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Review article

Evolutionary developmental transition from median to paired morphology of vertebrate fins: Perspectives from twin-tail goldfish

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A B S T R A C T

Vertebrate morphology has been evolutionarily modified by natural and/or artificial selection. The morphological variation of goldfish is a representative example. In particular, the twin-tail strain of ornamental goldfish shows highly diverged anal and caudal fin morphology: bifurcated anal and caudal fins. Recent molecular developmental genetics research revealed that a stop codon mutation in one of the two recently duplicated *chordin* genes is important for the highly diverged fin morphology of twin-tail goldfish. However, some issues still need to be discussed in the context of evolutionary developmental biology (evo-devo). For example, the bifurcated anal and caudal fins of twin-tail goldfish provided early researchers with insights into the origin of paired fins (pectoral and pelvic fins), but no subsequent researchers have discussed this topic. In addition, although the fossil jawless vertebrate species *Euphanerops* is also known to have had a bifurcated anal fin, how the bifurcated anal fin of twin-tail goldfish is related to that of fossil jawless vertebrate species has never been investigated. In this review, we present an overview of the early anatomical and embryological studies of twin-tail goldfish. Moreover, based on the similarity of embryonic features between the secondarily bifurcated competent stripe in twin-tail goldfish and the trunk bilateral competent stripes in conventional gnathostomes, we hypothesized that they share the same molecular developmental mechanisms. We also postulate that the bifurcated anal fin of *Euphanerops* might be caused by the same type of modification of dorsal-ventral patterning that occurs in the twin-tail goldfish, unlike the previously suggested evolutionary process that required the co-option of paired fin developmental mechanisms. Understanding the molecular developmental genetics of twin-tail goldfish allows us to further investigate the evolutionary developmental mechanisms of the origin of paired fins.

1. Introduction

Vertebrate species possess structurally and functionally complex appendages (so called median fins, pectoral and pelvic fins and limbs). These appendages consist of musculoskeletal systems that are established via highly sophisticated molecular developmental mechanisms (Dolle et al., 1993; Fallon et al., 1994; Niswander et al., 1994; Laufer et al., 1994; Sordino et al., 1995; Cohn and Tickle, 1996; Martin, 1998; Rodriguez-Esteban et al., 1999; Takeuchi et al., 1999; Capdevila and Izpisua Belmonte, 2001; Liem et al., 2001; Tickle, 2002; Kardong, 2006). More significantly, these appendages have evolved over 400 million years (Coates, 2003), showing highly divergent variation, as consequences of adaptation to various different types of selective pressures deriving from not only natural but also artificial environments. In fact, goldfish (*Carassius auratus*) is also known as a famous example of diverged appendages as a consequence of artificial selection (Smartt, 2001; Ota and Abe, 2016).

Goldfish have been bred all over the world (Smartt, 2001; Ota and Abe, 2016). According to analyses of Chinese archives, goldfish domestication for ornamental purposes began more than 1000 years ago (Chen, 1956; Smartt, 2001). During the domestication process, several morphologically diverged strains, such as *Ranchu*, *Ryukin*, *Oranda*, and *Demekin*, have been established due to their attractiveness and commercial value (Smartt, 2001; Ota and Abe, 2016). Most of these ornamental goldfish strains also possess bifurcated anal and caudal fins; they are collectively termed the “twin-tail goldfish”. More significantly, the bifurcated caudal and anal fins of the twin-tail goldfish consist of duplicated rays, skeletal structures and muscular

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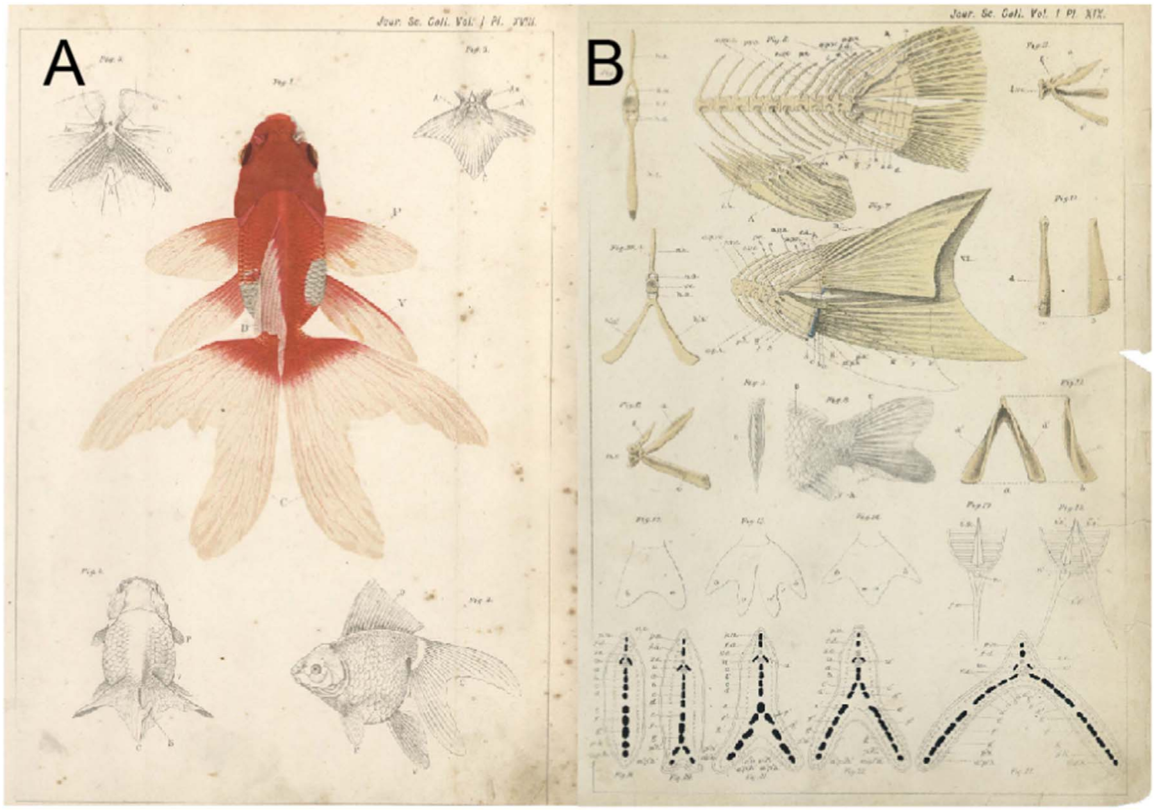

