004, 2007; Marthe et al. 2007; Martins et al. 2009, 2013, 2014; Barth et al. 2011; Correa et al. 2014).

The first report about the existence of B chromosomes in Meliponini was made by Costa et al. (1992) in *Partamona helleri*. Since then, analyses revealed the presence of up to 12 different B chromosomes in this species (Martins et al. 2014), and have demonstrated B distribution patterns that indicate the occurrence of geographical variation between populations (Martins et al. 2009). These analyses also showed that these chromosomes are usually heterochromatic and have many AT-rich sequences (Brilo et al. 1997, 2005; Brito-Ribon et al. 1999).

The combination of cytogenetic analyses with specific sequences of B chromosomes allowed the partial sequencing of a RAPD marker associated with the presence of these chromosomes in *P. helleri* (Tosta et al. 2004) and subsequently, the transformation of this into a SCAR marker (Tosta et al. 2007). Further analysis using the SCAR marker as a probe in dot-blot experiments, amplification of the SCAR marker and sequencing confirmed the presence of these chromosomes in *P. helleri* and *Partamona rustica* larvae and indicated their presence in adults of *Partamona cupira* and *Partamona criptica* (Tosta et al. 2014). With regard to *P. cupira*, the presence of B chromosomes had already been detected by Marthe et al. (2010) in some individuals from two colonies from Guimarães/Minas Gerais. These data show that the SCAR marker can facilitate the study of B chromosomes in this genus, because it

eliminates the need to work with larvae, which sometimes preclude analyses.

In addition, B chromosomes have also been identified in species of two other genera of stingless bees, *Melipona* and *Tetragonisca*. In populations of *M. quinquefasciata*, a variation of 0 to 4 B chromosomes between individuals of the same colony, as well as between individuals in different locations has been verified (Rocha 2002; Silva et al. 2013a, b). Lopes et al. (2008), in turn, described the presence of a small chromosome B in some individuals (male and female) of an *M. rufiventris* colony from Guimarães/Minas Gerais and Barth et al. (2011) detected the presence of 0–3 B chromosomes in some individuals from 10 of the 11 *Tetragonisca fiebrigi* colonies from Tangará da Serra/Mato Grosso do Sul. It is emphasized that these chromosomes were not detected in any of the *T. angustula* colonies analysed in different works (Rocha et al. 2003a; Barth et al. 2011; Miranda 2012).

We can then see that, to date, the B chromosomes of *P. helleri* were the best studied. However, similar studies are beginning to be developed in other species.

### Karyotypic evolution

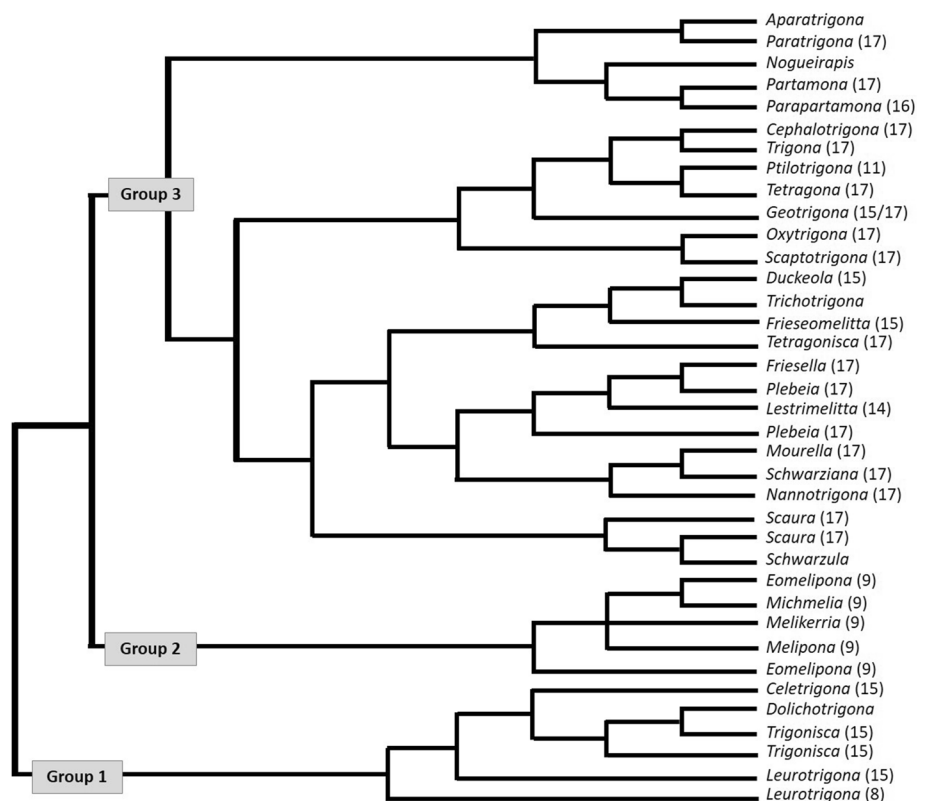
Kerr and Silveira (1972) were the first to propose a hypothesis to explain the chromosomal variation in Hymenoptera in general, and in Meliponini, in particular. Analysing the

cytogenetic data available for several species of bees, these authors found that their chromosome numbers ranged from 6 to 9 and from 12 to 20. They then suggested that these numbers could have arisen as a result of polyploidy events, from a basic number.

