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Distribution of sequences related to the *Bg* transposable element of maize in *Zea* and related genera

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Abstract Thirty-four accessions from *Zea* and 10 accessions from related genera were assayed for the presence of *Bg*, a transposable element originally found in maize (*Zea mays* ssp. *mays*). *Bg*-like sequences, identified as hybridizing bands on Southern blots, were visualized in all *Zea* accessions and were present in approximately equal numbers in teosinte and maize. With the exception of *Tripsacum dactyloides*, all accessions from related genera failed to hybridize with the *Bg* probes, even at reduced stringency. A comparison of the restriction patterns of related inbred lines revealed numerous common hybridizing fragments. An index of molecular similarity (MS) was used to determine the degree of similarity between pairs of inbred lines. Computed MS values endorse an inbred relationship and are in good agreement with published results of cluster analysis on these inbred lines.

Key words *Bg* transposable element · Molecular similarity · Maize · Teosinte · Southern analysis · *Zea*

Introduction

Transposable genetic elements are widespread in nature. The main features of these elements are their abilities to transpose to new chromosomal sites and to excise from the sites they occupy. As events of this kind can alter gene expression and gene product function in a variety of ways (Finnigan 1989), transposable element activity is a significant source of spontaneous mutation in various organisms, including bacteria, fungi, plants, and animals, thereby playing a role in the evolutionary process (Berg and Howe 1989; Peterson 1993).

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The transposable elements from maize were the first ones to be discovered (McClintock 1948). Since then, several independent families of maize transposable elements have been genetically described, and some of these have been characterized at the molecular level (for a review see Peterson 1993). Among the latter, the *Bg-rbg* transposable element system was first detected when studying a case of somatic instability at the *Opaque-2* (*O2*) locus (Salamini 1980, 1981). It was demonstrated that the instability encountered was due to the presence of a receptor element (*rbg*) at the *O2* locus. The responsive recessive allele, called *o2-m(r)*, was observed to be able to revert somatically to the wild type in the presence of a regulatory element termed *Bg*.

Both the autonomous and receptor element of the *Bg-rbg* system were isolated, the former at the *Waxy* (*Wx*) locus and the latter at the *o2-m(r)* allele, and characterized at the molecular level (Motto et al. 1989; Hartings et al. 1991). Molecular data obtained on the *Bg* and *rbg* components of the system have demonstrated that the receptor element resembles the autonomous element in size and that both elements share extensive sequence homology (Hartings et al. 1991). Moreover, Southern analysis revealed that 10 to 12 copies of *Bg*-homologous sequences are present in the maize genome (Motto et al. 1989).

One feature of the *Bg-rbg* transposable element system is its apparent widespread occurrence in natural maize populations. A search for the presence of *Bg* elements based on their ability to induce instability of the *o2-m(r)* allele revealed active autonomous elements in maize populations from distinct geographical areas (Montanelli et al. 1984).

In this paper, the distribution of *Bg*-like sequences among maize inbred lines and races, teosintes, and related genera has been investigated at the molecular level. The copy number and distribution of *Bg*-like sequences suggest a not too recent development of the *Bg* element in maize. *Bg*-homologous sequences are indeed present in a similar number in all of the *Zea* taxa analyzed.

Materials and methods

Plant material, DNA preparation and Southern analysis

The accessions of the genus *Zea* and of related genera which have been included in our analyses are listed in Table 1.

Genomic DNA for Southern analysis was extracted from 2-week-old, greenhouse-grown seedlings. In the case of maize inbreds, approximately 25 seedlings were pooled, while teosinte taxa and maize races were analyzed as single plants. Plant material was harvested in liquid nitrogen and genomic DNA extracted as previously described (Motto et al. 1988). Southern blotting of *Zea* and *Tripsacum* samples was performed essentially as described by Hartings et al. (1995), while Southern analyses of related genera were performed at reduced stringency. Hybridization of these blots was performed at 60 °C, while filters were washed in 2 × SSPE, 0.1% SDS for 20 min at room temperature and in 1 × SSPE, 0.1% SDS for 20 min at 65 °C. Filters were exposed for 16 h to Kodak XAR-5 films using intensifying screens. In order to accurately evaluate more weakly hybridizing bands, filters were exposed for 72 h when needed.