Fig. 1. Description of adult anatomy of twin-tail goldfish by Watase (1887). Goldfish caudal and anal fins (A), skeletal anatomy of twin-tail goldfish (B) as described by Watase (1887).

tissues (Fig. 1A and B). Considering the evolutionarily highly conserved architecture of the caudal fin skeleton of teleost fish, in which the skeleton is located in the sagittal plane of the body (Liem et al., 2001; Kardong, 2006), it is presumed that an exceptionally rare mutation had occurred in the ancestor of the twin-tail goldfish. It is also known that the twin-tail goldfish was first documented in 1596 C. E. (Chen, 1956; Smartt, 2001), suggesting that this morphological variation emerged approximately 600 years after the start of breeding goldfish for ornamental purposes. These lines of evidence indicated that the morphological mutation was genetically fixed during a relatively short time in the comparison with the time periods that are required for large-scale skeletal morphological evolution in nature (Abe et al., 2014). The drastically altered morphology of caudal and anal fins in the ornamental goldfish strains prompted us to investigate their molecular developmental background (Abe et al., 2014).

In our previous study, molecular genetic techniques were applied to the twin-tail goldfish, and the gene responsible for twin-tail morphology was successfully identified as one of two recently duplicated *chordin* genes (Abe et al., 2014). This allowed us to discuss how the twin-tail morphology was established during evolution and how gene (and/or genome) duplication and morphological evolution are related (Abe et al., 2014, 2016; Ota and Abe, 2016). However, there are some unexamined problems derived from early studies and recent paleontological data. For example, Watase (1887) firstly presumed an evolutionary developmental relationship between the goldfish twin-tail morphology and paired fins from his detailed description of anatomical and embryological morphology. His presumption was rejected by several researchers from the late 19th to early 20th centuries (Cori, 1896; Braus, 1906; Storch, 1911), and no subsequent reports have addressed this topic. However, it seems that re-interpretation of his presumption at the level of molecular developmental biology will provide insight into the evolutionary origin and process of the paired fins. Moreover, there is no comparative study of bifurcated anal fins between the twin-tail goldfish and the fossil agnathan *Euphanerops* (Janvier and Arsenault, 2007; Sansom et al., 2013). Based on the unusual morphology of the anal fin of *Euphaneropus*, it has been hypothesized that the developmental mechanisms of paired fins were co-opted for anal fin development (Sansom et al., 2013). However, this hypothesis has never been examined at the level of molecular developmental biology, presumably due to the paucity of analogous examples in extant vertebrates.

In this review, we present an overview of the early studies of twin-tail morphology in goldfish and revisit our previous molecular study, figuring out argument points for an evolutionary developmental relationship between the twin-tail morphology and paired fins. Moreover, we presume that the molecular developmental mechanism underlying the twin-tail morphology of goldfish, which might be shared with that of paired fins during embryonic field formation, is the enlargement of the ventral field caused by mutation in the *chordin* gene, changing the fin-formation competence from a single line into paired stripes. We also interpret the developmental mechanisms of the bifurcated anal fin of *Euphanerops* based on the developmental genetic mechanisms in twin-tail goldfish, and we suggest that the bifurcation of midline fins can occur in nature.

2. Early studies of twin-tail goldfish

To our knowledge, Watase is the one who first provided a detailed description of the skeletal anatomy and embryological morphology of the twin-tail goldfish (Watase, 1887). His careful anatomical analyses of the anal and caudal fins of twin-tail goldfish revealed that almost all of the skeletal elements of anal and caudal fins showed duplication (Fig. 1A and B). Moreover, bifurcated median fin primordia (bifurcated median fin folds) were observed in the caudal part of the twin-tail goldfish embryo (Fig. 2), showing consistency with the adult morphology and recently reported embryonic features (Fig. 2) (Abe et al.,