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Deep ancestry of programmed genome rearrangement in lampreys

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ABSTRACT

In most multicellular organisms, the structure and content of the genome is rigorously maintained over the course of development. However some species have evolved genome biologies that permit, or require, developmentally regulated changes in the physical structure and content of the genome (programmed genome rearrangement: PGR). Relatively few vertebrates are known to undergo PGR, although all agnathans surveyed to date (several hagfish and one lamprey: *Petromyzon marinus*) show evidence of large scale PGR. To further resolve the ancestry of PGR within vertebrates, we developed probes that allow simultaneous tracking of nearly all sequences eliminated by PGR in *P. marinus* and a second lamprey species (*Entosphenus tridentatus*). These comparative analyses reveal conserved subcellular structures (lagging chromatin and micronuclei) associated with PGR and provide the first comparative embryological evidence in support of the idea that PGR represents an ancient and evolutionarily stable strategy for regulating inherent developmental/genetic conflicts between germline and soma.

1. Introduction

Programmed genome rearrangement has been observed in several vertebrate and invertebrate taxa and appears to have arisen multiple times over the evolutionary history of eukaryotes (Wang and Davis, 2014). Notably, PGR has been previously observed within two deeply diverged vertebrate groups (jawless vertebrates). Reproducible differences in the structure and content of germline and somatic cells have been reported for all hagfish species surveyed to date (Nakai et al., 1995). More recently, PGR was also discovered and characterized in the sea lamprey (*Petromyzon marinus*) (Smith et al., 2009, 2012; Timoshevskiy et al., 2016; Bryant et al., 2016). The lineage leading to *P. marinus* diverged from the ancestral lineage of all other extant (jawed) vertebrates and the lineage leading to hagfish approximately 500 million years ago (MYA) (Orlov and Beamish, 2016), raising questions as to the ancestry and evolutionary significance of PGR in *P. marinus*, ancestral gnathostome lineages and the ancestral vertebrate lineage.

Recent efforts have made progress in identifying the gene targets and cellular mechanisms of PGR in *P. marinus* (Smith et al., 2012; Timoshevskiy et al., 2016; Bryant et al., 2016). These analyses indicate that PGR contributes to early differentiation events in the embryo that define somatic and germline lineages, wherein DNA elimination acts to permanently silence “germline” genes in somatic cell lineages. Notably, lamprey PGR parallels differentiation events that occur early in gnathostome development, with respect to the genes that are relegated to the germline (Smith et al., 2012; Bryant et al., 2016) and with respect to the earliest epigenetic modification events that mediate these events (Timoshevskiy et al., 2016). Given the available data, it is possible that observation of PGR in hagfish and sea lamprey reflects the inheritance and maintenance of PGR from their common ancestor, inheritance from the common ancestor of all extant vertebrates, or the independent evolution of superficially similar genome biologies in two deeply diverged vertebrate lineages akin to that observed for closely related finch species (del Priore and Pigozzi, 2014). While several embryological and genetic details of PGR have been characterized in *P. marinus*, analogous datasets do not currently exist for any other rearranging vertebrate, which has precluded direct comparative analyses that are necessary to begin evaluating these alternate evolutionary scenarios.

Here we describe the development of new hybridization-based approaches for performing comparative embryological studies of PGR and use these methods to further resolve the ancestry of PGR in the lamprey lineage. These studies reveal several conserved cellular/developmental features of PGR in two divergent lamprey species (lagging chromatin and micronuclei), observations that are interpreted as strong evidence that PGR has occurred in lampreys for at least the last 40 million years.

