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ORIGINAL PAPER

Are the TTAGG and TTAGGG telomeric repeats phylogenetically conserved in aculeate Hymenoptera?

Rodolpho S. T. Menezes[1] · **Vanessa B. Bardella**[2] · **Diogo C. Cabral-de-Mello**[2] · **Daercio A. A. Lucena**[1] · **Eduardo A. B. Almeida**[1]

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Abstract Despite the $(TTAGG)_n$ telomeric repeat supposed being the ancestral DNA motif of telomeres in insects, it was repeatedly lost within some insect orders. Notably, parasitoid hymenopterans and the social wasp *Metapolybia decorata* (Gribodo) lack the $(TTAGG)_n$ sequence, but in other representatives of Hymenoptera, this motif was noticed, such as different ant species and the honeybee. These findings raise the question of whether the insect telomeric repeat is or not phylogenetically predominant in Hymenoptera. Thus, we evaluated the occurrence of both the $(TTAGG)_n$ sequence and the vertebrate telomere sequence $(TTAGGG)_n$ using dot-blotting hybridization in 25 aculeate species of Hymenoptera. Our results revealed the absence of $(TTAGG)_n$ sequence in all tested species, elevating the number of hymenopteran families lacking this telomeric sequence to 13 out of the 15 tested families so far. The $(TTAGGG)_n$ was not observed in any tested species. Based on our data and compiled information, we suggest that the $(TTAGG)_n$ sequence was putatively lost in the ancestor of Apocrita with at least two subsequent independent regains (in Formicidae and Apidae).

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✉ Rodolpho S. T. Menezes
rstmenezes@gmail.com

[1] Laboratório de Biologia Comparada e Abelhas, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras (FFCLRP), Universidade de São Paulo (USP), Av. Bandeirantes, 3900, Ribeirão Preto, SP 14040-901, Brazil

[2] Instituto de Biociências/IB, Departamento de Biologia, Universidade Estadual Paulista (UNESP), Av. 24A, 1515, Rio Claro, SP 13506-900, Brazil

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Introduction

A telomere is an essential nucleoprotein composed of a short and tandemly arrayed motif present at each end of eukaryotic chromosomes (Blackburn 1991). It prevents chromosome ends from degrading and avoids chromosomal rearrangements, such as end-to-end fusions by distinguishing natural chromosome ends from chromosomal breaks. Telomeres also compensate for chromosome shortening resulting from incomplete DNA replication at chromosome ends (Blackburn 1991; Greider and Blackburn 1996). Additionally, telomeres are involved in important cell functions including cell proliferation, aging, carcinogenesis, gene repression, and association of chromosomes to nuclear periphery (Zakian 1995; Krupp et al. 2000).

Telomere sequences are relatively G-rich at the 3′ strand and generally follow the $(T)_nA(G)_n$ pattern of repetition (Zakian 1995). In vertebrates, the $(TTAGGG)_n$ telomeric repeat is highly conserved, and for this reason, it is referred to as "the vertebrate telomeric sequence" (Meyne et al. 1989). Conversely, four different types of sequences acting as telomeres have been already identified among insects. The pentanucleotide $(TTAGG)_n$ first discovered in silkworm, *Bombyx mori* (Linnaeus), called insect telomeric motif, is the most phylogenetically widespread in insects as well as other arthropods (Okazaki et al. 1993; Sahara et al. 1999; Mason et al. 2016). Due to the broad phylogenetic occurrence of $(TTAGG)_n$, it has been suggested that this sequence is the ancestral motif of telomeres in insects (Vítková et al. 2005). However, this telomeric motif has been lost at least 15 times during insect diversification (Frydrychová et al. 2004; Mason et al. 2016) and it has been replaced, for example, by

$(TCAGG)_n$ or other repetitive DNA, like transposable elements (TEs) and long tandem repeats (Zhang et al. 1994; Mason and Biessmann 1995; Rossato et al. 2007; Madalena et al. 2010; Mravinac et al. 2011; Fernandes et al. 2012; Mason et al. 2016).