Later studies, however, have shown that several species of Meliponini had an intermediate number of chromosomes in addition to differences related to the quantity and location of heterochromatic regions along the chromosome arms, which could not be explained by polyploidy (Pompolo 1992, 1994). Thus, the Minimum Interaction Theory that was initially postulated to explain the karyotype evolution of Australian ants by Imai et al. (1986, 1988, 1994) also began to be used to explain the karyotype evolution of other organisms, including some genera of stingless bees.

The Minimum Interaction Theory predicts the occurrence of changes in karyotypes to minimize deleterious interactions between chromosomes. These modifications would be through a cycle in which centric fissions increase the number of chromosomes, reducing their size and consequently, reducing the interactions between them. After fission, the in tandem growth of heterochromatin occurred in one of the chromosomal arms, restoring the stability of the telomeres. According to this theory, therefore, the karyotypes of ancestral species would consist of a small number of large chromosomes and over time, the descendants' species would present karyotypes with a larger number of

**Fig. 1** Distribution of the three main chromosomal numbers (n=9, 15 and 17) found in the Meliponini on the phylogenetic tree proposed for the Neotropical Meliponini (modified of Rasmussen and Cameron 2010)



smaller chromosomes with telocentric and acrocentric morphology, resulting from fissions. Accordingly, Pompolo (1992, 1994), Costa et al. (1992), Hoshiba and Imai (1993), Pompolo and Campos (1995), Caixeiro (1996, 1999), Brito (1998), Rocha and Pompolo (1998), Mampumbu (2002), Rocha et al. (2003a), Krinski et al. (2010) and Godoy et al. (2013) used this theory to explain the changes observed in various groups of Hymenoptera.

Pompolo and Campos (1995), for example, used the Minimum Interaction Theory to explain the karyotypic differences (number and morphology) found between *L. muelleri* ( $2n=16$ ) and *L. pusilla* ( $2n=30$ ). According to the authors, in *L. muelleri* predominate metacentric chromosomes with both arms predominantly euchromatic (only the centromeric region of a metacentric pair and the short arm of an acrocentric pair showed heterochromatic regions). The karyotype of *L. pusilla*, which has a predominance of acro/submetacentric chromosomes and a greater amount of heterochromatin in one arm, would have emerged from centric fissions and the addition of heterochromatin.

However, the Minimum Interaction Theory does not explain the variations found in species of *Melipona* (Rocha and Pompolo 1998) or *Euglossa* (Fernandes et al. 2013) and not even in other hymenopteran groups, e.g. the parasitoid superfamily Chalcidoidea (Gokhman and Gumovsky 2009) and the tribe Epiponini (=Polybiini) of the family Vespidae (Menezes et al. 2014). In *Melipona*, for example, karyotype evolution does not seem to be related to fission centric events, because although most species present  $n=9$  chromosomes, a large variation has been observed in the amount of heterochromatin and location of heterochromatic blocks (Rocha and Pompolo 1998; Rocha et al. 2007). The karyotype of *M. seminigra*, with  $n=11$ , however, could have originated from an ancestor with  $n=9$ , through the fission of two chromosomes.

Therefore, as the chromosomal variations observed in karyotypes of different Meliponini groups do not seem to be explained by a single theory or a single type of structural change, in the present study, we aimed to analyse the karyotype variations, verifying how these variations are related to the phylogenetic relationships among the different genera of this tribe.

In this sense, phylogenetic analysis based on molecular data (Rasmussen and Cameron 2010), considering the different taxa of Meliponini, reinforced the separation of this tribe into three monophyletic lineages: Afrotropical, Indo-Malayan/Australasian and Neotropical. These authors also recognize the presence of three distinct clades in the Neotropical lineage: *Trigonisca* sensu lato (including *Celétrigona*, *Dolichotrigona*, *Trigonisca*, and *Leurotrigona* - called in this work “Group 1”), *Melipona* sensu lato (“Group 2”) and the other Meliponini (“Group 3”). Cytogenetic analyses, in turn, show that the most common

karyotypes discussed above ( $n=9$ , 15 or 17) are well separated in these three groups of Neotropical Meliponini (Fig. 1).

In this scenario, it is noteworthy that the *Melipona* clade has been extensively studied from different biological aspects. Taxonomically, the species of this clade can be grouped into four subgenera: *Melikerria*, *Melipona*, *Michmelia* and *Eomelipona* (Kerr et al. 1967; Moure 1992). Considering the amount and distribution of heterochromatin between different species of this clade, Rocha and Pompolo (1998) and Rocha et al. (2002) proposed dividing it into two groups. Group I comprises species that have less than 50% heterochromatin in their chromosomes (*M. marginata*, *M. quadrifasciata*, *M. bicolor*, *M. asilvae*, *M. subnitida*, *M. mandacaia*, *M. puncticolis* and the A complement of *M. quinquefasciata*). All of these species, except *M. quinquefasciata*, belong to the subgenera *Eomelipona* and *Melipona*. Group II, in turn, includes species of the subgenera *Michmelia* and *Melikerria*, which have a high content of heterochromatin, spread over almost the entire length of the chromosomes (*M. scutellaris*, *M. fuscopilosa*, *M. capixaba*, *M. captiosa*, *M. crinita*, *M. rufiventris*, *M. mondury*, *M. fasciculata*, *M. flavolineata* and *M. fuliginosa*).