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2. Results and discussion

To shed light on the deeper evolutionary history of PGR in the lamprey lineage, we obtained early-stage embryos from the Pacific lamprey (*Entosphenus tridentatus*). The species *E. tridentatus* was selected as a representative of a clade of lampreys (genera *Entosphenus*, *Lethenteron* and *Lampetra*) that diverged from the sea lamprey's lineage ~40 MYA, corresponding to the deepest divergence within the family Petromyzontidae (Northern Hemisphere lampreys) (Anon, 2016). Presumably features shared between *P. marinus* and *E. tridentatus* reflect aspects of their biology that were inherited from the common ancestor of all petromyzontids. Pacific lamprey embryos were generated using husbandry and *in vitro* fertilization methods optimized for the species (Anon, 2016). Embryos were sampled at 1, 2 and 3 days post fertilization (Tahara stages 7, 9/10 and 11, respectively) (Tahara, 1988), fixed and cleared according to protocols developed for *P. marinus* (Timoshevskiy et al., 2016). Examination of *E. tridentatus* embryos revealed anaphases with lagging chromatin at 2 days post fertilization and interphase cells with micronuclei similar to those observed in *P. marinus* embryos at the same developmental stages (Figs. 1 and 2). Lagging chromatin and micronuclei are considered hallmarks of PGR in *P. marinus* (Timoshevskiy et al., 2016). We interpret these observations as strong evidence that PGR occurs in both species through similar, highly orchestrated events. Notably, micronuclei and lagging segments appear to be smaller in *E. tridentatus* when compared to those in *P. marinus*. Given the large difference in genome size between *P. marinus* (< 2 Gb) and other petromyzontids (< 1.5 Gb) (Robinson et al., 1975) observed size differences may not be particularly surprising. This difference in genome size presumably reflects the recent expansion of repetitive elements within the *P. marinus* genome, which harbors an exceedingly large number of high-identity repeats (Smith et al., 2013; Mehta et al., 2013).

To further test the assumption that lagging chromatin in divergent lamprey species reflects a shared evolutionary origin of PGR, we developed probes that specifically label eliminated chromatin in *P. marinus* throughout embryogenesis. These probes were generated by first isolating lagging chromatin from individual anaphases via laser capture microdissection, then amplifying and labeling captured sequences. Hybridization to *P. marinus* embryos confirmed that these probes specifically label eliminated chromatin before and during PGR (Fig. 1). These probes yielded strong and specific hybridization to lagging chromosomes within elimination anaphases and to micronuclei

