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Review

Getting to the bottom of anal evolution

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ABSTRACT

The digestive tract is an essential organ system that allows animals to efficiently digest food and take up nutrients to maintain growth and sustain the body. While some animal groups possess a sack-like gut, others possess a tube shaped alimentary canal with an opening for food uptake, the mouth, and an opening for defecation, the anus. The evolutionary origin of the hindgut with the anal opening remains unclear. Bilaterally symmetric animals (Bilateria) have a great diversity of gut architectures and also show a great variety in the development of this important organ system. In this review, we summarize current knowledge about gut morphology, its development, and the underlying molecular mechanisms of the alimentary canal of Bilateria. We focus on gastrulation, the fate of the blastopore and its connection to hindgut and anus development in different animal taxa. We evaluate scenarios about bilaterian evolution on the basis of recent insights of animal phylogeny and widening knowledge about animal developmental diversity.

Contents

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1. Introduction

The digestive tract of animals is an essential organ system. It allows animals to efficiently digest food and take up nutrients to maintain growth and sustain the body. The animal gut can have different shapes and different degrees of specializations, and it is often connected to other organ systems, such as excretory organs (nephridia) and gonadal structures (Schmidt-Rhaesa, 2007; Yonge, 1937). While some animal lineages show the absence of a digestive tract (e.g., Porifera, Placozoa, Cestoda, Acanthocephala), others possess a sack-like gut with only one opening to the environment functioning both for food uptake and excretion (e.g., Ctenophora, Cnidaria, Acoelomorpha, Platyhelminthes, Gnathostomulida). The sack-like digestive tract can be elaborated by the evolution of additional branches of the digestive tract (e.g., triclads, polyclads), the evolution of additional holes, and subdivisions by lamellae-like structures.

Many animals possess an alimentary canal (through-gut), with an opening for food uptake, the mouth, and another opening for defecation, the anus. Such unidirectional gut is found in many bilaterian lineages, and is often subdivided in highly specialized regions (such as stomachs), since the food in general passes only once through each area. Specializations in the ectodermal mouth region (i.e., foregut) include muscular (pharynx) or cuticular (teeth) structures that help to grasp, suck and process food. The endodermal midgut is mainly specialized on the secretion of digestive enzymes by gland cells and absorption of nutrients through phagocytotic and pinocytic cells that can be aligned along the epithelia of different regions (stomachs, intestines) (Marianes and Spradling, 2013; Yonge, 1937). The midgut cells thus provide the nutrients to the rest of the body by using a blood-vascular system, coelomic cavities, active transportation, or diffusion. The hindgut and the anal opening are often of ectodermal origin, and correspond to the region where the remnants of food are discharged. A hindgut region is sometimes lacking, as the anal opening can get fused with the openings of the excretory system and/or reproductive organs (cloaca). A one-way gut enables the processing of food much more efficiently and allows the uptake of food while the animal is still digesting. The evolution of such alimentary canal was in some lineages likely connected to the evolution of larger or at least longer body sizes. However, despite this clear advantage for food digestion, some groups have secondarily reduced the alimentary canal to a sack-like gut (e.g., ophiuroid echinoderms, terebratellid brachiopods, nectonemaoid nematomorphs, asplanchnoid rotifers, urodasyoid gastrotrichs).

This review focuses on the morphology, development, and evolution of the opening that makes the one-way gut what it is – the anus. It is the anal opening that discriminates the sac-like gut from the unidirectional alimentary canal, since recent data suggest that the mouth openings of bilaterians seem to be homologous (see Arendt et al., 2001; Hejnol and Martindale, 2008a). Understanding the evolutionary origin(s) of the anus is key to understand the evolution and diversification of animal body plans, and thus, deserves special attention.