DNA probes

Bg probes for Southern analysis were prepared by polymerase chain reaction (PCR) amplification using a plasmid carrying the complete *Bg* sequence as a template. Oligonucleotides located at position 1681 and 2811, 939 and 1369, and 3448 and 4297 of the *Bg* sequence (Hartings et al. 1991) were used in PCR reactions to amplify probes

Table 1 List of accessions analyzed in this study

	Line or acquisition	Source	Comments[a]
Zea section *Luxuriantes*			
1.	*Z. perennis*	Collins	s.n.[d]
2.	*Z. diploperennis*	Guzman	777
3.	*Z. luxurians*	Iltis	G-42
4.	*Z. luxurians*	Iltis	30919
Zea section *Zea*			
5.	*Z.m.* ssp. *parviglumis*	Beadle	s.n.
6.	*Z.m.* ssp. *parviglumis*	Kato	K-77-13
7.	*Z.m.* ssp. *huehuetenangensis*	Iltis & Lind	G-120
8.	*Z.m.* ssp. *huehuetenangensis*	Beadle	s.n.
9.	*Z.m.* ssp. *mexicana*	Doebley	625
10.	*Z.m.* ssp. *mexicana*	Doebley	642
11.	*Z.m.* ssp. *mexicana*	Beadle	s.n.
	Z.m. ssp. *mays*		
12.	Chapalote	ISC[b]	Mexico
13.	Black Mexican Sweet	ISC	Mexico
14.	Pisanckalla	IAO[c]	Bolivia
15.	Pura	IAO	Bolivia
16.	Purito	IAO	Bolivia
17.	Morocho chico	IAO	Bolivia
18.	Morocho de Tarija	IAO	Bolivia
19.	H99	ISC	Illinois Synt. 60c
20.	Mo17	ISC	187.2 × C103
21.	C103	ISC	LSC[e]
22.	Va17	ISC	WF9 × T8
23.	Va22	ISC	Va17 × $C103^2$
24.	WF9	ISC	Wilson Farm Reid
25.	B73	ISC	BSSS[f]
26.	B37	ISC	BSSS
27.	Oh43	ISC	LSC
28.	A619	ISC	A171 × $Oh43^2$
29.	HY	ISC	Illinois High Yielding
30.	Lo881	ISC	C103 synthetic
31.	Lo904	ISC	B37 × $B73^2$
32.	Lo924	ISC	Mo17 × $H99^2$
33.	Lo951	ISC	BSSS [P3183]
34.	Lo1055	ISC	Lo950 × Lo951
Other *Andropogoneae*			
35.	*Tripsacum dactyloides*	ISC	s.n.
	Sorghum bicolor		
36.	P721	ISC	
37.	NK121A	ISC	
Other *Gramineae*			
38.	*Hordeum vulgare*	ISC	
39.	*Avena sativa*	ISC	
40.	*Secale cereale*	ISC	
41.	*Triticum spelta*	ISC	
42.	*Triticum durum*	ISC	
43.	*Triticum aestivum*	ISC	
44.	*Oryza sativa*	ISC	

[a] Denotes: Collection tag of teosintes (1–11 and 35); geographic origin of maize races (12–18); pedigree of inbred lines (19–34)
[b] Istituto Sperimentale per la Cerealicoltura
[c] Istituto Agronomico dell'Oltremare
[d] Sine numero, not numbered
[e] Lancaster Sure Crop
[f] Iowa Stiff Stock Synthetic

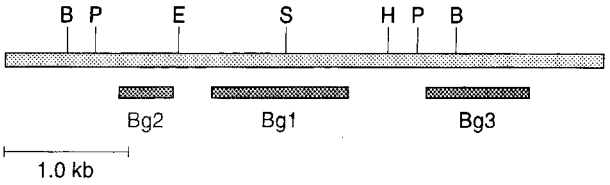

Fig. 1 Map of the *Bg* element. The *Eco*RI (*E*), *Hin*dIII (*H*), *Pvu*II (*P*), *Bst*EII (*E*), and *Sal*I (*S*) restriction sites are shown. The relative position of fragments used as molecular probes (*Bg1*, *Bg2*, and *Bg3*) are indicated *under* the *Bg* map