Analysis of the genome sizes of these species (Tavares et al. 2010, 2012) confirmed the classification proposed by Rocha and Pompolo (1998) and Rocha et al. (2002), showing that species with low amounts of heterochromatin also have a lower amount of DNA per haploid nucleus (subgenera *Melipona* and *Eomelipona*), whereas those having high amounts of heterochromatin have a greater amount of DNA (subgenera *Melikerria* and *Michmelia*). Together, these data show that differences in DNA content represent genomic changes that have occurred through the addition or deletion of heterochromatin. It is noteworthy, however, that the resulting grouping of cytogenetic analysis and DNA quantification differ from the phylogenetic proposal of Rasmussen and Cameron (2010), which shows that *Eomelipona* and *Michmelia* are the two closest subgenera, although the four subgenera form a single clade.

Furthermore, cytogenetic data available in the literature showed the presence of species with higher chromosome numbers in the Afrotropical ( $n=17-18$ —Kerr and Araújo 1957; Kerr 1969, 1972) and Indo-Malayan/Australasian lineages ( $n=18-20$ —Hoshiba and Imai 1993; Travenzoli et al. 2015) as well as in *Bombus*, the sister genus of the stingless bees ( $n=18-19$ —Owen et al. 1995), *Apis* ( $n=16$ —Hoshiba and Kusanagi 1978) and solitary species such as *Euglossa* ( $n=21$ —Fernandes et al. 2013) and *Eulaema* ( $n=21$ —Pompolo et al. 1986).

Therefore, considering that karyotypes with high chromosome numbers are the most common among the above groups, including Neotropical stingless bees ( $n=17$ ),

it is suggested that the ancestor of the karyotype of all Meliponini had a high chromosome number ( $n=17-20$ ). Thus, in some groups, the ancestral karyotype may have been maintained. For example, if the ancestral karyotype was comprised of 17 chromosomes, this number would have been maintained in most current genera that comprise “Group 3” (Fig. 1). Karyotypes with lower haploid numbers than 17, such as those found in the genera *Duckeola* ( $n=15$ ), *Frieseomelitta* ( $n=15$ ), *Geotrigona* ( $n=15$ ), *Lestrimelitta* ( $n=14$ ), *Parapartamona* ( $n=16$ ) and *Ptilotrigona* ( $n=11$ ), in turn, must have originated through additional fusions that occurred subsequent to the initial event that gave rise to the current characteristic chromosome number of this group. Centric fusion events could also help explain the current karyotypes found in species of *Melipona* (“Group 2”), *Celetrigona*, *Leurotrigona* and *Trigonisca* (“Group 1”). These fusion events occurred very early in the separation of Neotropical Meliponini, as they seem to have contributed to the karyotype organization of various genera.

In some cases, more than one type of chromosomal rearrangement has been used to account for these variations. Domingues et al. (2005), for example, found that *Trigona fulviventr* had  $2n=32$  chromosomes, differently from other *Trigona* species already karyotyped ( $2n=34$ ). As the first chromosome pair of this species is much larger than the others and has a metacentric morphology and heterochromatin restricted to the pericentromeric region, the authors attributed the reduction of chromosome number to a centric fusion of two pseudoacrocentric chromosomes. In this case, however, it is noteworthy that the species analysed was possibly *Trigona braueri* because *T. fulviventr* is not found in Brazil.

A similar situation was proposed by Domingues (2005) when analysing the karyotype of *Scaura latitarsis*. In this case, the author proposed that a pericentromeric inversion of a pseudoacrocentric chromosome (AM), followed by elimination of heterochromatin could explain the presence of one metacentric pair in the karyotype of this species, which was not detected on the karyotype of two other species of the genus (*S. longula* and *S. atlantica*).

In conclusion, cytogenetic analysis performed to date with Neotropical Meliponini has identified three different groups that gather most species and are congruent with the clades *Melipona* ( $n=9$ ), *Trigonisca* ( $n=15$ ) and other Meliponini ( $n=17$ ) as proposed by Rasmussen and Cameron (2010). It is noteworthy, however, that in the latter clade, although species with  $n=17$  predominate, there is also a sub-group with  $n=15$  consisting by the genera *Frieseomelitta* and *Duckeola*, that are phylogenetically close to each other. Therefore, the karyotypes with  $n=15$  must have originated independently, because *Trigonisca* and *Frieseomelitta/Duckeola* are

phylogenetically distant and most genera of the group with which *Frieseomelitta/Duckeola* is associated have  $n=17$  (Fig. 1). So, after its origin, each clade/group followed their own route of karyotype evolution, i.e., several rearrangements occurred during the chromosomal karyotype evolution of different groups of the tribe Meliponini. Consequently, the chromosomal karyotype variations observed in different groups seem not to be explained by a single theory or a single kind of structural change. In many cases, more than one type of rearrangement is necessary to explain the variations detected.

## Concluding remarks and prospects

The data presented show that, in spite of the early cytogenetic studies being restricted to description of the chromosome number, current studies involve the content and location of the heterochromatic regions as well as the molecular characterization of chromatin (AT and CG bases content), localization of genes and even whole chromosomes by molecular cytogenetic techniques (Brito et al. 2005; Martins et al. 2013; Lopes et al. 2014). In situ hybridization, for example, has been used for the location of ribosomal DNA sequences (Rocha et al. 2002; Mampumbu 2002; Brito et al. 2005; Ferreira 2015) and other repetitive sequences (Ferreira et al. 2015; Travenzoli et al. 2015) whereas microdissection has allowed the construction of probes from specific regions or entire chromosomes, thereby contributing to studies on chromosome evolution of Meliponini (Fernandes et al. 2011; Martins et al. 2013). It is worth noting that these advances have been accompanied by increases in informatics technology, with the development of capture and image analysis software. These software applications have allowed more precise measurements in addition to permitting more refined analyses of the patterns of chromosomal banding and composition of chromatin.

