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Review article

Embryonic hematopoiesis under microscopic observation

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ABSTRACT

Hematopoietic stem cells (HSCs) are at the origin of adult hematopoiesis, providing an organism with all blood cell types needed throughout life. During embryonic development a first wave of hematopoiesis (independent of HSCs) allows the survival and growth of the embryo until birth. A second wave of hematopoiesis that will last into adulthood depends on the production of HSCs that begins at mid-gestation in large arteries such as the aorta. HSC production occurs through a hemogenic endothelial to hematopoietic transition (EHT) process and the formation of hematopoietic clusters in most vertebrate species. Advances in understanding EHT, cluster formation and HSC production were triggered by combined progresses made in the development of *in vivo* assays, microscopy, imaging and fluorescence tools. Here, we review the current knowledge on developmental hematopoiesis with a focus on the first step of HSC production in the aorta and how microscopic approaches have contributed to a better understanding of the vital process of blood cell formation.

1. Introduction

The initial discovery of blood producing cells concurs with the progresses made in the field of microscopy in the early 20th century. Modern microscopes allowed direct visualization of individual cells and tissue structure leading to important scientific dogma. On the basis of his observations, the German pathologist Franz E.C. Neumann identified in the mid 19th century the bone marrow as the site of adult hematopoiesis and proposed the concept of a unique cell at the foundation of the entire blood system. The Russian scientist Alexander A. Maximow coined the term “hematopoietic stem cell” (HSC) for this very particular cell type (Maximow, 1909). At the same time, another partisan of the stem cell concept, Vera Dantschakoff, observed clusters of “hemoblasts” attached to the endothelial layer of the aorta of a chicken embryo (Dantschakoff, 1909). Those clusters rapidly appeared as a common feature of early vertebrate development since they were observed in the aorta of most animal species, including human (Dieterlen-Lievre et al., 2006; Jordan, 1917). The close proximity of clusters to the endothelium soon led to the hypothesis that cluster cells might be originating from or descendants of the endothelium. Finding the origin of clusters, the process of their formation and the connection between clusters and HSCs has been the focus of intense research for decades. In this review, we will report the current knowledge on HSC-independent and dependent hematopoiesis as it occurs during embryonic development and how microscopic (besides cellular and molecular) approaches have been crucial to better understand blood formation.

2. How microscopy development and fluorescence discovery have revolutionized developmental research

The development of microscopes and the discovery of fluorescence have been crucial to pave the way to our current research discoveries and techniques, especially in the field of developmental biology. Formally, the history of microscopy begins in the first century when glass was invented and the Romans discovered that primitive glass lenses could magnify objects (Fig. 1). In the 13th century, Salvino D'Armate made the first eye glass. The Dutch lens grinders Zacharias Jansen and his father built the first compound microscope featured with several lenses connected to a hollow cylinder (originally magnifying 3×–9×) in 1590–1595. However, it was in the late 17th century that the Dutch tradesman and scientist Antoni van Leeuwenhoek first made and used a microscope with an impressive (for his time) magnifying power of 270X. While the early microscopes were mainly used for merriments, van Leeuwenhoek investigated unicellular (such as bacteria and yeast) and multicellular organisms. Among his many important discoveries was the blood corpuscules that he could observe circulating in the tail capillaries of a living fish, emphasizing the close relation between the discoveries made in the hematopoietic field and microscopy. Van Leeuwenhoek's work was confirmed and further advanced by the English scientist Robert Hooke who published the first work of microscopic studies in 1665 (Title: “Micrographia: or some physiological descriptions of minute bodies made by magnifying glasses with observations and inquiries thereupon”). Over the two next

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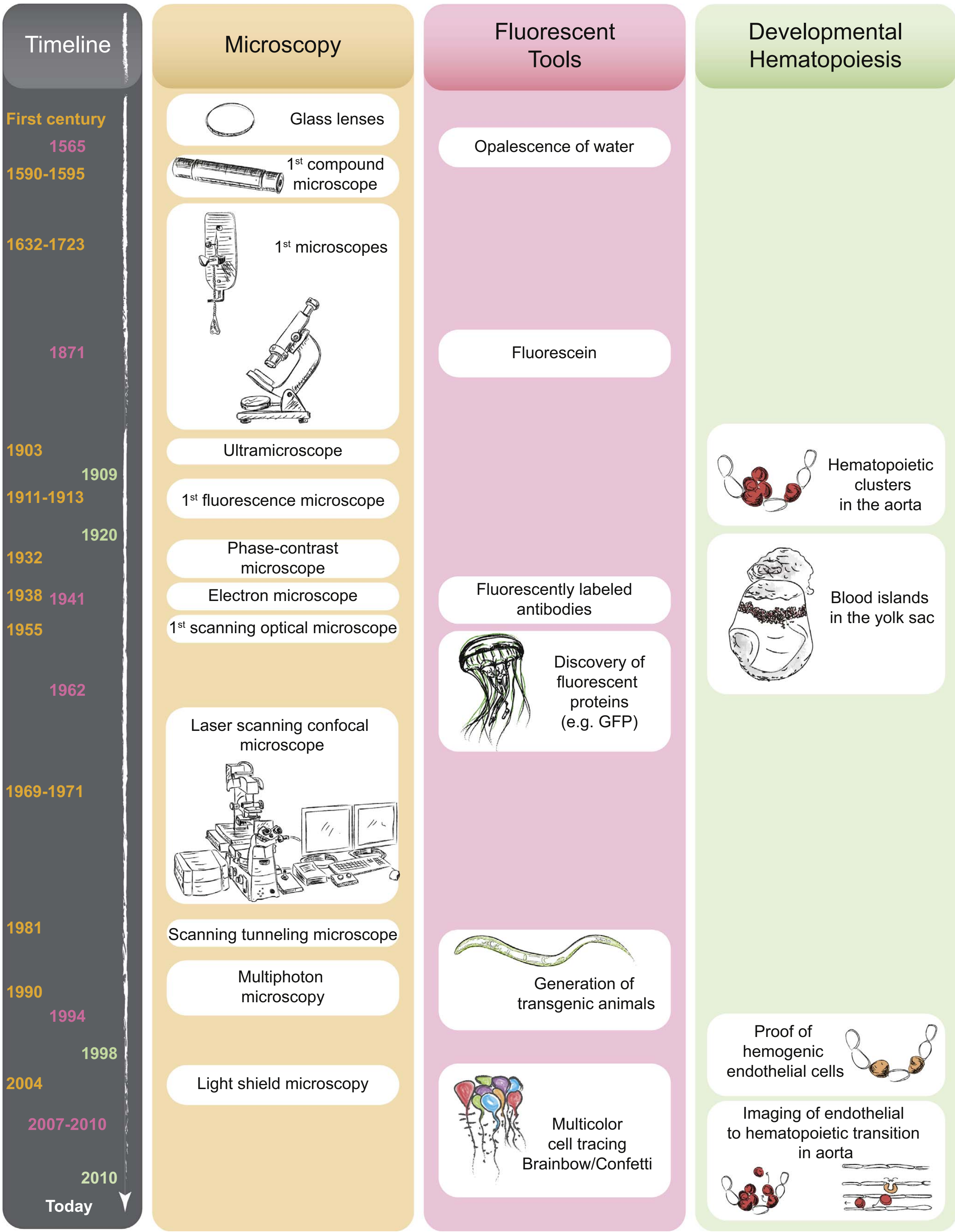

Fig. 1. Historic timeline. Chronological list of particularly important or significant inventions and discoveries in microscopy that allowed crucial observations to advance the field of developmental hematopoiesis.

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