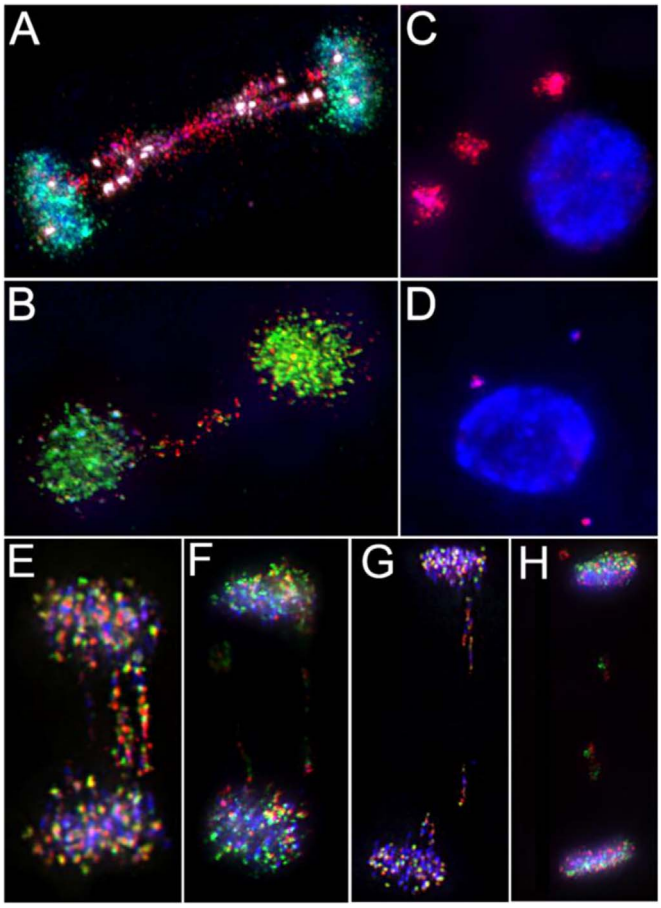

Fig. 2. Evidence for PGR in Northern Hemisphere lampreys. A-H) Cells undergoing DNA elimination in *P. marinus* and *E. tridentatus* embryos. Cells are hybridized with probes generated from amplified lagging chromatin that was isolated by laser capture from *P. marinus* (eliminated DNA: red) and counterstained with DAPI (blue). **A**) An elimination anaphase from *P. marinus*. This anaphase is also labeled with somatic CoT_2 DNA (green) and the eliminated element Germ1 (white). **B**) An elimination anaphase from *E. tridentatus*, counter-labeled with *E. tridentatus* CoT_2 DNA. **C-D**) Post-elimination interphase cells showing localization of eliminated DNA to micronuclei in **C**) *P. marinus* and **D**) *E. tridentatus*. **E - H)** Elimination anaphases from *E. tridentatus*, counter-labeled with *P. marinus* somatic CoT_2 DNA (green). **E)** early/mid anaphase **F)** mid anaphase **G,H)** late anaphase.

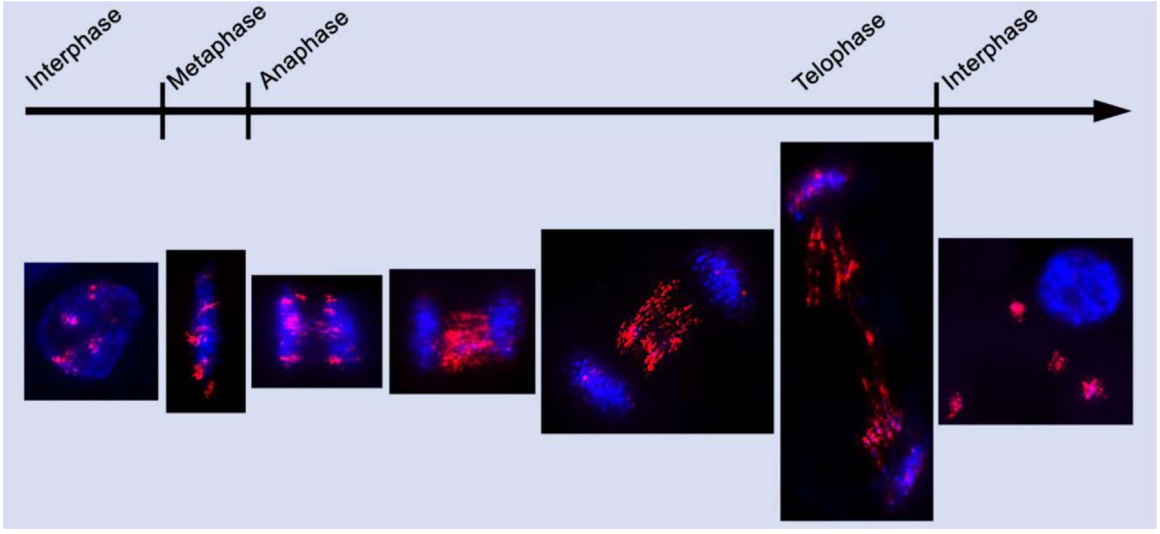

Fig. 1. Tracking germline-specific DNA before and during programmed elimination. Laser-capture FISH probes mark eliminated sequences during all phases of the cell cycle, including those that precede the first cellular events known to be associated with programmed genome rearrangement (lagging of eliminated chromatin). Cells are hybridized with probes generated from amplified lagging chromatin that was isolated by laser capture from *P. marinus* (eliminated DNA: red) and counterstained with DAPI (blue).

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