Within Hymenoptera, the telomeric sequence occurrence and chromosomal distribution have been investigated through fluorescence in situ hybridization (FISH) and/or Southern blotting in only a reduced number of species, representing eight hymenopteran families and only three of the 27 extant aculeate Hymenoptera families (sensu classification of Grimaldi and Engel 2005). In aculeate hymenopterans, the insect telomeric repeat was found in honeybee, *Apis mellifera* Linnaeus (Apidae), and in 29 species of ants (Formicidae) (Okazaki et al. 1993; Meyne et al. 1995; Sahara et al. 1999; Lorite et al. 2002; Wurm et al. 2011); although in *Myrmecia* ants, there was also telomeric hybridization (despite it was significantly weak) with the vertebrate telomeric repeat (Meyne et al. 1995). Notably, representatives of five distinct families of parasitoid hymenopteran and of one aculeate social wasp, *Metapolybia decorata* (Gribodo) (Vespidae), were shown to lack the insect telomeric repeat (Werren et al. 2010; Menezes et al. 2013; Gokhman et al. 2014). Those data raise the question of whether the insect telomeric repeat is phylogenetically predominant in aculeate Hymenoptera. To address this question, we tested the occurrence of both the putative insect telomere sequence $(TTAGG)_n$ and the vertebrate telomere sequence $(TTAGGG)_n$ using dot-blotting hybridization in 25 aculeate Hymenoptera species. The analysis included various lineages distributed in different phylogenetic positions within the hymenopteran tree of life (see Branstetter et al. 2017a; Peters et al. 2017) and comprising representatives of the following eight families of Aculeata: Ampulicidae, Bethylidae, Chrysididae, Crabronidae, Pompilidae, Scoliidae, Sphecidae, and Vespidae.

Material and methods

Sampled specimens and genomic DNA extraction

We investigated the occurrence of $(TTAGG)_n$ and $(TTAGGG)_n$ telomeric repeats in 25 species representing eight families of aculeate Hymenoptera. Vespidae was the most represented (15

Table 1 List of species studied and the locality of the specimens

Dot-blotting ID	Family	Species	Locality
01	Chrysididae	*Ipsiura tropicalis*	Ribeirão Preto, São Paulo, Brazil
02		*Caenochrysis paranaca*	Ribeirão Preto, São Paulo, Brazil
03	Bethylidae	*Epyris* sp.	Itirapina, São Paulo, Brazil
04	Vespidae	*Metapolybia decorata*	Santa Terezinha, Bahia, Brazil
05		*Epipona media*	Santa Terezinha, Bahia, Brazil
06		*Parachartergus pseudapicalis*	Rio Branco, Acre, Brazil
07		*Apoica* sp.	Ilhéus, Bahia, Brazil
08		*Angiopolybia pallens*	Ilha de Itaparica, Bahia, Brazil
09		*Polybia ruficeps*	Ribeirão Cascalheira, Mato Grosso, Brazil
10		*Chartergus* sp.	Ribeirão Cascalheira, Mato Grosso, Brazil
11		*Synoeca ilheensis*	Itacaré, Bahia, Brazil
12		*Polistes versicolor*	Estrela Velha, Rio Grande do Sul, Brazil
13		*Mischocyttarus consimilis*	Dourados, Mato Grosso do Sul, Brazil
14		*Mischocyttarus drewsini*	Dourados, Mato Grosso do Sul, Brazil
15		*Mischocyttarus cerberus*	Dourados, Mato Grosso do Sul, Brazil
16		*Zethus cylindricus*	Naviraí, Mato Grosso do Sul, Brazil
17		*Pachymenes ater*	Ribeirão Grande, São Paulo, Brazil
18		*Paragia vespiformis*	Eurardy Station, Western Australia, Australia
19	Scoliidae	*Campsomeris* sp. 1	Itirapina, São Paulo, Brazil
20		*Campsomeris* sp. 2	Ribeirão Cascalheiras, Mato Grosso, Brazil
21	Pompilidae	*Pepsis* sp.	Maturéia, Paraíba, Brazil
22		*Priochilus* sp.	Ribeirão Cascalheiras, Mato Grosso, Brazil
23	Crabronidae	*Bicyrtes cingulata*	Barra do Garças, Mato Grosso, Brazil
24	Sphecidae	*Sceliphron* sp.	Teodoro Sampaio, São Paulo, Brazil
25	Ampulicidae	*Ampulex* sp.	Ribeirão Preto, São Paulo, Brazil

species). Chrysididae, Pompilidae, and Scoliidae had two species each and Ampulicidae, Bethylidae, Crabronidae, and Sphecidae had one species each (see Table 1). Since telomeric repetitive sequence is characteristic for whole taxonomic groups and conservative between species and also intraspecifically (as verified in vertebrates), we used only one specimen per species. Voucher specimens are deposited at Coleção Entomológica "J.M.F. Camargo" (RPSP) (FFCLRP-USP, Ribeirão Preto, Brazil). We used thorax or hind leg tissue samples from each specimen and extracted total genomic DNA using the DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia, California, USA). Subsequently, the total genomic DNA from each specimen was treated with RNAse 100 μg/ml for 30 min at 37 °C.