2. Gut morphology in the Bilateria

A tripartite digestive tract that comprises an ectodermal foregut or stomodaeum, an endodermal midgut, and an ectodermal hindgut or proctodaeum is widely distributed in the Bilateria (Schmidt-Rhaesa, 2007). However, the digestive tract architectures in this group of animals differ in its cell type composition and lineage specific specializations, which result in an astonishing variation that sometimes makes it difficult to distinguish the different gut parts in certain animals (Fig. 1).

2.1. The beneficial architecture of a unidirectional alimentary canal

The common structure of an alimentary canal is a tube that extends from the anterior mouth to the posterior anus (Schmidt-Rhaesa, 2007). Several sessile taxa, of which some of them live in tubes, possess a so-called U-shaped gut with a curved midgut and the mouth and anus are close to one another. Examples are found in bryozoans, entoprocts, brachiopods, phoronids, pterobranchs, and sipunculans. The close proximity of mouth and anus does not seem to be a problem, with ciliary structures and a concerted regulation preventing the interference between food uptake and defecation. The subdivision of the alimentary canal into foregut, midgut, and hindgut usually follows embryological criteria in which fore- and hindgut are invaginations of the ectoderm and solely the midgut is of endodermal origin. However, in different animal groups this separation is not as “clear cut”. In arthropods, the foregut and hindgut are covered with cuticle of ectodermal origin and are molted. Here, cuticular specializations such as the chitinuous ridges of the mastax indicate its ectodermal origin. In other animal groups, it is more difficult to draw a border between the ectodermal and endodermal parts of the digestive system (Zorn and Wells, 2009). The inclusion of molecular data makes the traditional discrimination between midgut and hindgut more difficult since the molecular boundaries do not always coincide with the morphological and developmental boundaries (see e.g., *Capitella*, Fröbius and Seaver, 2006; Meyer et al., 2010). Furthermore, it has been shown that in some cases a malfunction of a single gene can change the fate of midgut precursors to cells with hindgut properties (see e.g., Reuter, 1994).

Despite the fact that a through gut is of great advantage as it allows the unidirectional movement of the food throughout the body, several mostly-parasitic lineages and several species that live in anoxic environments have secondarily completely reduced the digestive tract. Major groups to name are acanthocephalans, cestodes, *Acholades asteris* (rhabdocoel platyhelminth) (Jennings, 1989), siboglinids (Katz et al., 2011), and also rare cases in other groups such as in oligochaetes (Giere, 1985), rhizocephalan crustaceans, and molluscs (Felbeck, 1983). Such complete loss of the digestive tract is usually connected with the ectodermal uptake of nutrients in parasites, and the hosting of symbiotic bacteria responsible for novel biochemical pathways for reducing sulfate in anoxic environments.

2.2. The blind gut – a common theme in the Bilateria

In other bilaterally symmetrical animals, the digestive tract is composed out of a sack-like gut that lacks the anal opening, similar to that in cnidarians and ctenophores. We find such a blind gut in xenoturbellids, acoelomorphs, gnathostomulids, platyhelminthes and micrognathozoans. It remains an open question whether the absence of an anal opening is plesiomorphic for the Bilateria (Hejnol and Martindale, 2008a,b, 2009; Schmidt-Rhaesa, 2007), since it largely depends on progress in resolving the phylogenetic framework of the major bilaterian groups (Dunn et al., 2014; Edgecombe et al., 2011).

2.2.1. The case of Acoelomorpha

Acoelomorphs are simple, bilateral worms that lack coeloms and a through gut (Bourlat and Hejnol, 2009). The lack of an anal opening was one of the few morphological arguments that were used to group acoel flatworms into the Platyhelminthes (Ax, 1996; Ehlers, 1985; Hyman, 1951; von Graff, 1891). With the emergence of the alternative hypothesis of the phylogenetic position of acoels as sister group to all remaining Bilateria (Carranza et al., 1997; Ruiz-Trillo et al., 1999), the absence of an anus in this group of animals was interpreted as a reflection of the bilaterian ancestral state