Investigating Developmental System Drift in germ-layer specification in the lamprey *Lethenteron camtschaticum*.

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Introduction

Homology, the similarity of form in species of common descent, is a central concern of evolutionary-developmental biology. It is suggested that the developmental pathways conjuring homology are largely static, however a new concept, Developmental System Drift (DSD), states that multiple, varying developmental pathways can give rise to the same phenotype. DSD, then, is the competence of a developmental pathway to undergo modification and manipulation by the environment without changing the phenotype (Fig1).

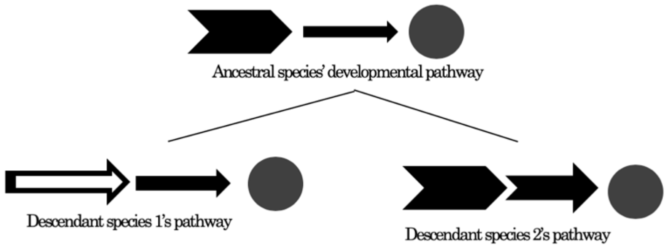

Fig1. DSD of ancestral pathway in descendants. Developmental pathway altered, but trait is conserved. Arrows indicate genes and circle indicates phenotype (homology). Adapted from True and Haag (2001).

Gastrulation is one of the most instrumental and evolutionarily conserved processes in the course of development. The emergence of the germ layers is marked by the deployment of ancestral specifiers such as *ets1*, *hex* and *tgif1* across the deuterostome invertebrate lineages. The jawed vertebrate lineage (gnathostomes), however, breaks this tradition. Ancestral specifiers *ets1*, *hex* and *tgif1* are replaced by homeobox, species-specific genes (orphan genes) such as *dharma* in zebrafish and *siamois* in *Xenopus* (Fig2). This shift in the developmental mechanism of germ-layer formation from that of the invertebrates (ancestral) to that of the gnathostomes (derived) presents itself as an example of DSD.

This research works with the agnathostome lamprey radiated intermediate to the deuterostome invertebrates and the gnathostomes. Possessing homeobox genes (*orphan 1* and *2)* similar to *dharma* and *siamois* in their orphan nature of not having homologues in other species, and expression at gastrulation, lampreys present a possibility of adhering to the gnathostome-like form of derived germ layer specification. Uncovering if, as hypothesised, they exhibit a derived or, alternatively, an ancestral from of germ layer specification is the central aim of this endeavor, where it can help approximate the emergence of the same DSD in the evolutionary history of deuterostomes.

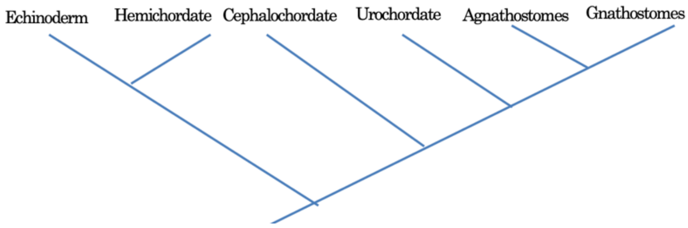

Fig.2 Deuterostome Phylogenetic tree. Echinoderms to Urochordates (deuterostome invertebrates) show ancestral (*ets1, hex, tgif1* inclusive) while Gnathostomes show a derived (*siamois, dharma* characterised) germ-layer specification. DSD seen for the same in deuterostome evolution.

Methodology

L.camtschaticum adults, collected from Hokkaido, were artificially fertilised, and their embryos incubated until gastrula stage and later fixed. *In situ hybridisation* using riboprobes done to look for *ets1*, *hex*, *tgif1*, *orphan1* and *orphan2* gene expression. Orphan genes selected on the basis on lack of homologues in other species and homeobox nature.

Expected Results and Implications

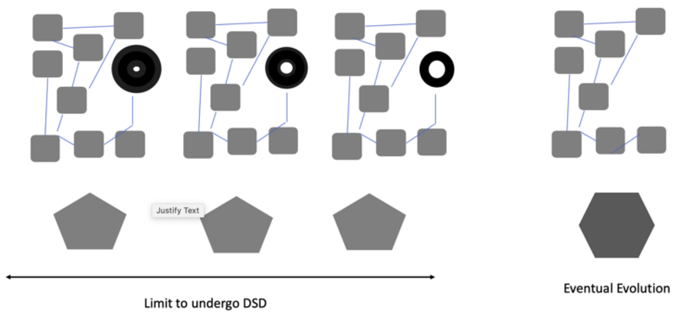

Fig3. Limit of a Developmental Pathway to undergo DSD. Change can be buffered (circle disappearing/ gradual inactivity) up to a limit before it affects the phenotype and leads to evolution and speciation.

Given the presence of orphan genes, expressed exclusively at gastrulation, lampreys are expected to conform to the derived germ-layer specification, as seen in gnathostomes. If so, then this could point to the lineage associated with the origin of this DSD.

As more examples of DSD emerge, they add weight to the new understanding of developmental mechanisms that minuscule changes in developmental pathways pile up over time before the end product is altered. Tracing these changes at molecular and genetic levels can eventually show the extent to which a pathway can undergo DSD before changing the phenotype, i.e. giving rise to a new species and phenotypic and developmental diversity (Fig3).