These studies have shown that although chromosome number in general is conserved among species of a certain genus, other aspects, such as chromosome morphology, quantity, distribution and composition of heterochromatin, may vary between them, which can aid in making taxonomic and evolutionary inferences from this tribe (Brito 1998; Rocha et al. 2002; Duarte et al. 2009; Barth et al. 2011; Miranda 2012; Miranda et al. 2013; Lopes et al. 2014). Thus, the emergence of techniques, such as molecular cytogenetic, may help clarify aspects not yet revealed by classical techniques.

**Acknowledgements** The authors are grateful to the Brazilian agencies FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais) and UFV (Universidade Federal de Viçosa) for financial support.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Almeida MG (1981) Estudo sobre o número de cromossomos e contagem de espermatozoides na abelha *Melipona scutellaris* Latreille, 1811. *Cien Cult* 33:539–542
- Barth A, Fernandes A, Rocha MP, Pompolo SG (2005) Caracterização citogenética da espécie *Trigona chanchamayoensis* (Hymenoptera, Apidae, Meliponina) do Cerrado Matogrossense. In: Resumos do 51° Congresso Brasileiro de Genética. Águas de Lindoia, São Paulo, p 178
- Barth A, Fernandes A, Pompolo SG, Costa MA (2011) Occurrence of B chromosomes in *Tetragonisca* Latreille, 1811 (Hymenoptera, Apidae, Meliponini): A new contribution to the cytotaxonomy of the genus. *Gen. Mol Biol* 34:7–79
- Bravo F, Arcos L (1991) O cariótipo das espécies de *Parapartamona* (Schwarz) (Hymenoptera, Apidae, Meliponinae) e comentários sobre a sistemática do grupo. *Rev Bras Ent* 35(4):755–759
- Brito RM (1998) Caracterização citogenética de duas espécies do gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Meliponinae). Dissertation, Universidade Federal de Viçosa
- Brito RM, Costa MA, Pompolo SG (1997) Characterization and distribution of supernumerary chromosomes in 23 colonies of *Partamona helleri* (Hymenoptera, Apidae, Meliponinae). *Braz J Gen* 20(2):185–188
- Brito RM, Caixeiro APA, Pompolo SG, Azevedo GG (2003) Cytogenetic data of *Partamona peckolti* (Hymenoptera, Apidae, Meliponini) by C banding and fluorochrome staining with DA/CMA3 and DA/DAPI. *Gen. Mol Biol* 26:53–57
- Brito RM, Pompolo SG, Magalhães MFM, Barros EG, Sakamoto-Hojo ET (2005) Cytogenetic characterization of two *Partamona* species (Hymenoptera, Apidae, Meliponini) by fluorochrome staining and localization of 18 S rDNA clusters by FISH. *Cytologia* 70(4):373–380
- Brito-Ribon RM, Miyazawa CS, Pompolo SG (1999) First karyotype characterization of four species of *Partamona* (Friese, 1980) (Hymenoptera, Apidae, Meliponinae). *Cytobios* 100:19–26
- Caixeiro AP (1996) Contribuição ao estudo citogenético do gênero *Plebeia* (Hymenoptera, Meliponini). Monografia, Universidade Federal de Viçosa
- Caixeiro AP (1999) Caracterização citogenética da heterocromatina constitutiva e sua implicação na evolução do cariótipo de espécies do gênero *Plebeia* (Hymenoptera: Apinae: Meliponini). Dissertation, Universidade Federal de Viçosa
- Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. <http://www.moure.cria.org.br/catalogue>. Accessed 10 July 2016
- Carvalho AF, Costa MA (2011) Cytogenetic characterization of two species of *Frieseomelitta* Ihering, 1912 (Hymenoptera, Apidae, Meliponini). *Gen Mol Biol* 34(2):237–239
- Cassinela EK, Ferreira RP, Oliveira FPM, Lopes DM (2013) Cytogenetic analysis in *Melipona paraensis* (Hymenoptera: Apidae). In: Anais do II Simpósio de Integração dos Programas de Pós-graduação em Biologia Celular e VI Simpósio de Biologia Celular da Universidade Federal de Minas Gerais. Belo Horizonte, Minas Gerais
- Correa AM, Fernandes A, Campos LAO, Lopes DM (2014) Análise da presença do marcador SCAR associado ao cromossomo B em espécies de abelha sem ferrão do gênero *Partamona*. *Braz J Biosc* 12:196–200
- Costa MA, Pompolo SG, Campos LAO (1992) Supernumerary chromosomes in *Partamona cupira* (Hymenoptera, Apidae, Meliponinae). *Rev Bras Genet* 15(4):801–806
- Costa KF, Brito RM, Miyazawa CS (2004) Karyotypic description of four species of *Trigona* (Jurine, 1807) (Hymenoptera, Apidae, Meliponini) from the state of Mato Grosso, Brazil. *Gen. Mol Biol* 27(2):187–190
- Crossa RP, Hernandez M, Caraccio MN, Rose V, Valente SAS, Valente VC, Mejia JM, Angulo VM, Ramirez CMS, Roldan J, Vargas F, Wolff M, Panzera F (2002) Chromosomal evolution trends of the genus *Panstrongylus* (Hemiptera, Reduviidae), vectors of Chagas disease. *Infect Genet Evol* 2:47–56
- Domingues AMT (2005) Estudos citogenéticos comparativos entre espécies de *Scaura* (Hymenoptera, Apidae, Meliponini). Dissertation, Universidade Estadual de Santa Cruz
- Domingues AMT, Bertão MR, Costa MA (2004) Cariótipo e caracterização de heterocromatina na espécie *Scaura atlantica* (Hymenoptera, Meliponini). In: Anais do 50° Congresso Brasileiro de Genética. Florianópolis Santa Catarina, p 195
- Domingues AMT, Waldschmidt AM, Andrade SE, Andrade-Souza V, Alves RMO, Silva Junior JC, Costa MA (2005) Karyotype characterization of *Trigona fulviventrtris* Guérin, 1835 (Hymenoptera, Meliponini) by C banding and fluorochrome staining: Report of a new chromosome number in the genus. *Gen Mol Biol* 28(3):390–393
- Duarte OMP, Martins CCC, Santana SEA, Domingues AMT, Costa MA, Alves RNO, Silva-Junior JC, Waldschmidt AM (2005) Caracterização citogenética da espécie *Paratrigona incerta* (Camargo and Moure, 1994) (Hymenoptera, Meliponina). In: Anais do 51° Congresso Brasileiro de Genética. Águas de Lindoia, São Paulo, p 143
- Duarte OMP, Martins CCC, Waldschmidt AM (2009) Occurrence of multiple nucleolus organizer regions and intraspecific karyotype variation in *Scaptotrigona xanthotricha* Moure (Hymenoptera, Meliponini). *Gen Mol Res* 8(3):831–839
- Eardley CD (2004) Taxonomic revision of the African stingless bees (Apoidea: Apinae: Meliponini). *Afr Plant Protect* 10(2):63–96
- Elizeu AM., Silva AA, Tavares MG (2013) Estudos citogenéticos de *Frieseomelitta doederleini* (Hymenoptera: Apidae) de Urbano Santos—Maranhão. In: Anais do IV Simpósio de Entomologia. Viçosa, Minas Gerais, p 142
- Fernandes A, Sampaio WMS, Campos LAO, Lopes DM (2011) Análise citogenética em *Tetragonisca angustula* (Hymenoptera, Apidae, Meliponini): uma proposta populacional. In: Anais da 2ª Reunião Brasileira de Citogenética. Águas de Lindoia, São Paulo, CA063
- Fernandes A, Lopes DM, Campos LAO (2012) Diferentes tipos de cromatina detectada pela combinação de banda C e análise de imagens em *Partamona chapadicola* (Hymenoptera, Apidae). In: Anais do II EPACITO, Encontro Paulista de Citogenética. Ribeirão Preto, São Paulo, p 35
- Fernandes A, Werneck HA, Pompolo SG, Lopes DM (2013) Evidence of separate karyotype evolutionary pathway in *Euglossa* orchid bees by cytogenetic analyses. *An Acad Bras Cienc* 85(3):937–944
- Ferreira RP (2015) Análise citogenética de abelhas do gênero *Trigona* Jurine, 1807 (Hymenoptera, Meliponini). Thesis, Universidade Federal de Viçosa
- Ferreira RP, Godoy DC, Lopes DM (2012) Caracterização cariotípica da abelha sem ferrão *Plebeia phrynostoma* (Hymenoptera, Meliponini). In: Anais do II EPACITO, Encontro Paulista de Citogenética. Ribeirão Preto, São Paulo, p 17

