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Wnt, *Frizzled*, and *sFRP* gene expression patterns during gastrulation in the starfish *Patiria (Asterina) pectinifera*

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ABSTRACT

By the initial phase of gastrulation, Wnt pathway regulation mediates endomesoderm specification and establishes the animal-vegetal axis, thereby leading to proper gastrulation in starfish. To provide insight into the ancestral mechanism regulating deuterostome gastrulation, we identified the gene expression patterns of *Wnt*, *Frizzled* (*Fz*), and secreted frizzled-related protein (*sFRP*) family genes, which play a role in the initial stage of the Wnt pathway, in starfish *Patiria (Asterina) pectinifera* embryos using whole mount *in situ* hybridization. We identified ten *Wnt*, four *Fz*, and two *sFRP* paralogues. From the hatching blastula to the late gastrula stage, the majority of the *Wnt* genes and both *Fz5/8* and *sFRP1/5* were expressed in the posterior and anterior half of the embryo, respectively. *Wnt8*, *Fz1*, and *Fz4* showed restricted expression in the lateral ectoderm. On the other hand, several genes were expressed *de novo* in the restricted domain of the archenteron at the late gastrula stage. These results suggest that the canonical and/or non-canonical Wnt pathway might implicate endomesoderm specification, anterior-posterior axis establishment, anterior-posterior patterning, and archenteron morphogenesis in the developmental context of starfish embryos. From comparison with the expression patterns observed in *Patria miniata*, we consider that the Wnt pathway is conserved among starfishes.

1. Introduction

Gastrulation is the first dynamic process to establish the body plan and axis during embryogenesis. During gastrulation, embryos specify multiple germ layers to form the outer and inner organs and the multilayered body plans of organisms. The body axis is established and morphologically developed throughout this process. In many animals, the Wnt pathway plays an important role in the initial phase of gastrulation. In this pathway, Wnt and frizzled (Fz) proteins act as secreted ligand and receptor, respectively, and secreted frizzled related proteins (sFRPs) function to moderate the effective range or region of Wnt pathway regulation by direct interaction with the Wnt protein (Mii and Taira, 2009). The Wnt pathway has two distinct signaling pathways based on intercellular signaling molecules; one is the canonical Wnt/β-catenin pathway, and the other is the non-canonical pathway that includes the calcium pathway and the planer cell polarity (PCP) signaling pathway. The conserved canonical Wnt/β-catenin pathway functions in axis formation and the specification of endomesoderm or endoderm during embryogenesis (Hudson et al., 2013; Imai et al., 2000; Logan et al., 1999; Momose et al., 2008; Petersen and Reddien, 2009; Rottinger et al., 2012). On the other hand, the non-canonical Wnt pathway regulates morphogenetic events during embryogenesis, for example gastrulation movement including the convergent extension and orientation of cell polarity (Chen et al., 2012; Niwano et al., 2009; Roszko et al., 2009). Therefore, Wnts, Fzs, and sFRPs are important components for the regulation of many morphogenetic and developmental events.

Echinoderms are one of the animals positioned at the most ancestral branch in deuterostome evolution. Thus, these animals would appear to be suitable to provide evolutionary insight into the ancestral mechanism regulating the initial phase of gastrulation. In sea urchins and starfishes, Wnt pathway regulation mediates endomesoderm specification and establishes the animal-vegetal axis (Logan et al., 1999; McCauley et al., 2015; Miyawaki et al., 2003; Wikramanayake et al., 1998). Accordingly, the sea urchin embryo has been intensively studied and several mechanisms for morphogenesis have been revealed through developmental and molecular biological analyses (Ben-Tabou de-Leon and Davidson, 2009; Ettensohn, 2006; Range, 2014). In contrast, little is