Dot-blotting hybridization

The dot-blotting hybridization technique was used in order to determine the presence/absence of both telomeric motifs $(TTAGG)_n$ and $(TTAGGG)_n$. The telomeric motifs were labeled with biotin-14-dATP (Invitrogen) through non-template PCR based on self-complementary primers following the conditions as described by Ijdo et al. (1991) and posteriorly used as probes in the dot-blotting technique. One hundred nanograms of genomic DNA was placed in each dot of Hybond-N^+ nylon filter (Amersham Biosciences) with the help of a manifold (Bio-Dot Microfiltration Apparatus, Bio-Rad) and suction device. Dot-blotting followed the protocol as proposed by Anjos et al. (2016). The genomic DNA from each sample in the membrane was denatured with NaOH 0.5 M for 2 min and the membranes were washed in 5× SSC for 1 min. The genomic DNA in the membrane was then fixed by baking at 80 °C for 90 min. The hybridization was carried out overnight (~ 16 h) at 37 °C using ~ 200 ng of denatured labeled probe diluted in ECL gold hybridization buffer (GE Healthcare Life Science), with the addition of bovine serum albumin (0.05% *w*/*v*) and NaCl (2.5 M). The post-hybridization washes were performed as follows: 5× SSC for 5 min at 42 °C; three times in primary buffer containing 6 M urea, 0.4% SDS (*w*/*v*), and 0.1× SSC for 10 min at 42 °C each; and 20× SSC for 5 min at room temperature. Finally, we used the biotin chromogenic detection kit (K0661, Thermo Scientific) for detection, following the manufacturer's recommendations.

Results

Dot-blotting hybridization essay with both $(TTAGG)_n$ and $(TTAGGG)_n$ probes revealed no hybridization in genomic DNA of any tested species (see Fig. 1 and Table 2). Thus, we have not found any trace of the $(TTAGG)_n$ sequence in any of the eight aculeate hymenopteran families examined (Fig. 1), raising the number of Hymenoptera families lacking this telomeric sequence to 13 of the 15 tested families to date (Fig. 2 and Table 2).

