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The origin and evolution of the term "clone"

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In biology, the term "clone" is most widely used to designate genetically identical cells or organisms that are asexually descended from a common progenitor. The concept of clonality in hematology-oncology has received much attention in recent years, as the advent of next-generation sequencing platforms has provided new tools for detection of clonal populations in patients, and experiments on primary cells have provided fascinating new insights into the clonal architecture of human malignancies. The term "clone" is used more loosely by the general public to mean any close or identical copy. Cloning of humans has been a staple of science fiction films and dystopian novels since Aldous Huxley's *Brave New World* was published in 1932. Here I trace the origin and evolution of the word clone, from its first use as an agricultural and botanical term in 1903, to its widespread adoption in biology, adaptation by artists, and contemporary use in hematology-oncology.

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1. Introduction

Clonal expansion of cells – i.e., growth of a group of genetically identical cells, often without respect to anatomical or physiological constraints – is a hallmark of malignancy [1]. However, clonal expansion is not by itself synonymous with malignancy. Clonal expansion of B lymphocytes in response to antigen exposure is an important process in normal immunity, for example, and numerous pre-malignant clonal states such as adenomatous colon polyps or lobular carcinoma in situ of the breast usually have an indolent natural history and can precede frank tissue-invasive disease by many years.

Recently, a substantial fraction of older adults (~10% by age 70 years) were found to have clonal hematopoiesis characterized by somatic mutations in potential pre-leukemic driver genes, raising questions about where the border should be drawn between clonal hematopoiesis and hematological cancers such as the myelodys-plastic syndromes (MDS) [2–6]. More generally, tumor composition is now known to be complex, with numerous derivative subclones with distinct genomic profiles evolving and branching off from an ancestral transformed cell, making for a convoluted architecture,

and one with subclones serving as sources of anti-cancer therapy resistance [7–9].

A deep understanding of the concept of cell clones and clonal behavior is now central to the practice of hematology and oncology, just as cloning of DNA (a different use of the term) has been an essential tool in molecular genetics labs for decades. In addition to the various scientific uses of the term "clone" in biology and medicine, this word has also been adopted widely by the general public to mean any identical or near-identical copy, in the same confusing way that "gene" has come to have a variety of meanings and nuances distinct from the formal definition of a gene as a unit of heredity [10,11]. Clones and cloning have also become staples of science fiction and dystopian fantasy literature. In computer science, a hard disk drive or a program subroutine can be cloned, and functionally similar but non-identical hardware systems are often called clones (e.g. the many "IBM PC clones" of the 1980s). Where did this useful and versatile term originate?

2. Clone: origin in agriculture

In 1903, a widely respected US Department of Agriculture plant breeder named Herbert J. Webber (1865–1946) (Fig. 1) was looking for a word to describe asexual propagation of plants by grafting or transplant of cuttings [12]. The botanical concept of asexual propagation was not a new one – a 6th century C.E. Alexandrian philosopher, John Philoponus ([']I ωάννηz ὸ Φiλόπονoz), had described the process using the term clados (κλάdων, meaning





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Fig. 1. A. Herbert John Webber (1865–1946) was a noted plant breeder and botanist who worked for the US Department of Agriculture from 1892 to 1907 after graduating from the University of Nebraska, then directed Cornell University's New York State College of Agriculture Department of Plant Breeding for 5 years. From 1912 until his retirement in 1929, Webber served as director of the University of California's Citrus Experiment Station. His 1903 letter to *Science* proposed the term "clone

"twig" or "branch"), which is the origin of the contemporary taxonomy term "clade" [13]. Hybridization and grafting with resistant American rootstock saved the French wine industry after European grape cultivars were decimated by grape phylloxera insect infestation in the Great French Wine Blight of the late 19th century [14]. But there was no term in common use before the 20th century to collectively describe agricultural practices such as grafting, budding, and root and tuber transplant. A portmanteau that Webber had previously proposed, "strace" (an amalgam of "strain" and "race"), failed to catch on, so he wrote a seminal letter to *Science*, suggesting a new term:

"Mr. O. F. Cook, of the Department of Agriculture, has called the writer's attention to the Greek word clon $(\kappa\lambda\omega\nu)$ meaning a twig, spray, or slip, such as is broken off for propagation, which could be used in the connection desired. After careful consideration, the writer believes this word much better suited to the purpose than the word *strace* which he previously suggested.... *Clon*, plural *clons* (pronounced with long o), is a short word, easily pronounced, spelled phonetically, and with a derivation which at least suggests its meaning. The writer would urge it as a suitable term to adopt into general usage"[12].

While Webber is usually credited with coining the term clone in most secondary sources on biological etymology, it is notable that in his initial proposal he claimed he had obtained the term from a fellow botanist, Orator Fuller Cook, Jr. (1867–1949). Cook was a taxonomist who also coined the term "speciation". Both Cook and Webber valued terms like clone that were easy to pronounce and simple to use, which may have been part of why clone later came to be employed in so many different ways [11]. Both botanists also published hundreds of articles on plant biology and cultivation in the early 20th century; while Cook's primary focus was cotton, Webber's studies of grafting citrus plants to promote disease resistance were extremely helpful in growing the American citrus industry in Florida and California.

In 1905, botanist Charles Pollard (1872–1945) proposed in a follow-up letter to *Science* that the spelling of the word should be clone, rather than clon as Webber had proposed, in order to emphasize that the verb sound for the o was long [15]. Pollard was influential in botanical language as the editor of the journal *Plant World* and also as consultant to the publisher of the Merriam-Webster dictionary, G. & C. Merriam Co. Therefore, the term clone was formally adopted as proposed by Webber (but with Pollard's suggested spelling) in 1905 by the Association of Agricultural Colleges and Experiment Stations [16].

3. Clone moves to the animal kingdom

While the term clone was initially suggested for agricultural purposes, it quickly took on a life of its own as its uses expanded. In 1912, George Harrison Shull (1874–1954), an eminent plant geneti-

[&]quot; to describe asexual propagation and reproduction. Image source: Herbert John Webber - Eustis, Florida. 19–. Black & white photonegative. State Archives of Florida, Florida Memory. Accessed 15 Feb. 2017.<https://www.floridamemory.com/items/ show/139924>. B. Herbert Weber standing under a carob tree. This picture was taken near Coconut Grove, Florida; in 1898, the first US Department of Agriculture Sub-Tropical Laboratory was started there by Webber and a colleague, Walter Tennyson Swingle (1871–1952). Source: Special Collections, USDA National Agricultural Library. Accessed February 13, 2017, https://www.nal.usda.gov/exhibits/ speccoll/items/show/303. C. Orator Fuller Cook, Jr. (1867–1949). This line drawing of a young Cook accompanied an article about the importance of scientific advance and agricultural education in securing the future of the young West African colony of Liberia, where Cook worked for a time in the 1890s. Image source: The Philipsburg Mail. (Philipsburg, Mont.), 23 May 1895. Chronicling America: Historic American Newspapers. Library of Congress. http://chroniclingamerica.loc.gov/lccn/ sn83025320/1895-05-23/ed-1/seq-3/.

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