Nigon element analysis of *Meloidogyne hapla*

Introduction

The genus *Meloidogyne* includes both diploid species and major clades of polyploid hybrids, with karyotypes of n=17 in diploids and n of up to 70 in polyploids. *Meloidogyne hapla* is diploid and has 17 chromosomes, defined by genetic mapping and karyotyping (Thomas et al., 2012). The genome assembly has been superscaffolded into 19 scaffolds using genetic cross mapping, with chromosomes 1 (mh_1A, mh_1B) and 2 (mh_2A, mh_2B) split in two. Each single superscaffold (e.g. "mh_10.12.8") corresponds to a single genetic linkage group. There are 275 short, unplaced scaffolds. The superscaffolds were analysed in detail, with the split chromosomes 1 and 2 kept as two fragments.

Methods

Nigon-unit defining loci were identified in *Meloidogyne hapla* and their mapping to superscaffolds recorded.

Results

Compared to the other nematode species analysed, the published genome sequence for *M. hapla* had a noticeably lower proportion of matches to the set of shared orthologues (Figure 6 B,C). Of 2191 Nigon-defining loci, 1688 (or 77%) had matches in the *M. hapla* genome. The mapping rate was lowest for Nigon set X (68%) and highest for Nigon set B (81%) (Table S12). Three quarters (75%) of the mapped loci from the Nigon-defining sets were present in the chromosome-sized contigs, with the highest proportion of Nigon set matches in these unplaced contigs from the X set (38%). Most of the unplaced scaffolds had a single Nigon locus mapped (range 1-17, mean 1.54).

The number of Nigon-defining loci mapped to each chromosomal molecule ranged from 8 to 157. The two chromosome 1 contigs had a total of 201 loci mapped and the two chromosome 2 contigs had a total of 144 loci mapped. Four of the shorter chromosome-mapped scaffolds had <40 Nigon-defining loci mapped, and these were not analysed further. Assessment of possible assignment to ancestral Nigon elements using simple counts or proportions of mapped Nigon-defining loci (Table S12) biased assignment to those Nigon elements that contained more loci (e.g. the number of loci used to define Nigon X is less than one sixth the number used to define Nigons A and C). Thus we normalised Nigon-defining locus counts per chromosomal scaffold by expressing them as the proportion of Nigon-defining loci from each Nigon set.

Using normalised proportions, a few chromosomal superscaffolds could be assigned to ancestral Nigon elements with some confidence. Thus chromosome

mh_16 contained 50% of all the NigonE set loci mapped to the chromosomes, and chromosome mh_8 contained 38% of the mapped NigonX set. Other chromosomes showed a bias towards one or a few Nigon-defining sets. Chromosome mh_5 had overrepresentation of NigonB, mh11 of NigonN, mh4 of NigonC, mh5 of NigonB and mh_5 of NigonX loci. Notably, the assignments of the two halves of chromosome 1 (mh-1A and mh_1B) were congruent (highest proportion to NigonA in both), while the mappings of mh_2A and mh_2B from chromosome 2 were discordant (highest proportions to NigonB and NigonD respectively).

Discussion

Overall, the assignment of *M. hapla* chromosomal superscaffolds to Nigon origin is complex. No scaffold was simply assigned to one Nigon, but only seven had content where one Nigon set constituted a majority of mapped loci, and these counts were biased by the count of loci in each set. In *Strongyloides ratti* and *Steinernema carpocapsae*, we identified a shared fusion of NigonB, NigonD and NigonX to form the X chromosome of each species, with additional complex rearrangements in *S. ratti*. In the *M. hapla* assignments there is no signal of this predicted fusion as NigonX-derived loci are not particularly associated with either NigonB or NigonD loci. The two scaffolds on which a majority of NigonX loci were mapped (mh6 and mh8) had very few NigonD loci (zero and 1 loci respectively). The additional fusions predicted in *S. ratti* (fusions of C+E+N and of A+C+D+E+N) were also not evident.

Thus we conclude that, if the chromosomes of *M. hapla* contain a remnant signature of their derivation from ancestral Nigon elements, the fragmentation implied in going from seven ancestral to seventeen extant chromosomes also involved a large number of translocations. It will be very informative to examine additional high-quality genomes from additional *Meloidogyne* species, and other chromosomally-contiguous genomes from the Heteroderidae. Many *Meloidogyne* species are complex triploid and tetraploid hybrids, making assembly and interpretation difficult, but recent progress with long read data generation shows promise in generation of high quality genome estimates (Susič et al., 2020; Szitenberg et al., 2017).