Gene Expression Patterns 21 (2016) 1–6

Contents lists available at ScienceDirect

Gene Expression Patterns

journal homepage: http://www.elsevier.com/locate/gep

Spatiotemporal expression pattern of the zebrafish *aquaporin 8 family* during early developmental stages

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ARTICLE INFO

Article history:
Received 9 March 2016
Received in revised form
31 May 2016
Accepted 1 June 2016
Available online 3 June 2016

Keywords:
Zebrafish
Aquaporin8
Intestinal tract
Liver
Vascular system
Nephrogenesis

ABSTRACT

Aquaporin 8 (Aqp8) is a transmembrane protein that is selectively permeated by water and some small solutes, and physiologically contributes to acid-base equilibrium in the gastrointestinal tract. Here, we described the characterization and spatiotemporal expression pattern of zebrafish *aqp8* (*zaqp8*) gene family, including *zaqp8a.1*, *zaqp8a.2*, and *zaqp8b*, during the early developmental stages. The expression of *zaqp8a.1* started first in the lateral plate mesoderm at the 12-somite stage (ss) and then expanded sequentially to the dorsal aorta, intersegmental blood vessels and then to the dorsal longitudinal anastomotic vessel at 24 h post fertilization (hpf). At 28 hpf, expression of *zaqp8a.1* was also detected in the embryonic heart tube. Four days post fertilization (dpf), strong *zaqp8a.1* expression was detected in the gastrointestinal tract and liver. By 72 hpf, the expression of *zaqp8a.2* was first detected in the primitive gut region but not detected in the liver. The expression of *zaqp8b* was first detected in the intermediate mesoderm at 10 ss. From 24 hpf to 6 dpf, the proximal convoluted segment of the embryonic kidney was marked by *zaqp8b* expression Overall, these differential expression patterns of *aqp8a.1*, *aqp8a.2*, and *aqp8b* suggest that they possibly play distinct roles throughout the embryonic development by controlling or maintaining organ-specific cellular water homeostasis. Our study provides new evidence that organogenesis requires differential roles of Aqp8 proteins in zebrafish.

1. Introduction

Aquaporins (AQPs) are a family of membrane-channel proteins that facilitate the movement of water and small solutes across the cell membrane. Therefore, AQPs are important for maintaining normal body fluid volume by regulating water homeostasis in different cells and organs. The AQP family can be categorized into two subfamilies, water-transporting members (aquaporins) and glycerol-transporting members (aquaglyceroporins). Members of AQPs include AQP0, AQP1, AQP2, AQP4, AQP5, AQP6, and AQP8, while the aquaglyceroporins include AQP3, AQP7, AQP9, and AQP10 (King et al., 2004).

AQP8 is expressed in diverse tissues and organs; therefore, mice *AQP8* (*mAQP8*) is detected in the pancreas, lung, kidney, submandibular gland, diaphragm, testis, spleen, stomach, and brain, and is reported to facilitate transport of water and urea, but not glycerol, across the cell membrane (Ma et al., 1997). In rat, *rAQP8* expression was detected in the liver, pancreas, and salivary gland, and facilitates water transport (Koyama et al., 1997). Recent studies indicate that human AQP8 (hAQP8) stimulates diffusion of hydrogen peroxide across plasma membranes (Bienert et al., 2007). Similarly, mitochondrial AQP8 also facilitates hydrogen peroxide release from the mitochondria and modulates redox signaling pathways evoking diverse biological process, including cell survival or death (Marchissio et al., 2012).

In contrast to mammals, three kinds of Aqp8s (zAqp8a.1, zAqp8a.2 and zAqp8b) were reported in zebrafish. Among their genes, *zaqp8a.1* was highly expressed in cardio-vascular system and associated with the development of hematopoietic cells (Sumanas et al., 2005). However, comprehensive expression patterns for *zaqp8a.2* and *zaqp8b* over different developmental stages has not been elucidated.

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http://dx.doi.org/10.1016/j.gep.2016.06.001
1567-133X/