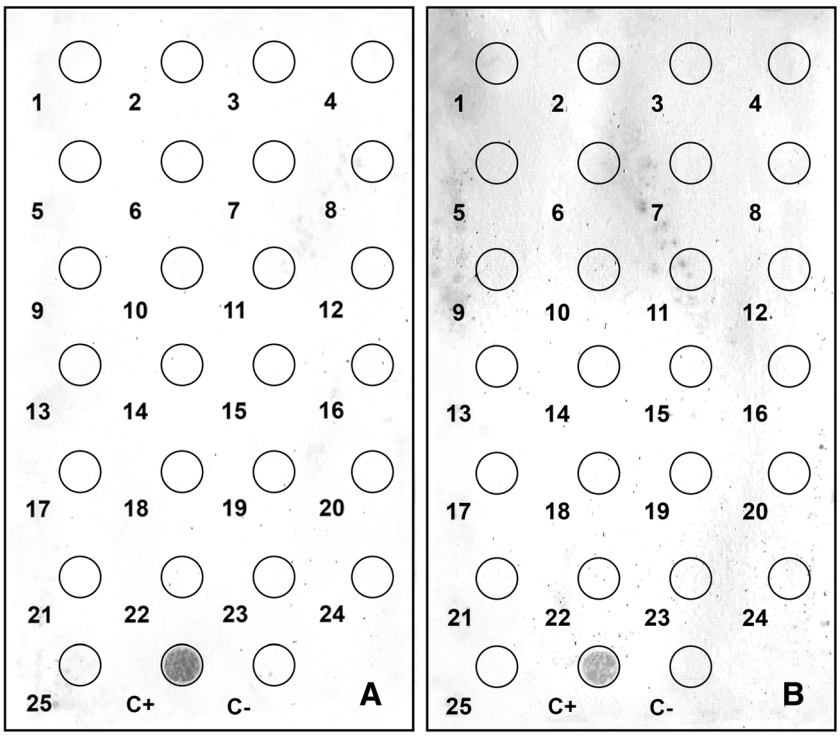

Fig. 1 Dot-blotting hybridization of genomic DNA from 25 aculeate Hymenoptera species to the $(TTAGG)_n$ (**a**) and $(TTAGGG)_n$ (**b**) probes. Species names are given in Table 1. C+ and C− are the positive and negative controls, respectively. Genomic DNA from *Gryllus assimilis* (Gryllidae cricket) and *Oreochromis niloticus* (Cichlidae fish) were used as positive control in (**a**) and (**b**), respectively

Table 2 List of the Hymenoptera species tested about the presence of both $(TTAGG)_n$ and $(TTAGGG)_n$ telomeric motif

Superfamily	Family	Species	$(TTAGG)_n$	$(TTAGGG)_n$	Reference
Ichneumonoidea	Ichneumonidae	*Ichneumon amphibolus*	–	?	a
Cynipoidea	Cynipidae	*Diplolepis rosae*	–	?	a
Chalcidoidea	Eurytomidae	*Eurytoma robusta*	–	?	a
		Eurytoma serratulae	–	?	a
		Eurytoma compressa	–	?	a
	Torymidae	*Torymus bedeguaris*	–	?	a
	Pteromalidae	*Nasonia vitripennis*	–	–	b
		Nasonia giraulti	–	–	b
		Nasonia longicornis	–	–	b
Vespoidea	Vespidae	*Metapolybia decorata*	–	–	c, d
		Synoeca ilheensis	–	–	d
		Epipona media	–	–	d
		Parachartergus pseudapicalis	–	–	d
		Apoica sp.	–	–	d
		Angiopolybia pallens	–	–	d
		Polybia ruficeps	–	–	d
		Chartergus sp.	–	–	d
		Polistes versicolor	–	–	d
		Mischocyttarus consimilis	–	–	d
		Mischocyttarus drewsini	–	–	d
		Mischocyttarus cerberus	–	–	d
		Pachymenes ater	–	–	d
		Zethus cylindricus	–	–	d
		Paragia vespiformis	–	–	d
Chrysidoidea	Chrysididae	*Ipsiura tropicalis*	–	–	d
		Caenochrysis paranaca	–	–	d
	Bethylidae	*Epyris* sp.	–	–	d
Scolioidea	Scoliidae	*Campsomeris* sp. 1	–	–	d
		Campsomeris sp. 2	–	–	d
Pompiloidea	Pompilidae	*Pepsis* sp.	–	–	d
		Priochilus sp.	–	–	d
Apoidea	Crabronidae	*Bicyrtes cingulata*	–	–	d
	Sphecidae	*Sceliphron* sp.	–	–	d
	Ampulicidae	*Ampulex* sp.	–	–	d
	Apidae	*Apis mellifera*	+	–	e
Formicoidea	Formicidae	*Myrmecia* sp.	+	+*	f
		Myrmecia haskinsorum	+	+*	f
		Myrmecia pilosula	+	+*	f
		Myrmecia gulosa	+	+*	f
		Myrmecia chasei	+	+*	f
		Myrmecia fulvipes	+	+*	f
		Myrmecia forficata	+	+*	f
		Myrmecia croslandi	+	+*	f
		Manica yessensis	+	–	g
		Tapinoma nigerrimum	+	–	h
		Bothriomyrmex gibbus	+	–	h
		Linepithema humile	+	–	h
		Camponotus micans	+	–	h
		Camponotus pilicornix	+	–	h

Table 2 (continued)

Superfamily	Family	Species	$(TTAGG)_n$	$(TTAGGG)_n$	Reference
		Cataglyphis velox	+	–	h
		Crematogaster auberti	+	–	h
		Crematogaster laestrygon	+	–	h
		Formica cunicularia	+	–	h
		Formica subrufa	+	–	h
		Lasius niger	+	–	h
		Aphaenogaster gibbosa	+	–	h
		Aphaenogaster senilis	+	–	h
		Messor bouvieri	+	–	h
		Messor structor	+	–	h
		Monomorium subopacum	+	–	h
		Pheidole pallidula	+	–	h
		Tetramorium semilaeve	+	–	h
		Tetramorium hispanicum	+	–	h
		Solenopsis invicta	+	+*	i