Bg1, *Bg2*, and *Bg3*, respectively (Fig. 1). PCR amplification reactions were performed in a 100 µl final volume and contained 50 m*M* Tris. HCl pH 8.3; 50 m*M* KCl; 1.5 m*M* $MgCl_2$; 250 µ*M* each of dATP, dTTP, dCTP, and dGTP; 0.5 m*M* of 5' oligo; 0.5 m*M* of 3' oligo; 0.5 units of *Taq* polymerase; 1 ng of plasmid DNA was used as a template. Mineral oil was used to prevent evaporation of the samples at high temperatures. Amplification was obtained through 25 cycles with the following temperature profile: 94 °C for 30 s; 55 °C for 30 s; 72 °C for 1 min. Products were run on a 0.8% agarose gel, bands were cut out, and probes further purified by electroelution.

Statistical analysis

In order to quantify the degree of similarity between the inbred lines, indexes of molecular similarity (MS) were calculated according to the following equation: $MS = 200N_{xy}/(N_x + N_y)$, where MS is the molecular similarity coefficient between inbred lines x and y, N_{xy} is the number of common bands for x and y, and N_x and N_y are the total number of bands detected in x and y, respectively. Since MS reflects the proportion of bands that cannot be distinguished between inbreds, a MS value of 100 indicates identity of 2 lines, whereas a MS value of 0 indicates maximum diversity between 2 lines.

Results

Copy number

To analyze the distribution and copy number of *Bg*-like sequences among maize inbreds, Southern analyses were performed on 16 elite lines using two restriction enzymes (*Eco*RI and *Hin*dIII) in combination with probes *Bg1*, *Bg2*, or *Bg3* (Table 2). As expected, the results of these analyses confirmed the variability in band number with both the restriction enzyme and molecular probe. However, the average band numbers calculated for each combination of probe and enzyme did not show significant differences, although probe *Bg3* did reveal a slightly larger number of hybridizing fragments. In fact, upon joint evaluation of the band numbers obtained with both *Eco*RI and *Hin*dIII, the 16 inbred lines revealed an average band number of 7.3 ± 1.4 with probe *Bg1*, 8.5 ± 1.9 with probe *Bg2*, and 10.2 ± 1.9 with probe *Bg3*. The overall average of *Bg*-homologous bands for the inbred lines was 8.7 ± 2.1.

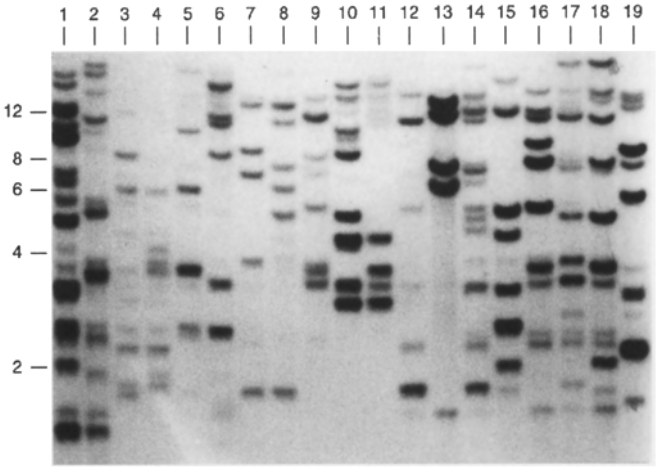

Fig. 2 Southern analysis of teosintes and maize races. Genomic DNA was restricted with *Hin*dIII endonuclease and hybridized with probe *Bg1*. *Lane 1 Z. perennis*, *2 Z. diploperennis*, *3 Z. luxurians*, *4 Z. luxurians*, *5 Z. m. mexicana*, *6 Z. m. mexicana*, *7 Z. m. mexicana*, *8 Z. m. parviglumis*, *9 Z. m. parviglumis*, *10 Z. m. huehuetenangensis*, *11 Z. m. huehuetenangensis*, *12* Chapalote, *13* Black Mexican Sweet, *14* Pisankalla, *15* Purito, *16* Pura, *17* Morocho Tarija, *18* Morocho chico, *19 Tripsacum dactyloides*. Molecular weights are indicated (in kb)

