



## Review

## Origins of neurogenesis, a cnidarian view

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## ABSTRACT

New perspectives on the origin of neurogenesis emerged with the identification of genes encoding post-synaptic proteins as well as many “neurogenic” regulators as the NK, Six, Pax, bHLH proteins in the Demosponge genome, a species that might differentiate sensory cells but no neurons. However, poriferans seem to miss some key regulators of the neurogenic circuitry as the Hox/paraHox and Otx-like gene families. Moreover as a general feature, many gene families encoding evolutionarily-conserved signaling proteins and transcription factors were submitted to a wave of gene duplication in the last common eumetazoan ancestor, after Porifera divergence. In contrast gene duplications in the last common bilaterian ancestor, Urbilateria, are limited, except for the bHLH Atonal-class. Hence Cnidaria share with Bilateria a large number of genetic tools. The expression and functional analyses currently available suggest a neurogenic function for numerous orthologs in developing or adult cnidarians where neurogenesis takes place continuously. As an example, in the *Hydra* polyp, the *Clytia* medusa and the *Acropora* coral, the *Gsx/cnox2/Anthox-2* ParaHox gene likely supports neurogenesis. Also neurons and nematocytes (mechanosensory cells) share in hydrozoans a common stem cell and several regulatory genes indicating that they can be considered as sister cells. Performed in anthozoan and medusozoan species, these studies should tell us more about the way(s) evolution hazards achieved the transition from epithelial to neuronal cell fate, and about the robustness of the genetic circuitry that allowed neuromuscular transmission to arise and be maintained across evolution.

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## Introduction

*Urbilateria and its older sisters Cnidaria and Ctenophora*

In 1978, Ed Lewis in his seminal Nature paper (Lewis, 1978) predicted the evolutionary conservation of DNA-binding regulatory proteins that would control patterning along the anterior–posterior axis through cis-regulatory elements. Since then, the accumulation of molecular and genetic data indeed proved the wide conservation of the genetic networks regulating shared developmental processes among bilaterians, not only for the specification of the anterior to posterior axis but also the dorso-ventral axis, the head patterning and the eye specification (De Robertis, 2008). As anticipated, the main cellular differentiation processes in bilaterians also make use of evolutionarily-conserved genetic circuitries as those used for myogenesis (Yun and Wold, 1996), neurogenesis (Bertrand et al., 2002; Acampora et al., 2005; Denes et al., 2007; Tessmar-Raible et al., 2007), gametogenesis (Cox et al., 1998). Since 1991, orthologs of these bilaterian regulatory genes were identified not only in cnidarians (see

below) but also in poriferans (Larroux et al., 2006, 2008) and some could even be traced in choanoflagellates (King et al., 2008).

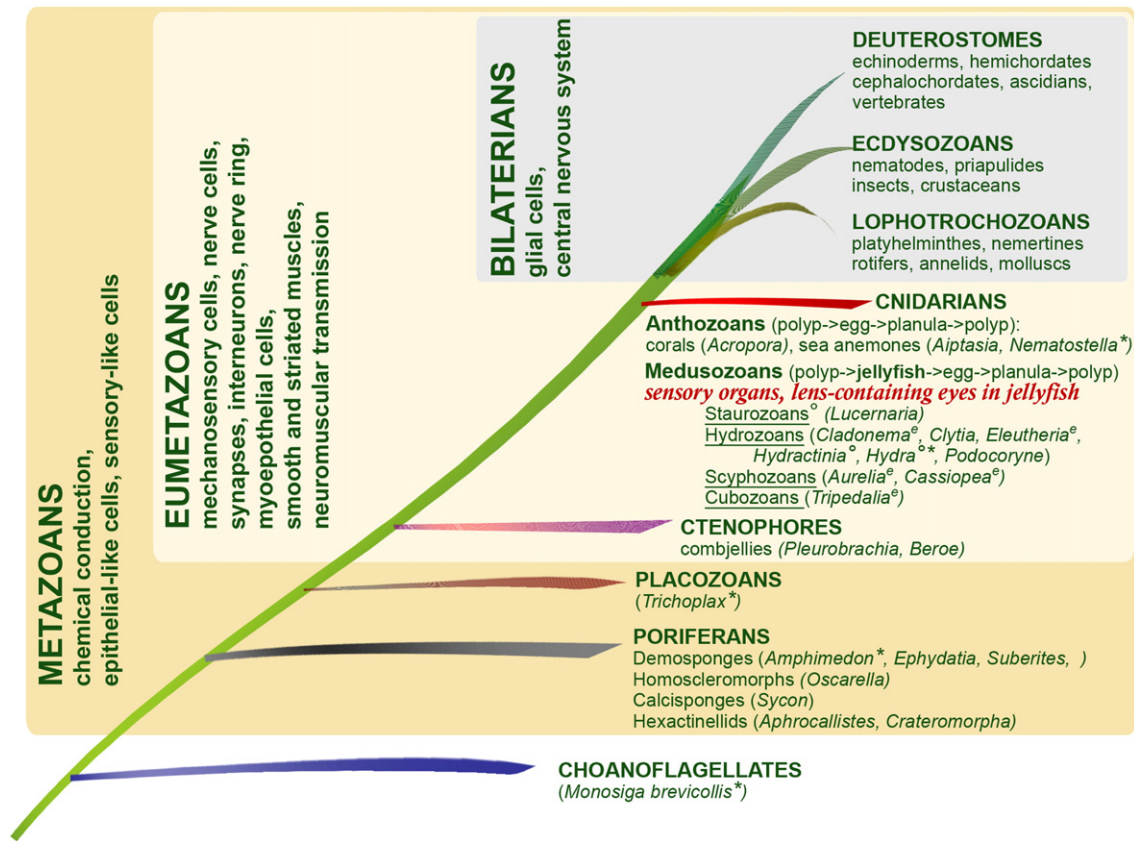
The Zootype hypothesis proposed first that a same set of regulatory genes, namely homeobox genes, define the anterior to posterior (AP) axis in all animal species at an early and transient developmental stage (Slack et al., 1993). Subsequently the Urbilateria hypothesis proposed that, beside the AP axis, deuterostomes and protostomes also received from a common putative ancestor, named Urbilateria a genetic toolkit that specifies their dorso-ventral axis, including their neural tube (De Robertis, 2008). In the absence of extant Urbilaterian species, the Ctenophora and Cnidaria that diverged earlier in animal evolution but display anatomical polarities and differentiate a nervous system, are obvious candidates to test these hypotheses (Fig. 1). In fact the initial expression analyses performed at the cellular level supported the hypothesis of a common origin for neurogenesis and also for the specification of the apical nervous system in cnidarians and anterior nervous system in bilaterians (Gauchat et al., 1998; Galliot and Miller, 2000). However this simple rule of the universal conservation of developmental genetic toolkits between animal phyla received some assault when it appeared that the zootype hypothesis could not be verified in cnidarians (Gauchat et al., 2000; Schierwater and Desalle, 2001; Chourrout et al., 2006; Kamm et al., 2006; Lee et al., 2006; Ryan et al., 2007; Chiori et al., 2009; Quiquand et al., 2009), and it is nowadays admitted that the specification of the embryonic AP axis by the Hox gene families only arose after Cnidaria divergence.

