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Featured letter

Evolution of DNA origami scaffolds

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ABSTRACT

Nanoscale materials made using DNA have been increasingly used for applications ranging from biosensors to nanoelectronics. Specifically, DNA origami – where one long single-stranded DNA scaffold is folded into nanoscale shapes and structures using short 'staple' oligonucleotides – typically relies on a single-stranded DNA scaffold derived from a viral genome. The sizes of structures that are made rely on the length of the scaffold strand; the most frequently used DNA scaffold is the single-stranded 7249-nucleotide circular M13mp18 genome. Modern techniques used in genome tailoring are now widely exploited for the creation of DNA scaffolds of various lengths for use in DNA origami. DNA scaffolds of lengths ranging from ~700-nucleotides to ~51,000 nucleotides have been prepared using biotechniques such as polymerase chain reaction, a combination of site-directed mutagenesis and site- and ligation independent cloning, and using the molecular toolbox of restriction and ligation enzymes. Such tailor-made DNA scaffolds allow the creation of origami nanostructures of desired sizes.
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1. Introduction

Since the time it was proposed that DNA can be used as a framework for periodic positioning of guests [1], the molecule has been used for the construction of two-[2–4] and three dimensional lattices [5–8], nanomachines and devices [9,10], topologically linked arrays [11,12] and biosensors [13,14]. The advent of DNA origami [15] spawned the creation of complex shapes out of DNA [16,17] that have been used as scaffolds for proteins [18] and for use in biological applications [19]. The field of DNA nanotechnology has also exploded since DNA origami became a feasible technique for the creation of nanoscale platforms [20]. DNA origami structures are made from a long single-stranded DNA (ssDNA) scaffold that is designed to fold into desired shapes and held together by "staple strands" that bind to complementary regions of the scaffold (Fig. 1A). Larger assemblies have been made using other techniques [21] but the ease of preparation of DNA origami makes it a widely used procedure for spatial arrangement of molecules at the nanoscale. The establishment of the DNA origami technique has democratized the fabrication of finite nanometer-sized DNA objects which promise a wide range of applications in life sciences and the development of novel materials [22,23]. One current limitation results from limited availability of suitable ssDNA scaffolds. The use of entire genomes constrains origami designs to discrete available lengths, which are typically several thousand or more nucleotides long. The vast majority of origami structures are made using the single-stranded 7249-nucleotide (nt) circular M13mp18 genome, which is commercially available in amounts of up to hundreds of micrograms. Production of ssDNA scaffolds of various lengths and sequences could lead to preparation of nanostructures of desirable sizes (Fig. 1B).

The reliance of DNA origami sizes on the availability of suitable DNA scaffolds can be addressed using current techniques that allow precise modification of a genome for use in a variety of biotechnology applications, a process known as genome tailoring. The success of genome manipulation is a result of easy access to genomic sequences in the databases and availability of extent genetic and recombinant tools to modify the genome. Readily available viral genomes [24] and a combination of the "molecular toolbox" of enzymes can be used to tailor suitable genomes for use as scaffolds for DNA origami nanostructures of various sizes (Fig. 2).

2. Strategies to create tailor-made DNA scaffolds

To overcome the limitation of scaffold length, several approaches have been explored. For instance, polymerase chain reaction (PCR)-based techniques have been applied to generate single-stranded scaffolds for origami assembly [25,26]. PCR-based

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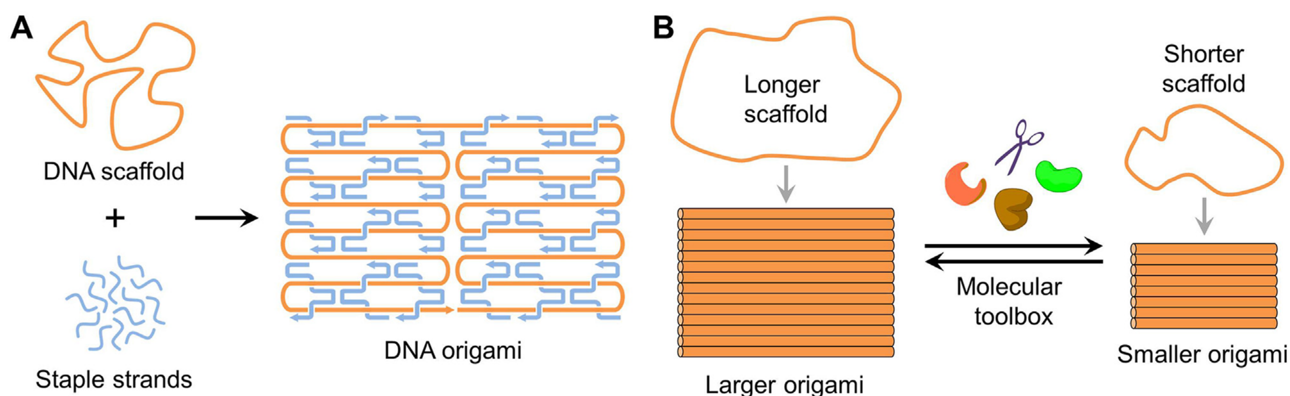

