



# Unravelling the deep homology of gill slits and the origin of bilaterian body plans

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#### Overview

Bilaterians comprise the vast majority of animal diversity and disparity and can be divided into three main clades: ecdysozoans (moulting animals like arthropods), spiralians (e.g. annelid worms and molluscs) and deuterostomes (including us and starfish). The extant representatives of these groups are so morphologically divergent that identifying shared derived characters that would have been present in their common ancestors is extremely difficult, obfuscating what features may have been present in the ancestral bilaterian. This has hampered efforts to uncover the origin of bilaterian body plans.

While it is well established that ecdysozoans and spiralians are sister taxa, the phylogenetic position of deuterostomes is less certain. Recent work has challenged the traditional view that the deuterostomes are monophyletic, instead inviting the possibility that they are a paraphyletic grade at the base of the Bilateria (Kapli *et al.* 2021). If correct, this would imply that the ancestor of all or much of bilaterian diversity was deuterostome-like.

Deuterostomes are a divergent group of animals, encompassing forms as different as starfish, vertebrates and sea squirts, and there are almost no morphological characters which unite them to the exclusion of other animal groups. Gill slits are an iconic deuterostome character that play an important role in respiration in most aquatic vertebrates (i.e. fish), but are absent in extant echinoderms (i.e. starfish, sea urchins and their relatives), which instead breathe through their tube feet. Fossil echinoderms first appear over half a billion years ago during the Cambrian Explosion, revealing a diverse array of extinct forms with body plans unlike their living relatives (Zamora and Rahman 2014; Deline et al. 2020). Intriguingly, multiple different extinct echinoderm lineages show a variety of often serialised structures which have been interpreted as respiratory and might be homologous to gill slits seen in other deuterostomes (Álvarez-Armada et al. 2022). However, there is some uncertainty regarding the function of these structures across echinoderms, and it is not clear whether they are deeply homologous (share common ancestry) with each other and/or true gill slits in extant deuterostomes, or if they evolved independently in different lineages, perhaps in response to environmental drivers like oxygen concentration.



Examples of extinct echinoderms with putative respiratory structures. On the left, Macrocystella (which looks like living crinoids) shows plates with additional folds interpreted to be respiratory; on the right Kinzercystis shows minute pores between plates also interpreted as respiratory.

This project aims to resolve the nature of these putative respiratory structures in ancient echinoderms and determine their relationship to gill slits in other deuterostomes. This will involve first characterising the morphology of gill slits in living deuterostomes to establish a set of criteria for recognising them in fossils. The student will then characterise the spectrum of possible respiratory structures in fossil echinoderms both anatomically and functionally. These different lines of evidence will be used to assess homology and produce a new morphological phylogenetic framework in which the deep homology of these structures can be assessed. Ultimately, this will help reveal the nature of the deuterostome and perhaps bilaterian ancestors.

# Methodology

The student will characterise the diversity of gill slits in living deuterostomes using a combination of confocal microscopy and X-ray tomography, including dice-CT (diffusible iodine-contrast enhanced computed tomography). These data will allow the student to characterise the morphological variation in gill slits today before applying this new knowledge to understanding the earliest fossil echinoderms.

The student will examine fossils from museum collections including OUMNH, the Natural History Museum, London, the University of Zaragoza and the Smithsonian Museum of Natural History and identify crucial specimens for further study with micro-CT and/or synchrotron tomography. Putative respiratory structures will be virtually reconstructed as 3D models and analysed quantitatively to assess shape variation in morphospace. Additionally, the student will perform computational fluid dynamics simulations – which will involve placing the structures of interest in a virtual flume tank to assess hydrodynamic performance – to determine whether they played a role in respiration or were more likely to function in different ways.

These data will be used in conjunction with new phylogenetic data which the student will build on to perform phylogenetic analyses and ancestral state reconstructions for echinoderms, deuterostomes and possibly bilaterians using Bayesian methods.

#### Timeline

**Year 1**: Doctoral training courses (10 weeks), literature review, beamtime applications and study of living deuterostome anatomy.

**Years 2 and 3**: Fossil dataset construction, tomography, construction of morphospace and computational fluid dynamics. Phylogenetic dataset construction. Presentation of results at national conference.

**Year 4**: Phylogenetic analyses, ancestral state reconstructions, data integration, thesis completion and papers for international journals/conference presentation.

### Training & Skills

The supervisory team includes expertise in echinoderms and early deuterostome evolution (F. Dunn, I. Rahman, S. Shimeld) and phylogenetic methods (L. Parry) with complementary skills in 3D morphology (I. Rahman, F. Dunn, L. Parry) and computer simulation (I. Rahman). The student will learn how to select and prepare specimens for 3D imaging, process tomographic data to create virtual models, and a variety of other techniques in digital morphology (Cunningham et al. 2014). The student will learn to perform computational fluid dynamic simulations as well as integrate observations of extinct and extant taxa in comparative analyses. Lastly, they will be trained in carrying out phylogenetic analyses.

## **References & Further Reading**

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