- Ferreira RP, Novaes CM, Travenzoli NM, Lopes DM (2015) Intraspecific variation revealed by chromosomal mapping of microsatellite in stingless bee *Trigona spinipes*. In: 10th European Cytogenetics Conference, Strasbourg. Chromosome Res 23:130
- Francini IB, Gross MC, Nunes-Silva CG, Carvalho-Zilse G (2011) Cytogenetic analysis of the Amazon stingless bee *Melipona seminigra merrillae* reveals different chromosome number for the genus. Sci Agric 68(5):592–593
- Godoy DC, Ferreira RP, Lopes DM (2013) Chromosomal variation and cytogenetics of *Plebeia lucii* and *P. phrynostoma* (Hymenoptera: Apidae). Florida Entomol 96(4):1559–1566
- Godoy DC, Lopes DM, Ferreira RP (2014) Caracterização cariotípica de duas espécies de Meliponini da região Amazônica. In: Anais do Simpósio de Integração Acadêmica de 2014 da Universidade Federal de Viçosa. Viçosa, Minas Gerais, ID3431
- Gokhman VE, Gumovsky AV (2009) Main trends of karyotype evolution in the superfamily Chalcidoidea (Hymenoptera). Comp Cytogenet 3:63–69
- Heard TA (1999) The role of stingless bees in crop pollination. Annu Rev Entomol 44:183–206
- Hoshihara H (1988) Karyological analysis of a stingless bee, *Melipona favosa* (Apidae, Hymenoptera). Cytologia 53:153–156
- Hoshihara H, Imai HT (1993) Chromosome evolution of bees and wasps (Hymenoptera: Apocrita) on the basis of C-banding pattern analyses. Jpn J Entomol 61:465–492
- Hoshihara H, Kusanagi A (1978) Karyological study of honeybee. J Apic Res 17:105–109
- Imai HT (1991) Mutability of constitutive heterochromatin (C-bands) during eukaryotic chromosomal evolution and their cytological meaning. Jpn J Gen 66:635–661
- Imai HT, Maruyama T, Gojobori T, Inoue Y, Crozier RH (1986) Theoretical bases for karyotype evolution. The minimum-interaction hypothesis. Am Nat 128:900–920
- Imai HT, Taylor RW, Crosland MWJ, Crozier RH (1988) Modes of spontaneous evolution in ants with reference to the minimum interaction hypothesis. Jpn J Gen 63:159–185
- Imai HT, Taylor RW, Crozier RH (1994) Experimental bases for the minimum interaction theory. Chromosome evolution in ants of the *Myrmecia pilosula* species complex (Hymenoptera: Formicidae: Myrmecinae). Jpn J Gen 69:137–182
- Imai HT, Satta Y, Takahata N (2001) Integrative study on chromosome evolution of mammals, ants and wasps based on the minimum interaction theory. J Theor Biol 210:475–497
- Kerr WE (1948) Estudos sobre o gênero *Melipona*. An Esc Super Agric Luiz de Queiroz 5:182–276
- Kerr WE (1952) A variação do número de cromossomas na evolução dos Hymenoptera. Sci Gen 4:182–190
- Kerr WE (1969) Some aspects of the Evolution of social bees. Evol Biol 3:119–175
- Kerr WE (1972) Number of chromosomes in some species of bees. J Kansas Entomol Soc 45:111–122
- Kerr WE, Araújo VP (1957) Contribuição ao estudo citológico dos Apoidea. I. Espermatogênese em três espécies africanas. Garcia de Orta 3:431–433
- Kerr WE, Silveira ZV (1972) Karyotypic evolution of bees and corresponding taxonomic implications. Evol Int J org Evol 26:197–202
- Kerr WE, Pisani JF, Aily D (1967) Aplicação de princípios modernos à sistemática do gênero *Melipona* Illiger, com a divisão em dois subgêneros (Hymenoptera, Apoidea). Papeis Avulsos de Zoologia 20(13):135–145
- Krinski D, Fernandes A, Rocha MP, Pompolo SG (2010) Karyotypic description of the stingless bee *Oxytrigona cf. flaveola* (Hymenoptera, Apidae, Meliponina) of a colony from Tangará da Serra, Mato Grosso State, Brazil. Gen. Mol Biol 33(3):494–498