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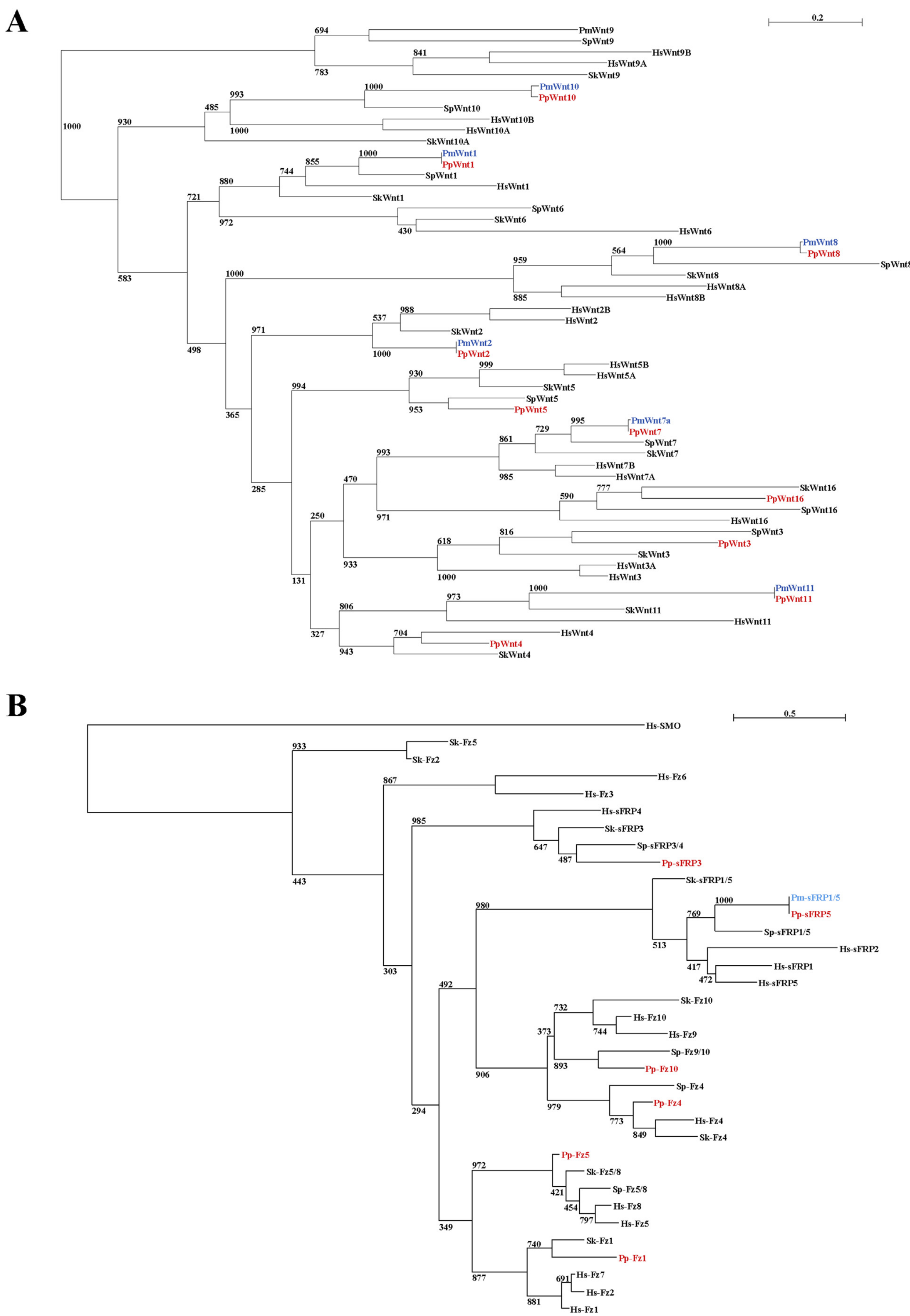

Fig. 1. Phylogenic analyses of *Wnt*, *Fz*, and *sFRP* genes in the starfish *P. pectinifera*. (A) Phylogenetic tree of *Wnt* paralogues generated by the maximum-likelihood method. (B) Phylogenetic tree of *Fz* and *sFRP* paralogues generated by the maximum-likelihood method. *P. pectinifera* and *P. miniata* genes are shown in red and blue text, respectively. Hs, Sp, and Sk indicate human, sea urchin *Strongylocentrotus purpuratus*, and the acorn worm *Saccoglossus kowalevskii* genes, respectively. The number at each branch indicates the percentage of times that a node was supported in 1000 bootstrap pseudoreplications. The scale bar indicates an evolutionary distance of 0.5 amino acid substitutions per position.