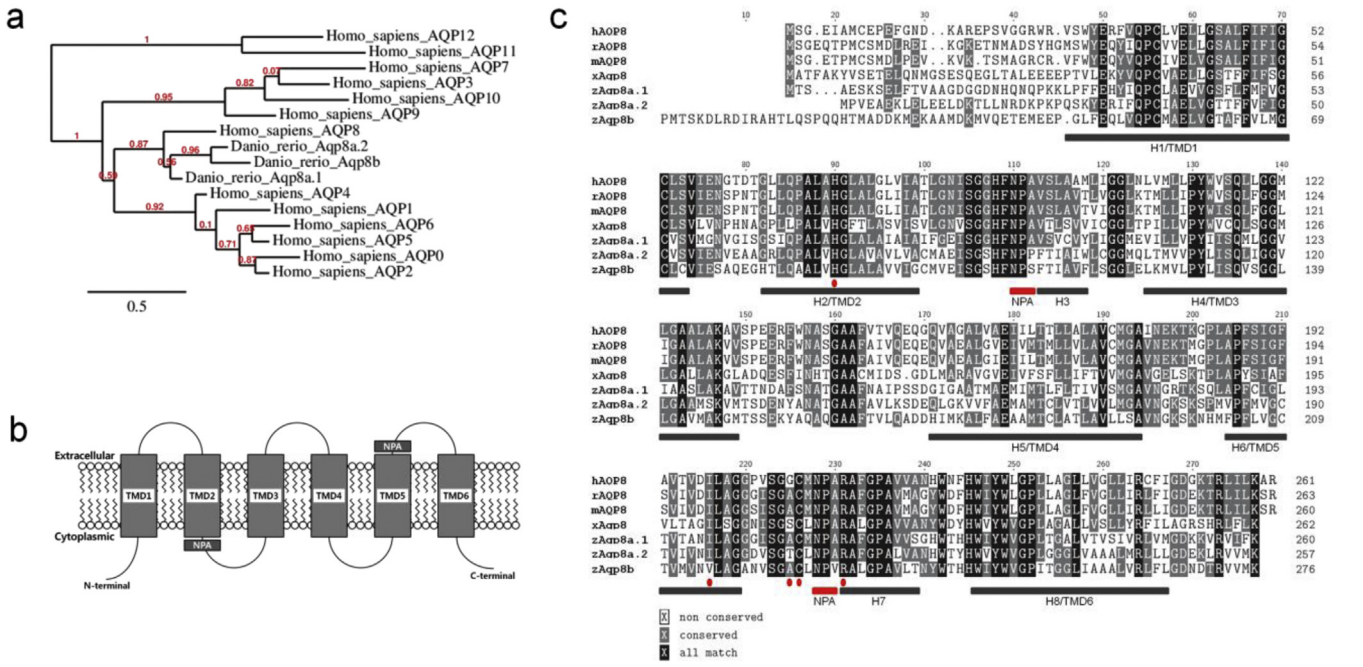

Fig. 1. Phylogenetic and amino acid homology analysis of aquaporins from animal sources. (a) Phylogenetic analysis of AQPs, including zAqp8s. The tree was constructed on the basis of percent identity at the amino acid level. (b) Schematic structure for zAqp8s. (c) High degree of amino acids identity in the NPA motif (red bars) and transmembrane domain (TMD) (black bars) in hAQP8, rAQP8, mAQP8, xAqp8 and zAqp8 families. The key residues for ammonium transportation are indicated by red circles.

Here, we report the detailed expression patterns of three *zaqp8* ortholog genes in early and late zebrafish developmental stages. We newly identified *zaqp8a.1* expression in the gastrointestinal tract and also found that *zaqp8a.2* and *zaqp8b* are mainly expressed in the gastrointestinal tract and pronephric duct, respectively. Taken together, these organ-specific expression patterns of the three *zaqp8* genes suggest differential roles in the formation of proper organ size by controlling or maintaining organ-specific cellular water homeostasis.

2. Results and discussion

2.1. Identification of the three zebrafish aqp8 genes

Three zebrafish *aqp8* genes were annotated as *zaqp8aa, zaqp8ab and zaqp8b* (Tingaud-Sequeira et al., 2010). These genes were more recently designated *zaqp8a.1*, *zaqp8a.2*, and *zaqp8b* and were mapped to chromosomes 12 and 3, respectively. A phylogenetic analysis of the three zAqp8 was consistent with hAQP8 (Fig. 1a).

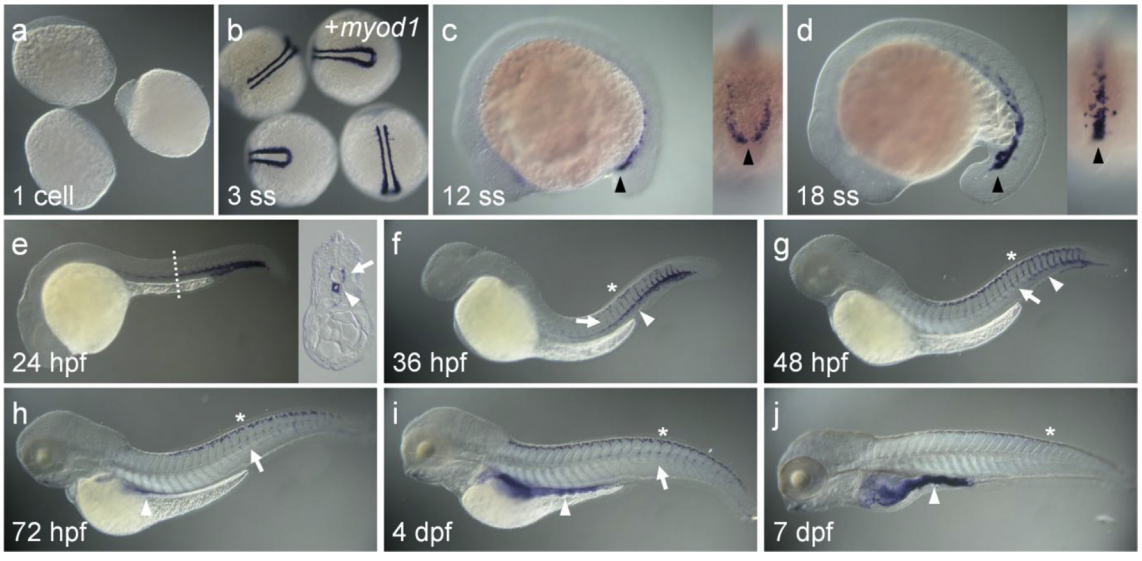

Fig. 2. Expression of *zaqp8a.1* in zebrafish embryos was analyzed by whole mount *in situ* hybridization. Lateral view with anterior to the left (c–j). (a, b) The expression of *zaqp8a.1* was not detected at the one cell stage or at 3 ss. For selection of 3 ss embryos precisely, embryos were co-stained with *myod1* (b). (c–d) The expression of *zaqp8a.1* was first detected in the posterior region of LPM at 12 ss and then anteriorly expanded at 18 ss (arrowhead). (e–j) The expression of *zaqp8a.1* was detected in blood vessels. (e) In DA (arrowhead) and ISV (arrow), expression of *zaqp8a.1* was seen at 24 hpf, but it greatly decreased in DA and ISV at 72 hpf (h) and 4 dpf (i), respectively. (f) Expression of *zaqp8a.1* in DLAV (asterisks) was firstly seen from 36 hpf, and persisted until 7 dpf (j).