Table 2 Number of bands per line, diversified by probe and restriction enzyme

Inbred	*Bg1*		*Bg2*		*Bg3*		Mean[a]
	*Eco*RI	*Hin*dIII	*Eco*RI	*Hin*dIII	*Eco*RI	*Hin*dIII	
H99	6	7	7	6	10	10	7.6 (1.7)[c]
Mo17	10	9	11	10	11	12	10.5 (1.0)
C103	9	8	10	7	9	9	8.6 (0.9)
Va17	9	8	10	9	9	11	9.3 (0.9)
Va22	7	8	8	9	8	9	8.2 (0.7)
WF9	4	6	6	6	7	6	5.9 (0.9)
B73	7	7	9	7	9	13	8.6 (2.1)
B37	7	7	11	9	11	13	9.6 (2.2)
OH43	6	6	9	6	10	11	8.0 (2.1)
A619	6	5	9	6	11	10	7.6 (2.4)
HY	7	6	10	6	9	10	8.0 (1.7)
Lo881	8	8	11	9	11	14	10.2 (2.1)
Lo904	7	8	11	8	10	14	9.6 (2.4)
Lo924	9	9	13	9	10	12	10.3 (1.6)
Lo951	10	9	9	6	7	12	8.8 (1.9)
Lo1055	6	6	9	6	8	11	7.6 (1.9)
Mean[b]	7.4 (1.6)	7.3 (1.2)	9.6 (1.6)	7.4 (1.4)	9.4 (1.3)	11.0 (2.0)	8.7 (2.1)

[a] Mean of band numbers across inbred lines
[b] Mean of band numbers across combinations probe-enzyme
[c] Standard deviation

Maize races and teosintes were assayed with probe *Bg1* in combination with the *Eco*RI and *Hin*dIII enzymes (Fig. 2). The band number for each accession was calculated as the rounded-off average of approximately 10 individual plants. Again, *Bg* copy number was directly correlated with *Bg*-homologous band numbers on Southern blots. Section *Luxuriantes* teosintes revealed an average band number of 16.4 ± 3.5, a value considerably higher than the average band number (7.3 ± 1.4) obtained for the inbred lines assayed with the same *Bg1* probe. However, this difference is at least in part due to the assignment of the tetraploid perennial *Zea perennis* to this group. Bearing in mind the heterozygous nature of the *Luxuriantes* accessions, this difference in band number is probably not significant. Section *Mays* teosintes displayed an average band number of 10.3 ± 2.8, a value close to that obtained for the inbred lines. Finally, the maize races displayed an average band number of 10.4 ± 3.3, a value in good agreement with that found for the inbred lines. When the data obtained for the 34 *Zea* accessions was combined, an average of 9.5 ± 3.1 bands hybridizing with the *Bg* element were present among strains.

From the 10 accessions of related genera, only *T. dactyloides* DNA hybridized with the *Bg1* probe, revealing 14 bands with *Eco*RI and 12 bands with *Hin*dIII (Table 3). These values are in agreement with the average band number obtained for the *Zea* accessions. All other accessions of related genera failed to hybridize with the *Bg* probes, even under conditions of reduced stringency (data not shown).

Table 3 Number of hybridizing bands per line or acquisition

	Accession	*Eco*RI	*Hin*dIII
1.	*Z. perennis*	22	21
2.	*Z. diploperennis*	19	15
3.	*Z. luxurians*	14	14
4.	*Z. luxurians*	12	14
5.	*Z. m. parviglumis*	11	8
6.	*Z. m. parviglumis*	15	9
7.	*Z. m. huehuetenangensis*	9	11
8.	*Z. m. huehuetenangensis*	6	8
9.	*Z. m. mexicana*	13	12
10.	*Z. m. mexicana*	16	10
11.	*Z. m. mexicana*	9	7
12.	*Z. m. mays* [Chapalote]	10	7
13.	*Z. m. mays* [Black Mexican Sweet]	8	5
14.	*Z. m. mays* [Pisanckalla]	13	5
15.	*Z. m. mays* [Pura]	11	10
16.	*Z. m. mays* [Purito]	8	12
17.	*Z. m. mays* [Morocho chico]	14	16
18.	*Z. m. mays* [Morocho de Tarija]	13	14
35.	*T. dactyloides*	14	12

Bg-like fragments display a conserved pattern

A comparison of the restriction patterns of related inbred lines, obtained with the *Eco*RI and *Hin*dIII enzymes in combination with the three *Bg* probes, revealed numerous hybridizing fragments in common.