+: Presence; −: absence; +*: showed trace of the $(TTAGGG)_n$; ?: not tested; a: Gokhman et al. (2014); b: Werren et al. 2010; c: Menezes et al. (2013); d: this study; e: Sahara et al. (1999); f: Meyne et al. (1995); g: Okasaki et al. (1993); h: Lorite et al. (2002); i: Wurm et al. 2011

Discussion

Telomeres are of great interest to evolutionary biologists since their shortening is linked to the biology of lifespan. However, with the exception of Vespidae, the other aculeate Hymenoptera families sampled had not been studied concerning the organization and/or presence of telomeric repeats so far. A body of evidence suggests $(TTAGG)_n$ sequence as the ancestral motif of telomeres in insect chromosomes but with repeated losses across several orders (e.g., Mason et al. 2016). The most emblematic case is within Diptera, in which the telomerase and telomerase-generated telomeric DNA sequences were lost and then replaced by other telomere maintenance mechanisms (e.g., homologous recombination and transposition) (Mason et al. 2011; Frydrychova et al. 2009). Moreover, $(TTAGG)_n$ have not been found in eight of 19 sampled coleopteran families (Mason et al. 2016), and within the superfamily Tenebrionoidea (in three closely related families), it was replaced by the $(TCAGG)_n$ sequence (Mravinac et al. 2011).

Our results show that the insect telomeric repeat probably is not phylogenetically predominant in aculeate Hymenoptera, especially considering the phylogenetic span of taxa sampled (although 17 aculeate Hymenoptera families have not been yet tested about the presence of telomeric repeats) (Fig. 2 and Table 2). According to Mason et al. (2016), the capping complex that binds to chromosome ends and distinguishes them from double-stranded chromosome breaks (De Lange 2009; Fulcher et al. 2014) might have a crucial role in the variability of telomeric DNA sequences. Thus, Mason et al. (2016) suggested that when the capping complex is inflexible in its DNA sequence binding preference, the telomeric sequence would not be allowed to change. Conversely, if the capping complex loses strict sequence specificity, the terminal DNA sequence may be allowed to vary, but possibly with some limitations. The other possibility is that the capping complex may lose all sequence specificity, allowing the presence of alternative telomere organizations. Thus, we suggest that probably the capping complex in the ancestor of Apocrita (or even the ancestor of Hymenoptera) lost the strict sequence specificity, allowing the telomeric DNA sequence to vary, but probably with some restrictions. This hypothesis is congruent with the remarkable lack of the insect telomeric repeat as we detected in Hymenoptera, as well as the presence of the both insect and vertebrate telomeric repeats in two distinct ant genera (see Fig. 2).

An alternative hypothesis assuming multiple independent losses of $(TTAGG)_n$ sequence should not be completely ruled out, but it seem as less likely considering the higher number of evolutionary transitions assumed in such scenario. Organisms that have telomerase-generated telomeric DNA sequences also appear to have an alternative mechanism for lengthening telomeres (Royle et al. 2009). For example, in yeast and human tumors, alternative process for the maintenance of telomeric sequences may occur readily even in the presence of telomerase (Teng and Zakian 1999; Cesare and Reddel 2010; Dlaska et al. 2013). Thus, it is not surprising that over evolutionary time, telomerase-generated telomeric DNA sequences have been independently lost in Hymenoptera and other insect groups.

Following our abovementioned hypothesis and bearing in mind the Hymenoptera phylogeny, we suggest in a more parsimonious evolutionary scenario that the insect telomeric repeat was putatively lost in the ancestor of

