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Embryonic expression of a *decapentaplegic* gene in the oligochaete annelid *Tubifex tubifex*

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Abstract

We have cloned and characterized the expression of a *decapentaplegic* homologue (designated *Ttu-dpp*) from the oligochaete annelid *Tubifex tubifex*. RT-PCR analysis and in situ hybridization revealed that *Ttu-dpp* begins to be expressed around the time of the onset of ectodermal germ band (GB) elongation (i.e., the onset of gastrulation). At this time, *Ttu-dpp* expression is detected in the anteriormost part of the GBs. As development proceeds and the GBs elongate, the domain of *Ttu-dpp*-expressing cells extends posteriorly. Then *Ttu-dpp*-expressing cells within the GB are divided into two groups: one group occurs along the ventral midline and coincides with the domain of ventral ganglia; the other is located more dorsally. The latter group of *Ttu-dpp*-expressing cells subsequently undergoes dorsalward expansion, which results in the formation of a lateral stripe of cells in every segment except the first (i.e., segment I). In embryos that undergo body elongation (that is one of the last morphogenetic movements occurring prior to hatchout), *Ttu-dpp* expression in the lateral region is confined to setal sacs, which are arranged in the same transverse plane around the periphery of each segment (except segment I).

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Decapentaplegic (dpp) and BMP2/4 (vertebrate version of dpp) encode signaling molecules (ligands) from the TGF- β family. Dpp/BMP2/4 have been known to play a central role in specification of dorsoventral axis during embryonic development in Drosophila and Xenopus (De Robertis and Sasai, 1996). Developmental significance of these ligands has also been implicated in cell fate specification in ascidians and axis specification during Drosophila imaginal disc development (Lawrence and Struhl, 1996; Miya et al., 1997). In insects (other than fruit fly) and spiders, it has also been suggested that Dpp is involved in leg development, which is accomplished by budding from the embryo proper (Sanchez-Salazar et al., 1996; Niwa et al., 2000; Akiyama-Oda and Oda, 2003; Prpic et al., 2003; Yamamoto et al., 2004).

Despite its obvious importance, the expression pattern of dpp in lophotrochozoans has only been described for

two molluses, *Ilyanassa obsoleta* (Lambert and Nagy, 2002) and *Patella vulgata* (Nederbragt et al., 2002). The former authors reported that *Ilyanassa dpp* mRNA, which associates with centrosomes temporarily, segregate asymmetrically to specific blastomeres during early cleavage stages, while the latter authors confined their observation to the larval stage, and reported that *Patella dpp* is expressed in cells surrounding the shell-forming cells.

In this study, we have isolated a *dpp* homologue from another lophotrochozoan, *Tubifex tubifex* (oligochaete annelid) and examined its expression from 1-cell stage to juveniles.

1. Results and discussion

1.1. Cloning of Tubifex homologue of decapentaplegic

Using a set of degenerate primers, we amplified a *decapentaplegic* (dpp) homologue from *T. tubifex* cDNA generated from mixed embryonic stages. The amplified

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fragment was 263 bp long, and the deduced amino acid sequence aligned well with mollusc Dpp and vertebrate BMP2/4 with more than 60% identity (Fig. 1A). An analysis of the phylogenetic relationships of the predicted amino acid sequence indicated that it clusters (though with low bootstrap support) with Dpp, as opposed to other mem-

bers of BMP family (Fig. 1B). We concluded that this fragment was a portion of the *T. tubifex dpp* orthologue designated *Ttu-dpp*.

We extended the *Ttu-dpp* fragments using gene-specific primers and 3' RACE. The fragments we obtained included the stop codon, 3' untranslated region (73 bp) and a poly-A



Fig. 1. Characterization of *Ttu-dpp*, a *decapentaplegic* homologue from *T. tubifex*. (A) Alignment of the C-terminal domain of Ttu-Dpp with known Dpp/ BMP2/4 class proteins. Asterisks represent amino acid identity. Numbers in parentheses indicate the percentage amino acid identity with Ttu-Dpp. (B) Molecular phylogenetic relationship of Ttu-Dpp to other TGF-β family proteins. The phylogenetic tree was generated by the neighbor joining method using PAUP*4.0b10. Numbers are bootstrap values (as percentages of 1000 replications). Lengths of branches are drawn to the scale indicated. Species abbreviations: Ate, *Archaearanea tepidariorum* (spider); Cel, *Caenorhabditis elegans* (nematode); Dme, *Drosophila melanogaster* (fruit fly); Hsa, *Homo sapiens* (human); Iob, *Ilyanassa obsoleta* (mollusc); Mmu, *Mus musculus* (mouse); Pvu, *Patella vulgata* (mollusc); Tca, *Tribolium castaneum* (beetle); Ttu, *T. tubifex* (annelid); Xla, *Xenopus laevis* (frog).

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