

Editorial

Amphioxus: a peaceful anchovy fillet to illuminate Chordate Evolution (I)

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The cephalochordate amphioxus occupies a central place in evolutionary thoughts to the origin of Vertebrates. With a prototypical vertebrate-like body plan and a preduplicative genome, the friendly lancelet seems to be in morphological and genetic motionless since its separation from the major branch of evolution that eventually ended up in our corner in the Animal Kingdom. This makes it an ideal model system with which, with the current development of genomic and experimental tools, an Evo-Devo approach to the understanding of the origin of vertebrates looks proper, reliable, and excitingly promising.

Key words: amphioxus, Evo-Devo, vertebrates, chordates

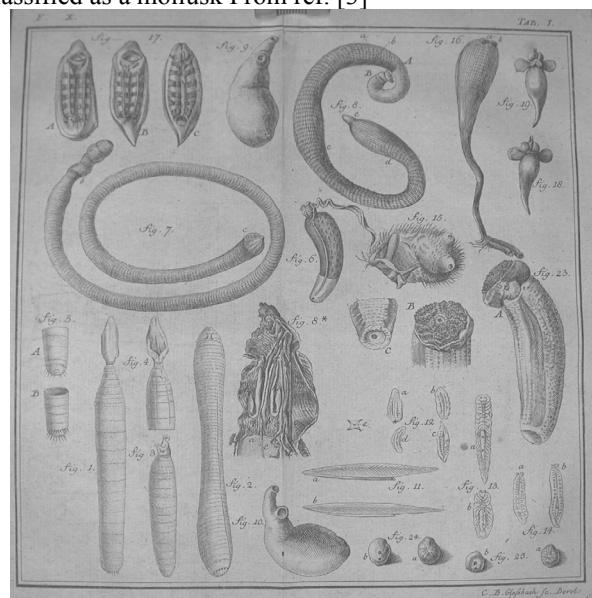
Introduction

The discovery in the 1980's that animals as diverse as flies and mouse shared a toolkit of basic developmental genes helped to reconcile developmental biologists and geneticists, which divorced in the beginning of the XX century after a romantic Darwinian-encouraged relationship ("community of embryonic structure reveals community of descent", Darwin 1859 [1]). This reconciliation has lead to the nativity of the new discipline of "Evo-Devo", or evolutionary developmental biology, that tries to explain the evolutionary change by means of changes in developmental genes and gene networks [2]. Among other main metazoan transitions, the one-hundred year discussions as how vertebrates originate from their closest invertebrate relatives are now being sponsored by studying genes and gene networks during embryonic development of lower deuterostomes: hemichordates, echinoderms, urochordates and cephalochordates.

Figure 1. Adult amphioxus of the species *Branchiostoma lanceolatum* with mature gonads (yellow).



Figure 2. Original drawing (fig No. 11) and description of the amphioxus, *Branchiostoma lanceolatum*, originally classified as a mollusk From ref. [3]



**Die
fischförmige naakte Seeschnecke.
(*Limax lanceolaris*.)**

Sch möchte fast alle diejenige Land- und Seegeschäfte unter das Geschlecht der nackten oder Häuslosen Schnecken (*Limaces*) rechnen, die einen ordentlichen Saugfuß haben, mit welchem sie an sich und sich fortbewegen. Gewiß genug gehören in ein Geschlecht die nackten Erdschnecken, mit den sogenannten Doriden des Herrn von Linne, und eben desselben *Laplysia* oder dem Seehasen der Mittelmeidischen See. Allein auch die mit einer schmalen Furche sich anlegenden weichen Seegeschäfte, z. B. das von Bohadic unter dem Namen *Argus* beschriebne, die im Seekroft des Oceans gemeine *Scyllaea* und dasjenige Thierchen endlich, welches ich hier beschreiben will, scheinen nur eine Abseitung des nehmlichen Geschlechts anzunehmen. Ich habe letzteres jedoch nicht lebendig zu betrachten Gelegenheit gehabt, sondern erhielt es aus der See um Cornwall in Weingeist. Vielleicht berichtet ein anderer mehrere Umstände davon.

The cephalochordate amphioxus (Fig. 1), described in 1778 as a mollusk (Fig. 2) [3] has been regarded as the closest invertebrate relative to the vertebrates, possessing a vertebrate-like body plan, with notochord, hollow dorsal nerve cord, segmented muscle blocks, perforated pharyngeal region and post anal tail.

However, amphioxus is devoid of most of the complex features of vertebrates, as an elaborated brain or paired fins. In words of Henry Gee, "the amphioxus looks like nothing more than a pallidly animated anchovie fillet" [4]. In the early XX century, amphioxus became a favourite of the summer students at the Biological Laboratories of the Cold Spring Harbor Laboratories on Long Island, New York, who invented the chorus of a song that became the "Its a long way from amphioxus" song (Fig. 3), authored by the marine biologist Philip Pope in 1921 and popularised by the folk singer Sam Hilton in 1961 [5].

Figure 3. The amphioxus song "Its a long way from amphioxus". From ref. [5]

A fish-like thing appeared among the annelids one day.
It hadn't any parapods nor setae to display.
It hadn't any eyes nor jaws, nor ventral nervous cord.
But it had a lot of gill slits and it had a notochord.

(chorus):

It's a long way from Amphioxus. It's a long way to us.
It's a long way from Amphioxus to the meanest human cuss.
Well, it's goodbye to fins and gill slits, and it's welcome lungs and hair!
It's a long, long way from Amphioxus, but we all came from there.

It wasn't much to look at and it scarce knew how to swim.
And Nereis was very sure it hadn't come from him.
The mollusks wouldn't own it and the arthropods got sore,
So the poor thing had to burrow in the sand along the shore.

He burrowed in the sand before a crab could nip his tail,
And he said "Gill slits and myotomes are all to no avail.
I've grown some metapleural folds and sport an oral hood,
But all these fine new characters don't do me any good.

(chorus)

It sulked awhile down in the sand without a bit of pep,
Then he stiffened up his notochord and said, "I'll beat 'em yet!
Let 'em laugh and show their ignorance. I don't mind their jeers.
Just wait until they see me in a hundred million years.

My notochord shall turn into a chain of vertebrae
And as fins my metapleural folds will agitate the sea.
My tiny dorsal nervous cord will be a mighty brain
And the vertebrates shall dominate the animal domain.

(chorus)

The first developmental genetics record in amphioxus dates of 1992 [6], and since then, it seems clear that, at the genetic level, amphioxus represents the best preduPLICATIVE stand-in of the vertebrate genome [7]. Very recently, the position of cephalochordates as the closest invertebrate relative of vertebrates has been challenged [8], and phylogenomic data suggest that amphioxus may in fact be the earlier chordate, or even lower deuterostomes [9]. In this sets of special issues of *Int. J. Biol. Sci.*, research groups passionate in amphioxus genetics are contributing and giving insights into the genome organisation, developmental biology,

neurobiology and anatomy of lancelets, giving glimpses and rational hypothesis to understand the genetic mechanisms that underlie evolutionary change in Chordates. Whatever the proper position, amphioxus, at the genomic and morphological level, is an example of a "living fossil", for which it seems that time has not passed, escaping the, in words of the XIX century zoologist, E. Ray Lankester "the great destroyer: Time" [10]. Hence, amphioxus is invaluable to illuminate, after 500 M years, the origin of Chordates, our particular corner in the tree of life.

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Conflict of interest

The author has declared that no conflict of interest exists.

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