Data obtained for the LSC inbred lines H99, Lo924, and Mo17 revealed high similarity indexes (Fig. 3A). Considering the pedigree of Lo924, we expected this line to have a higher similarity with H99 than with Mo17. However, a comparison of the hybridization patterns revealed a high MS value (95.9) for Lo924 and Mo17. On the contrary, Lo924 and H99 exhibited a MS value of 58.8, while H99 and Mo17 revealed a MS value of 54.0. These results are in good agreement with earlier findings that indicate the prominence of Mo17 germ plasm in Lo924 despite its pedigree (Ajmone-Marsan et al. 1992; Livini et al. 1992).

Comparison of the restriction patterns obtained for the LSC inbred lines C103, Va17, and Va22 revealed a considerable degree of conservation, with the Va22 inbred line showing an intermediate pattern (Fig. 3B). In fact, Va22 and Va17 exhibited a MS of 82.6, a value only slightly higher than that calculated for Va22 and C103 (73.3), while C103 and Va17 revealed a MS value of 58.2. Again, these results were to some extent unexpected, considering the pedigree of line Va22, but were confirmed by cluster analysis performed on these inbreds that indicated a low association between Va22 and C103 (Ajmone-Marsan et al. 1992; Livini et al. 1992).

The BSSS lines B37, Lo904, and B73 displayed a high degree of similarity (Fig. 3C). Considering the Lo904 pedigree, we expected an intermediate position of this inbred with respect to the two parental lines, biased towards the B73 line. In fact, upon calculation of molecular similarity indexes, values of 87.9 for B73 and Lo904, 70.9 for B37 and Lo904, and 64.8 for B73 and B37 were obtained.

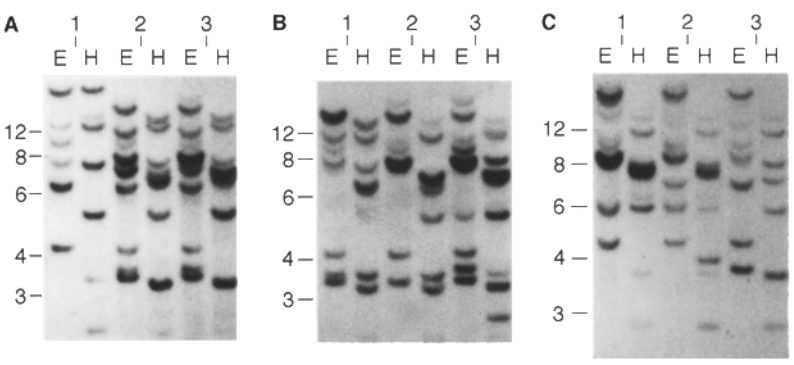

Fig. 3A–C Southern analysis of inbred lines. **A** *1* H99, *2* Lo924, *3* Mo17; **B** *1* C103, *2* Va22, *3* Va17; **C** *1* B73, *2* Lo904, *3* B37. Genomic DNA was restricted with the *Eco*RI (*E*) and *Hin*dIII (*H*) endonucleases and hybridized with probe *Bg1*. Molecular weights are indicated (in kb)

A similar approach was used to calculate the relationship between the seven maize races included in our studies. A comparison of the restriction patterns obtained with the *Eco*RI and *Hin*dIII enzymes in combination with the *Bg1* probe was used to calculate molecular similarities. In this way, a mean MS value of 50.0 was calculated for all seven races. While Mexican and Bolivian races could be divided into two clusters based on relative MS values (data not shown), no further separation of Bolivian races could be achieved. However, race Purito consistently showed the lowest MS values in combination with the other Bolivian races. Within the "Pisanckalla" complex, Purito gave MS values of 46.1 with race Pisanckalla and 46.5 with Pura, while Pisanckalla and Pura displayed a MS value of 58.8. Furthermore, MS values of Purito and Morocho Tarija (24.0) and Purito and Morocho Chico (37.5) were the lowest encountered among the Bolivian races, whereas Morocho Chico and Morocho Tarija showed a MS value of 59.3.

Discussion

Since their discovery in the 1940s (McClintock 1948), transposable elements have been identified in almost all species investigated (Berg and Howe 1989), and although subjected to extensive genetic and molecular study, their origin remains unclear. Little is known about their distribution among species and in different geographical regions, and about their polymorphism, both within a species and between species with various degrees of phylogenetic separation.

