

## Abstract

Aquatic larvae of many vertebrate lineages develop specialized, cranially located cement or attachment glands which allow them to remain attached to a substrate by means of polysaccharide secretion. The larvae can thus remain still and safe in well-oxygenated water out of reach of any predators until the digestive and locomotory apparatus fully develops. *Xenopus* cement gland is the most thoroughly studied example of this type of glands, since it was used as a model for the anteriormost patterning of the developing head. Based on shared expression patterns of key transcription factors and a similar ectodermal origin it has been repeatedly suggested that *Xenopus* cement gland is homologous to adhesive organs of teleosts and adhesive papillae of ascidians. The lack of comprehensive knowledge on this type of glands in other lineages however rendered any considerations of homology among such a distant lineages rather inconclusive.

In the present work I have focused on a detailed study of the cement glands and other corresponding structures in three representatives of basal actinopterygian lineages: Senegal bichir (*Polypterus senegalus*), sterlet (*Acipenser ruthenus*), and tropical gar (*Atractosteus tropicus*). Using a combination of *in vivo* fate-mapping approaches with a Micro-CT imaging of cranial endoderm to follow endoderm contribution to developing head structures I conclusively demonstrate an endodermal origin of cement glands in all three species. Despite different germ layer origin, cement glands of basal actinopterygians show the same expression patterns as *Xenopus* cement gland, suggesting that a developmental system drift might have occurred during cement gland evolution, resulting in a shift of their initiation from the anterior ectoderm to the immediately adjacent anteriormost endoderm.

Cement gland primordia in basal actinopterygians develop as diverticula of the anterior foregut wall, subsequently migrating towards the embryonic surface where they incorporate into the surface ectoderm in the preoral region. These results thus allow us to characterize the preoral endoderm as a distinct morphogenetic domain, which substantially alters the standard mode of vertebrate head development. At the same time these findings represent the first thoroughly described example of endodermal contribution to craniofacial surface in vertebrates. The presence of preoral gut in all the three lineages implies that it represents an ancestral mode of development for the ray-finned fishes and indicates that this domain was secondarily lost in teleosts due to the radical transformation of their early development as a result of meroblastic cleavage. The presence of vestigial, preoral gut-like structures in other vertebrates, as well as in the lancelet or acorn worms suggests that the endodermal origin of cement glands in basal actinopterygians may represent an ancient blueprint of chordate head development.

**Keywords:** cement glands, bichir, sturgeon, gar, xenopus, embryonic development, head, endoderm, preoral gut, prechordal plate, actinopterygians, vertebrates, chordates, homology