Fig. 1. DNA origami. (A) The DNA origami strategy. (B) The molecular toolbox of restriction and ligation enzymes, combined with genome tailoring techniques can be used to create scaffolds of various lengths for DNA origami construction.

scaffolds (Fig. 3A) of lengths ranging from 756-nt to 4808-nt have been used to produce origami of variable sizes and shapes from two common DNA sources, M13mp18 and lambda [25]. These structures demonstrated that PCR amplification for scaffold strand generation enables the formation of DNA origami from a broad range of scaffold lengths. In addition, asymmetric PCR is also an efficient and economical way to generate ssDNA templates [27]. Another approach is to use a phosphorylated PCR primer to selectively introduce a phosphate group into one strand of the double-stranded DNA (dsDNA), which can then be preferentially digested by Phage lambda exonuclease III to produce ssDNA templates [28]. Conventional PCR using low fidelity Taq DNA polymerases enables reliable amplification of only < 4Kb of DNA, which limits its application for modifying larger DNA sequences [29]. Discovery of long-range PCR using high fidelity proofreading enzyme with exonuclease activity enables ten-fold increase in PCR product length [30]. Such a long-range PCR strategy has been used to amplify a 26,182-nt fragment of λ DNA in the dsDNA form; ssDNA was then obtained through selective enzymatic digestion [26]. PCR, as well as subsequent purification steps for separation of nucleotides, primers and template, impose severe limitations on accessible amounts of ssDNA material. However, the process allows the production of scaffold lengths between 100- and 10,000-nt, along with the ability to choose any section and source of DNA.

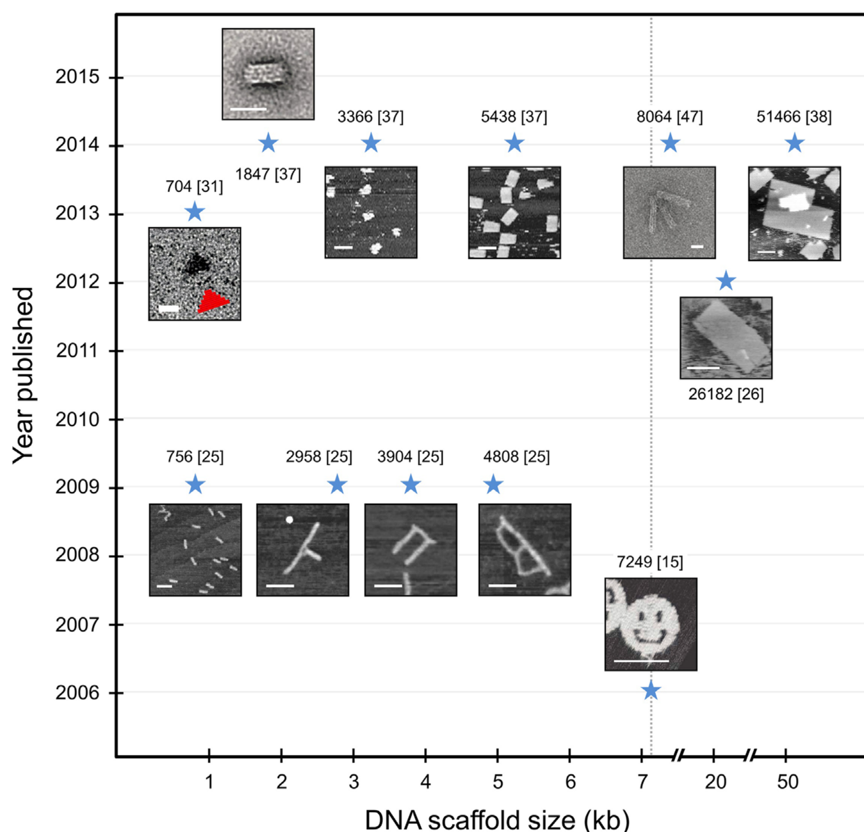

Fig. 2. DNA origami scaffolds developed over the years. Each star represents a scaffold: scaffold length and images of representative DNA origami shapes are shown for each case. References are indicated in brackets. The "traditional" scaffold length of 7249-nt from M13 is shown as a dotted line. Scale bars represent 100 nm in AFM images and 20 nm in TEM images. AFM and TEM images reproduced with permission from reference [15], Copyright 2006, Nature Publishing Group; [25,38], Copyright 2009 and 2014 respectively, American Chemical Society (ACS); [26,31], Copyright 2012, Royal Society of Chemistry (RSC); [37] Copyright 2013 WILEY-VCH and [47] Copyright 2014, American Association for the Advancement of Science.

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