The distribution of sequences homologous to the *Bg* transposable element from *Zea mays* ssp. *mays* was investigated in this paper among 34 accessions of the genus *Zea* and ten related species. *Bg*-like sequences, revealed as hybridizing fragments on Southern blots, could be identified in all *Zea* taxa, thereby demonstrating the wide-spread distribution of this element. Southern analyses performed on species of related taxa exposed bands hybridizing with *Bg* in *Tripsacum dactyloides*, which emphasizes the close relationship between this species and the *Zea* taxa. Because the maize ear lacks any seed dispersal mechanism, maize must be considered a strictly domesticated species. If we consider that the first evidence of human civilization in the New World dates back 15,000 years ago, maize must have originated from a teosinte progenitor within the past 15,000 years (Iltis and Doebley 1984). The presence of *Bg*-homologous sequences in teosintes and in *Tripsacum dactyloides* supports the hypothesis that *Bg* might already have existed as a transposable element before the maize-teosinte split, or even before the *Zea-Tripsacum* split, in a progenitor of today's *Maydeae*. This observation is in contradiction with phylogenetic studies on the distribution of various transposable elements among the *Drosophilideae* family and in nematodes indicating that these elements are distributed in a discontinuous fashion among related taxa and hence suggesting that: (1)) these elements can diverge rapidly and may be lost in some species by divergence or genetic drift (Dowsett 1983; Martin et al. 1983; Daniels et al. 1990); (2) their transmission does not seem to be strictly vertical, and some data might be explained by horizontal transfer between species (Daniels et al. 1990; Stacey et al. 1986; Simonelig et al. 1988; Abad et al. 1991).

An analysis of 16 inbred lines with two restriction enzymes in combination with three molecular probes that spanned 75% of the *Bg* sequence revealed an average copy number of 8.7 ± 2.1 *Bg*-homologous fragments per maize genome. It must be stressed, however, that our approach to the evaluation of the number of hybridizing fragments in Southern analysis as a means to calculate the *Bg* copy number will inevitably lead to an underestimation since the exact number of hybridizing bands is difficult to determine. To calculate the band numbers, we counted all of the bands without any consideration to differences in intensity; moreover, only visibly separated bands were counted as doublets.

The hybridization patterns obtained from related inbred lines showed a remarkable degree of similarity. Indexes of molecular similarity were calculated for LSC inbred lines H99, Lo924, and Mo17, and these revealed a degree of similarity as high as 95.9% for the inbreds Lo924 and Mo17. In contrast, Lo924 and H99 exhibited only 58.8% similarity. These results are in good agreement with earlier findings (Ajmone-Marsan et al. 1992; Livini et al. 1992) that indicate the prominence of Mo17 germ plasm in Lo924 despite its pedigree. LSC inbred lines C103, Va17, and Va22 also revealed a considerable degree of conservation, with the Va22 inbred line showing an intermediate pattern. Considering the pedigree of line Va22, these results were unexpected, but did confirm earlier studies performed on these inbreds that indicated a low association among Va22 and C103 (Ajmone-Marsan et al. 1992; Livini et al. 1992). Finally, the BSSS lines B37, Lo904, and B73 displayed a high level of identity with values of 87.9% for B73 and Lo904, 70.9% for B37 and Lo904, and 64.8% for B73 and B37, thereby confirming the pedigree of inbred Lo904.

The number of hybridizing bands detected in this study for the maize and teosinte accessions were, considering the degree of heterozygosity of the different accessions analyzed, similar. This is a noteworthy observation since maize and teosinte have had a very different history in the last 10,000 years. While maize, a domesticated form of teosinte, was heavily selected for a restricted number of traits, the latter evolved under natural selection (Doebley and Stec 1991 and references therein).

The finding that both maize and teosinte, despite their divergent past, reveal a similar number of *Bg*-like sequences, is open to different interpretations. First, it is possible that the majority of *Bg* sequences in the genome have lost the ability to transpose. Alternatively, *Bg* elements might transpose only rarely, due to the presence of a mechanism controlling transposition rate. This

would explain the relatively low and constant number of *Bg*-like sequences found in the taxa. Further investigation is necessary to assess the existence of such a mechanism and to evaluate whether it is imposed by the transposable element itself, or whether it depends on host factors.

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