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**Fig. 1.** Origin of neurogenesis and progressive acquisition of a central nervous system along animal evolution. The differentiation of cells with synaptic transmission can be traced back to the last common ancestor of eumetazoans, whereas the differentiation of sensory cells possibly emerged in the last common ancestor of choanoflagellates and metazoans; in Porifera choanocytes are proposed to correspond to sensory cells. Both Ctenophora and Cnidaria differentiate a nervous system; they diverged prior to Bilateria but their respective positions are controversial. Similarly the position of Placozoa in Metazoa is debated. \*Indicate species with sequenced genome; †species that differentiate eyes, ‡species that have lost the medusa stage.

However what is true for the AP axis might not be true for the specification of the nervous systems. Alain Ghysen wrote about the *Origin and Evolution of the Nervous System*: “The extreme variability of behaviors and survival strategies among triploblasts would be subordinate on the previous attainment by the urbilaterians of a high level of developmental stability in the building of elementary functional circuits. According to this view, the initial triploblast radiation may have been contingent upon reaching this highly evolved stage of neural development” (Ghysen, 2003). In other words, the neurogenic circuitry was already established in a very stable way in Urbilateria (Arendt et al., 2008), suggesting that it might be possible to trace back some features of this ancestral nervous system in cnidarians that differentiate a rather sophisticated nervous system with numerous cellular and functional similarities to bilaterian ones. In bilaterians, homologous tasks such as differentiating nerve cells (Simionato et al., 2008) and mechanosensory organs (Ghysen, 2003), developing eyes (Pichaud and Desplan, 2002; Gehring, 2004), regionalizing the neural tube along the dorso-ventral axis (Denes et al., 2007; Mieko Mizutani and Bier, 2008) or patterning the tripartite brain (Lichtneckert and Reichert, 2005) rely on a shared set of transcription factors. We propose here to review the current knowledge about the molecular mechanisms that support neurogenesis in cnidarians and discuss some scenario that led to this unique evolutionary transition.

#### The complex life cycle of cnidarians

Cnidaria is supposed to have diverged about 650 million years ago, preceding the Cambrian explosion, the period when ancestors to most extant bilaterian phyla arose from a common hypothetical ancestor

named Urbilateria (Fig. 1). Cnidarians are most often marine animals that commonly display a radial symmetry and are made up of two-cell layers, the ectoderm and the endoderm, separated by an extracellular matrix named mesoglea (Bouillon, 1994b). However this “diploblastic” criterion is disputed as numerous cnidarian species actually differentiate “mesodermal” derivatives as striated muscle at one or the other stage of their life cycle (Seipel and Schmid, 2006). Cnidarian species cluster in two distinct classes (Bridge et al., 1995; Collins et al., 2006): the anthozoans that live exclusively as polyps (sea pens as *Renilla*, stony corals as *Acropora*, sea anemones as *Aiptasia*, *Anthopleura*, *Nematostella*) and the medusozoans that display a complex life cycle with a parental medusa stage and a sessile polyp stage. Among those, the cubozoans (*Tripedalia cystophora*) and scyphozoans (*Aurelia aurita*, *Cassiopea xamachana*) predominantly live as medusae, whereas the hydrozoans (*Podocoryne*, *Clytia*, *Cladonema*, *Eleutheria*) usually follow a life cycle where they alternate between these two forms. However some hydrozoan species have lost the medusa stage as the marine *Hydractinia* and the freshwater *Hydra* polyps (Galliot and Schmid, 2002). Similarly the staurozoans that were only recently characterized as a group (Collins et al., 2006), live exclusively as polyps. Cnidarian polyps are basically a tube with a single opening circled by a ring of tentacles, which has a mouth–anus function. Cnidarians together with ctenophores (combjellies) are the first phyla where movements are governed by a neuromuscular system, as exemplified by their active feeding behavior that requires coordinated movements of their tentacles (Westfall and Kinnamon, 1984; Westfall, 1996). Therefore, cnidarians and ctenophores provide appropriate model systems to trace back the first-evolved nervous systems (Anderson and Spencer, 1989). In contrast, poriferans (sponges), which diverged earlier during evolution and are capable of chemical

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