- Lopes DM, Pompolo SG, Campos LAO, Tavares MG (2008) Cytogenetic characterization of *Melipona rufiventris* Lepeletier 1836 and *Melipona mondury* Smith 1863 (Hymenoptera, Apidae) by C banding and fluorochromes staining. Gen Mol Biol 31:49–52
- Lopes DM, Fernandes A, Campos LAO (2011a) Descrição cariotípica de *Partamona nhambiquara* e *Partamona chapadicola* (Hymenoptera, Meliponini) por técnicas convencionais e moleculares. In: Anais da 2ª Reunião Brasileira de Citogenética. Águas de Lindoia, São Paulo, CA049
- Lopes DM, Fernandes A, Praça-Fontes MM, Werneck HA, Resende HC, Campos LAO (2011b) Cytogenetics of three *Melipona* species (Hymenoptera, Apidae, Meliponini). Sociobiology 58:185–194
- Lopes DM, Fernandes A, Campos LAO (2012) Cytogenetic of stingless bee *Partamona rustica* (Hymenoptera, Apidae). In: Anais do X Encontro sobre Abelhas. Ribeirão Preto, São Paulo, p 324
- Lopes DM, Fernandes A, Diniz D, Scudeler PES, Foresti F, Campos LAO (2014) Similarity of heterochromatic regions in the stingless bees (Hymenoptera: Meliponini) revealed by chromosome painting. Caryologia 67(3):222–226
- Mampumbu AR (2002) Análise citogenética da heterocromatina e da NOR em populações de abelhas sem ferrão *Friesella schrottkyi* (Friese, 1900) (Hymenoptera: Apidae: Meliponini). Dissertation, Universidade Estadual de Campinas
- Marthe JB, Tavares MG, Campos LAO (2007) Genetic variability in *Partamona helleri* (Hymenoptera: Apidae) populations with and without B chromosomes. Biosci J 23:52–57
- Marthe JB, Pompolo SG, Campos LAO, Salomão TMF, Tavares MG (2010) Cytogenetic characterization of *Partamona cupira* (Hymenoptera, Apidae) by fluorochromes. Gen Mol Biol 33(2):253–255
- Martins CCC (2008) Caracterização citogenética em *Partamona helleri* (Friese, 1900) e *Partamona rustica* (Pedro and Camargo 2003) (Hymenoptera: Apidae: Meliponini) Dissertation, Universidade Estadual de Santa Cruz
- Martins CCC, Duarte OMP, Waldschmidt AM, Alves RMO, Costa MA (2009) New occurrence of B chromosomes in *Partamona helleri* (Friese, 1900) (Hymenoptera, Meliponini). Gen Mol Biol 32(4):782–785
- Martins CCC, Diniz D, Sobrinho-Scudeler PE, Foresti F, Campos LAO, Costa MA (2013) Investigation of *Partamona helleri* (Apidae, Meliponini) B chromosome origin. An approach by microdissection and whole chromosome painting. Apidologie 44:75–81
- Martins CCC, Waldschmidt AM, Costa MA (2014) Unprecedented record of ten novel B chromosomes in the stingless bee *Partamona helleri* (Apidae, Meliponini). Apidologie 45:431–439
- Mauricio BSS, Ferreira RP, Lopes DM (2012) Karyotypic description of the stingless bee *Celetrigona longicornis* (Friese, 1903) by C-banding. In: Anais do X Encontro sobre Abelhas. Ribeirão Preto, São Paulo, p 319
- Melo GAR (2016) *Plectoplebeia*, a new Neotropical genus of stingless bees (Hymenoptera: Apidae). Zoologia. doi:10.1590/S1984-4689zool-20150153
- Menezes RST, Carvalho AF, Correia JPSO, Silva TS, Somavilla A, Costa MA (2014) Evolutionary trends in the chromosome numbers of swarm-founding social wasps. Insect Soc 61(4):385–393
- Miranda AF (2012) Estudos citogenéticos e moleculares do gênero *Partamona*: filogenia e cromossomos B. Thesis, Universidade Federal de Viçosa
- Miranda RV, Fernandes A, Lopes DM (2013) Karyotype description of *Cephalotrigona femorata* Smith (Hymenoptera, Apidae) and the C-banding pattern as a specific marker for *Cephalotrigona*. Sociobiology 60(1):125–127
- Moure JS (1992) *Melikerria* e *Eomelipona*, dois subgêneros novos em *Melipona* Illiger, 1806 (Hymenoptera, Apidae). In: Cruz LC,