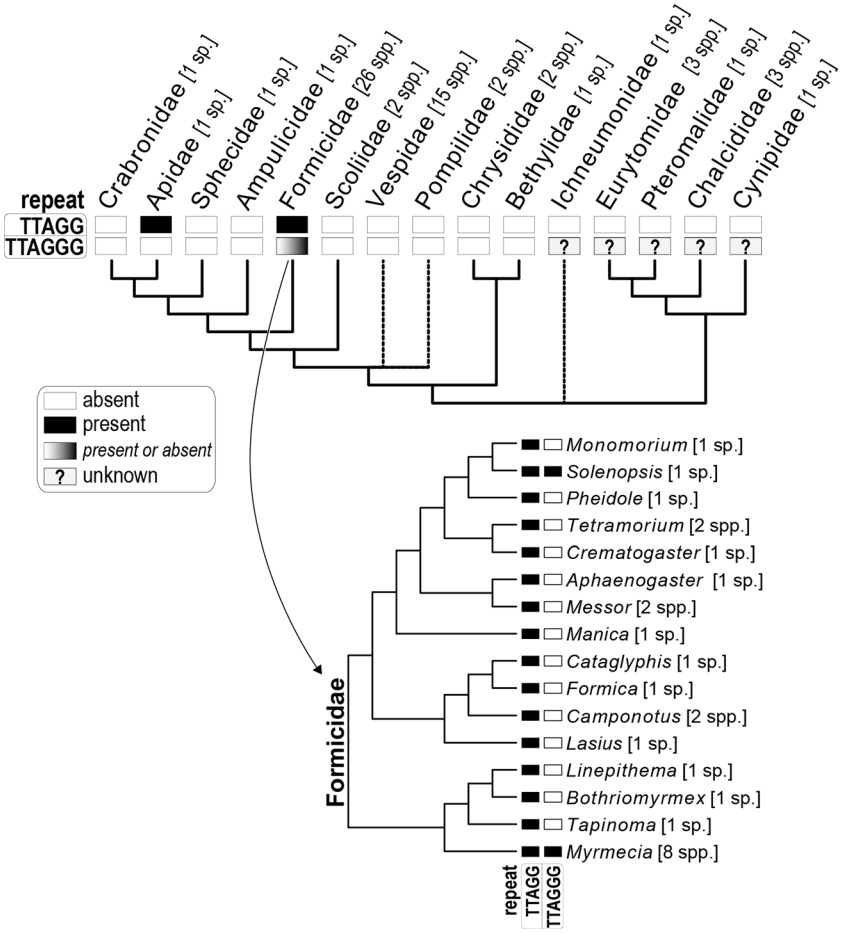

Fig. 2 Phylogenetic relationships among the lineages of Hymenoptera considered for this comparative study, depicting the distribution of telomeric repeats $(TTAGG)_n$ and $(TTAGGG)_n$. The presence or absence of these repeats indicated for each hymenopteran family derives from investigations of multiple species or single-representative species sampled for each taxon. Only *Apis mellifera* (Apidae) and ants (Formicidae) are known to have the $(TTAGG)_n$ repeat; whereas $(TTAGGG)_n$ was detected in some ant species but not all (the expanded ant phylogeny in the bottom shows the phylogenetic distribution of this repeat in ant genera studied thus far). Phylogenetic relationships at the family level is a summary of recent phylogenomic hypotheses by Klopfstein et al. (2013), Branstetter et al. (2017a), and Peters et al. (2017); dashed lines indicate lineages whose placement is conflicting or controversial when comparing the original studies; a list of species representing each family can be found in Table 2. The tree for ant genera is a simplification of the hypothesis by Branstetter et al. (2017b)

Apocrita (or even the ancestor of Hymenoptera) with subsequent two independent regains in Formicidae and Apidae (Fig. 2). A dated phylogeny for Hymenoptera (Peters et al. 2017) shows that extant apocritan lineages originated around 241 million years ago (mya). Considering that several families of Apocrita seem to lack the $(TTAGG)_n$ sequence (see Fig. 2 and Table 2), it is possible that this terminal DNA sequence was putatively lost in the Lower Mesozoic, when the radiation of Hymenoptera began (Grimaldi and Engel 2005). Sawfly wasps are good candidates for future analyses because they represent independent lineages that diversified during the early evolutionary history of the Hymenoptera, and the presence of $(TTAGG)_n$ in their chromosome ends has never been investigated. Further studies about organization and/or presence of telomeric repeats considering other Hymenoptera taxa will be necessary to corroborate our hypothesis. Moreover, further analyses integrating cytogenetics and genomics might reveal the existence of a new (e.g., TEs, satellite repeats) or other non-tested telomeric DNA sequences for Hymenoptera. Additionally, analysis of other representative taxa sampled here will contribute to the possible understanding of intrafamilial telomeric sequence loss.

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