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BMC[15]. The cells were divided into a Rh123^{bright} and a Rh123^{dull} population, each population containing 50% of all nucleated cells present in the blast cell window. It was the work of Ploemacher, who was technically assisted by Brons, that showed that MRA cells, CFU-S-12, and CFU-S-8 can be sequentially ordered on the basis of their Rh123 uptake, i.e., their mitochondrial activity[86,89,90]. The MRA could almost completely be separated from CFU-S-8/12 using the 15% most Rh123^{dull} cells vs. the 16% most Rh123^{bright} cells of all nucleated cells present in the light scatter blast cell window. Ninety-eight percent of all CFU-S-12 was not contained in the Rh123^{dull} fraction, while this fraction contained the majority (80%) of MRA. This indicates that, essentially, MRA cells and CFU-S-12 are two stem cell subpopulations with strictly distinct properties, MRA cells being the most primitive. This is not in agreement with the suggestion, done by others several years later, that HSC form a continuum of resting and activated CFU-S[102]. As a pre-enrichment step in the early studies on HSC of Ploemacher *et al.* counterflow elutriation, which sorts cells on the basis of size and density, was used. The enrichment of MRA in the Rh123^{dull} population, compared to fresh BMC, was 66.4 times for MRA[CFU-S-12], and 116.7 times for MRA[CFU-GM]. Interestingly, only 8% of all CFU-S-8 is in cell cycle[22,49,121,135], while 99% stain Rh123^{bright} [73,89]. This is probably due to differentiation processes within the CFU-S-8 which, as mentioned earlier, coincide with a high energetic state. Another feature that emerges from these studies is that MRA cells are pre-CFU-S. These are the cells that generate new CFU-S-12 without having the ability to form spleen colonies themselves, in contrast to the CFU-S-12 that hardly show any form of self-renewal, i.e., the generation of new CFU-S-12 by CFU-S-12. Therefore, earlier reports on the self-renewal ability of CFU-S[49,73,93,94,95,134] could, in retrospect, be explained by the assumption that pre-CFU-S were present in the precursor cell populations studied. A subpopulation of CFU-S-12, probably with marrow repopulating qualities, may also have contributed to observations of the self-renewal of CFU-S.

Both the Rh123^{bright} and Rh123^{dull} fractions contained progenitor cells able to generate cells of all differentiation lineages. However, Rh123^{bright} cells gave predominantly rise to macroscopic erythroid and megakaryocytic spleen colonies that disintegrated after day-12. The 15% most Rh123^{dull} cells, on the other hand, formed, in addition to new CFU-S, microscopic colonies in the spleen at day-12 after transplantation. These colonies, as the macroscopic spleen colonies found at day-16, were predominantly megakaryocytic and/or granulocytic[86]. The rapid generation of megakaryocytes and granulocytes by CFU-S is essential for the short-term survival of lethally irradiated animals. This is illustrated by the observation that the transplantation of only a few CFU-S-12 extend the survival time of these animals with several days[73,90]. By the *generation* of new CFU-S, the pre-CFU-S provide a prolonged survival, once the animals have overcome the first critical period. This indicates that radioprotection is a function of a combination of CFU-S and pre-CFU-S, and therefore is not a proper assay

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