- Chaud NJ (eds) Anais do Encontro Brasileiro de Biologia de Abelhas e outros Insetos Sociais. Homenagem aos 70 anos de Warwick Estevam Kerr. UNESP, São Paulo, pp 32–38
- Nascimento S (2005) Caracterização citogenética da espécie *Frieseomelitta trichocerata* Moure, 1988 (Hymenoptera; Apidae; Meliponina) coletada em Tangará da Serra—MT. Monografia, Universidade do Estado de Mato Grosso
- Oliveira MP, Ferreira RP, Oliveira FPM, Lopes DM (2013) Caracterização citogenética de *Tetragona dorsalis* (Hymenoptera: Apidae, Meliponini). In: Anais do IV Simpósio de Entomologia. Viçosa, Minas Gerais, p 140
- Owen RE, Richardfs KW, Wilkes A (1995) Chromosome numbers and karyotypic variation in bumble bees (Hymenoptera: Apidae; Bombini). *J Kansas Entomol Soc* 68:290–302
- Pedro SRM (2014) The stingless bee fauna in Brazil (Hymenoptera: Apidae). *Sociobiology* 61:348–354
- Pompolo SG (1992) Estudos citogenéticos em Meliponinae. Anais do Encontro Brasileiro sobre Biologia de Abelhas e outros Insetos Sociais. Naturalia, Ed. Especial, pp 62–66
- Pompolo SG (1994) Análise dos cariótipos de 19 gêneros de abelhas da subfamília Meliponinae. In: Anais do 1º Encontro sobre Abelhas. Ribeirão Preto, São Paulo, pp 143–146
- Pompolo SG, Campos LAO (1995) Karyotypes of two species of stingless bees, *Leurotrigona muelleri* and *Leurotrigona pusilla* (Hymenoptera, Meliponinae). *Rev Bras Genet* 18:181–184
- Pompolo SG, Takahashi CS, Kerr WE (1986) Os cromossomos de *Eulaema nigríta* (Apidae, Euglossini). *Cien Cult* 38(7):885–885
- Ramirez SR, Nieh JC, Quental TB, Roubik DW, Imperatriz-Fonseca VL, Pierce NE (2010) A molecular phylogeny of the stingless bee genus *Melipona* (Hymenoptera: Apidae). *Mol Phylog Evol* 56:519–525
- Rasmussen C (2008) Catalog of the Indo-Malayan-Australasian stingless bees (Hymenoptera, Apidae, Meliponini). *Zootaxa* 1935:1–80
- Rasmussen C, Cameron SA (2007) A molecular phylogeny of the Old world stingless bees (Hymenoptera: Apidae: Meliponini) and the non-monophyly of the large genus *Trigona*. *Syst Entomol* 32:26–39
- Rasmussen C, Cameron SA (2010) Global stingless bee phylogeny supports ancient divergence, vicariance, and long distance dispersal. *Biol J Linnean Soc* 99:206–232
- Ravaoarimanana IB, Tiedemann R, Montagnon D, Rumpel Y (2004) Molecular and cytogenetic evidence for cryptic speciation within a rare endemic Malagasy lemur, the Northern Sportive Lemur (*Lepilemur septentrionalis*). *Mol Phylogenet Evol* 31(2):440–448
- Rocha MP (2002) Análises citogenéticas em abelhas do gênero *Melipona* (Hymenoptera, Meliponini). Dissertation, Universidade Federal de Viçosa
- Rocha MP, Pompolo SG (1998) Karyotypes and heterochromatin variation (C-bands) in *Melipona* species (Hymenoptera, Apidae, Meliponinae). *Gen Mol Biol* 21:41–45
- Rocha MP, Pompolo SG, Dergam JA, Fernandes A, Campos LAO (2002) DNA characterization and karyotypic evolution in the bee genus *Melipona* (Hymenoptera Meliponini). *Hereditas* 136:19–27
- Rocha MP, Pompolo SG, Campos LAO (2003a) Citogenética da tribo Meliponini (Hymenoptera, Apidae). In: Melo GAR, Santos IA (eds) Apoidea Neotropica. Homenagem aos 90 anos de Jesus Santiago Moure. UNESC, Santa Catarina, pp 311–320
- Rocha MP, Cruz MP, Fernandes A, Waldschmidt AM, Silva-Junior JC, Pompolo SG (2003b) Longitudinal differentiation in *Melipona mandacaia* (Hymenoptera, Meliponini) chromosomes. *Hereditas* 138:133–137
- Rocha MP, Pompolo SG, Fernandes A, Campos LAO (2007) *Melipona*—six decade of cytogenetic. *Biosc J* 23:111–117
- Rodrigues TAS, Diniz D, Waldschmidt AM (2012) Estudos citogenéticos do gênero *Frieseomelitta* (Hymenoptera, Meliponini) da região sudoeste da Bahia. In: Anais do II Workshop de Genética, Biodiversidade e Conservação. Jequié, Bahia, pp 30–33
- Rossi AR, Gornung E, Sola L, Nirchio M (2005) Comparative molecular cytogenetics analysis of two congeneric species, *Mugil curema* and *M. liza* (Pisces, Mugiliformes), characterized by significant karyotype diversity. *Genetica* 125:27–32
- Silva JB, Brito RO, Miranda EA, Silva Junior JC (2007) Caracterização citogenética da abelha sem ferrão *Melipona flavolineata* como ferramenta para a preservação da espécie. In: Anais do VIII Congresso de Ecologia do Brasil. Caxambu, Minas Gerais, pp 1–2
- Silva WRT, Araújo ED, Scher R (2012) Caracterização do cariótipo de uma população de abelhas *Melipona quadrifasciata* (Hymenoptera: Meliponini), no município de Brejo Grande/SE. *Scientia Plena* 8(3):1–6
- Silva AA, Tavares MG, Elizeu AM (2013a) Análise de populações polimórficas de *Melipona quinquefasciata* (Hymenoptera: Apidae) quanto à presença de cromossomos B. In: Anais do IV Simpósio de Entomologia. Viçosa Minas Gerais, p 145
- Silva HB, Ferreira RP, Oliveira FPM, Lopes DM (2013b) Citogenética da abelha sem ferrão *Melipona puncticolis* (Hymenoptera, Meliponini) coletada em Altamira, Pará. In: Anais do IV Simpósio de Entomologia. Viçosa, Minas Gerais, p 147
- Silva HB, Ferreira RP, Lopes DM (2014) Análise citogenética da abelha *Melipona seminigra pernigra* (Hymenoptera, Meliponini) coletada em região de floresta amazônica. In: Anais do Simpósio de Integração Acadêmica de 2014 da Universidade Federal de Viçosa. Viçosa, Minas Gerais, ID 1832
- Silveira ZV (1971) Número de cromossomos em meliponídeos brasileiros. *Cien Cult* 23:105–106
- Silveira ZV (1972) Número de cromossomos em meliponídeos brasileiros. II. *Cien Cult* 24(6):160
- Tambasco AJ, Giannono MA, Moreira LMA (1979) Analyses of G-bands in chromosomes of the *Melipona quadrifasciata anthidioides* Lepeletier (Hymenoptera, Apidae, Meliponinae). *Cytologia* 44:21–27
- Tarelho ZVS (1973) Contribuição ao estudo citogenético dos Apoidea. Dissertation, Universidade de São Paulo
- Tavares MG, Carvalho CR, Soares FAF (2010) Genome size variation in *Melipona* species (Hymenoptera: Apidae) and sub-grouping by their DNA content. *Apidologie* 41:636–642
- Tavares MG, Carvalho CR, Soares FAF, Campos, LAO (2012) Genome size diversity in stingless bees (Hymenoptera: Apidae, Meliponini). *Apidologie* 43:731–736
- Tinni SR, Jessy NS, Hasan MM, Mustafa MG, Alam SS (2007) Comparative karyotype analysis with differential staining in two forms of *Anabas testudines* Bloch. *Cytologia* 72(1):71–75
- Tosta VC, Fernandes-Salomão TM, Tavares MG, Pompolo SG, Barros EG, Campos LAO (2004) A RAPD marker associated with B chromosomes in *Partamona helleri* (Hymenoptera, Apidae). *Cytogenet Genome Res* 106:279–283
- Tosta VC, Tavares MG, Fernandes-Salomão TM, Barros EG, Campos LAO, Camacho JPM (2007) Development of a SCAR marker for the analysis of B chromosome presence in *Partamona helleri* (Hymenoptera, Apidae). *Cytogenet Genome Res* 116:127–129
- Tosta VC, Marthe JB, Tavares MG, Fernandes-Salomão TM, Pompolo SG, Recco-Pimentel SM, Perfectti F, Campos LAO, Camacho JPM (2014) Possible introgression of B chromosomes between bee species (Genus *Partamona*). *Cytog Gen Res* 144:220–226
- Travanzoli NM, Brito RM, Oldroyd B, Lopes DM (2015) Description cytogenetics of *Austroplebeia australis* (Apidae, Meliponinae).

- In: Anais do XI Encontro sobre Abelhas. Ribeirão Preto, São Paulo, p 302
- Van Daele PAAG, Dammann P, Meier JL, Kawalika M, Van de Woestijne C, Burda H (2004) Chromosomal diversity in mole-rats of the genus *Cryptomys* (Rodentia: Bathyergidae) from the Zambezi region: with descriptions of new karyotypes. *J Zool Lond* 264:317–326
- Vicari MR, Artoni RF, Bertollo LAC (2005) Comparative cytogenetics of *Hoplias malabaricus* (Pisces, Erythrinidae): A population analysis in adjacent hydrographic basins. *Genet. Mol Biol* 28(1):103–110
- Waldschmidt AM, Duarte OMP, Martins CCC, Santana SEA, Miranda EA, Alves RNO, Silva-Junior JC, Carneiro PLS (2005) Análises citogenéticas em espécies de abelhas da subtribo Meliponina (Hymenoptera: Meliponina) da região sudoeste da Bahia. In: Anais do 51º Congresso Brasileiro de Genética. Águas de Lindoia, São Paulo, p 253