Symbiodinium microadriaticum (coral microalgal endosymbiont)

Christian R Voolstra[1], Manuel Aranda[2], Ye Zhan[3], Job Dekker[3,4]

[1] Department of Biology, University of Konstanz, Konstanz, Germany
[2] Biological and Environmental Sciences & Engineering Division (BESE), Red Sea Research Center (RSRC), King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia
[3] Program in Systems Biology, Department of Biochemistry and Molecular Pharmacology, University of Massachusetts Medical School, Worcester, MA, USA
[4] Howard Hughes Medical Institute, Chevy Chase, MD, USA

*Correspondence: christian.voolstra@uni-konstanz.de ; manuel.aranda@kaust.edu.sa ; Job.Dekker@umassmed.edu

Lessons Learned from the Genome

Photosynthetic single cell microalgae in the family Symbiodiniaceae [1] engage in endosymbioses with a broad range of marine invertebrates, including stony corals that sustain the immense productivity and biodiversity of coral reef ecosystems. More generally, dinoflagellates are ubiquitous aquatic protists and constitute main primary producers in the oceans [2]. Despite their ecological and economic importance, their biology remains enigmatic. For instance, dinoflagellates chromosomes appear permanently condensed and the bulk of their DNA is folded in the absence of nucleosomes, the basic structural unit of DNA packaging in other eukaryotes [3,4]. Dinoflagellates also display numerous other remarkable features including extensive DNA modifications rarely seen in other eukaryotes, such as replacement of a large fraction of thymines with hydroxymethyluracil, extensive RNA editing, and the presence of complex, but poorly characterized organelles. To gain further insight into the functional and genetic traits of Symbiodiniaceae dinoflagellates, we assembled 94 chromosome-scale scaffolds of the genome of the ancestral Symbiodiniaceae species *Symbiodinium microadriaticum* and analyzed their organization [5]. Contrary to the random order and direction of genes typically found in eukaryotic cells, genes are enriched towards the ends of chromosomes in alternating unidirectional blocks that are - in certain instances - enriched for genes involved in specific biological processes. Even more astonishingly, these gene blocks are co-expressed and separated by structural boundaries where transcription converges so that pairs of divergently transcribed gene blocks form chromosome structural domains, corroborated by another study [6]. These structural domains in turn comprise the transcription-dependent basic building blocks of the chromosomes that fold as linear rods. Such a highly ordered structure that links gene orientation, gene transcription, and spatial organization of chromosomes is exceptional, making dinoflagellates exciting model organisms to study mechanisms of chromosome folding. The assembly and annotation of the *Symbiodinium microadriaticum* genome will facilitate future studies to explore the remarkable biology of these critically important organisms.

Genome Facts

The *Symbiodinium microadriaticum* genome assembly has 94 chromosomes that jointly cover 624,473,910 bp (77%) of the starting 808,242,489 bp [7], featuring a scaffold N50 of 8.44 Mb and a contig N50 of 23.35 kb, with a fluctuating GC content: GC content increases towards the ends of the chromosomes and dips by ~6% to 46% to form small local minima at domain boundaries, suggesting that this chromosome architectural feature is encoded in the genome.

The chromosome number is close to previous estimates of 97±2 chromosomes based on electron microscopic analyses [8]. Chromosomes are small with lengths from tens of kb to just under 20 Mb (median about 6.6 Mb)

A total of 48,715 annotated protein-coding genes were identified (of the starting 49,109 gene models); a large number of genes was found present in subscaffolds that were present at higher copy number and at multiple chromosomes, highlighting the amplification of specific gene sets including those involved in retrotransposition [9].

A manually curated conservative assembly (Smic1.0), as well as a version where more repetitive sequences were included (Smic1.1N), are freely available at reefgenomics.org [10] at http://smic.reefgenomics.org and in NCBI's GEO [11] at https://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE152150 .

Species Facts

Symbiodinium microadriaticum is a prominent intra- and intercellular photosymbiont of many marine metazoan and protozoan hosts, including stony corals and jellyfish [12]. It is the type species of the genus *Symbiodinium* (Dinophyta) in the family Symbiodiniaceae [12], following the original (and invalid) description [13].

Symbiodinium microadriaticum is the ancestral species of the family Symbiodiniaceae that diverged over 160 mio years ago during the Jurassic Period and connects the rise of these symbiotic dinoflagellates with the emergence and evolutionary success of reef-building corals [1].

Symbiodinium microadriaticum cells are ~10µm in diameter and possess large genomes of > 1Gbp [8]; nevertheless, the genome is small in comparison to other dinoflagellates that typically possess genomes many times greater than the human genome (up to ~250Gbp) [8, 14].

Its cell color is golden-brown to greenish-brown and it has two major life cycle stages: the predominant coccoid (metabolically active) phase and the transient motile (mastigote) phase [12]. They can be living inside their hosts, mostly as coccoid cells, but can also be free living and then alternate between coccoid and mastigote states.

Symbiodinium microadriaticum has a haploid chromosome set in the vegetative coccoid state, which posits that mutations or any process that alters the coding sequence of proteins, such as RNA editing [15], directly affect the phenotype and are not 'buffered by diploidy'.

Fun Fact about the genome

Varying chromosome counts and polyploidy have been described for field and cultured specimens [16]. Considering our finding that (some) chromosomes are enriched for specific biological processes, the potential to alter chromosome numbers provides the opportunity for dynamic environmental adaptation through chromosome duplication or loss, which may explain their evolutionary success and promiscuous ability to form symbioses. This remains to be further investigated.

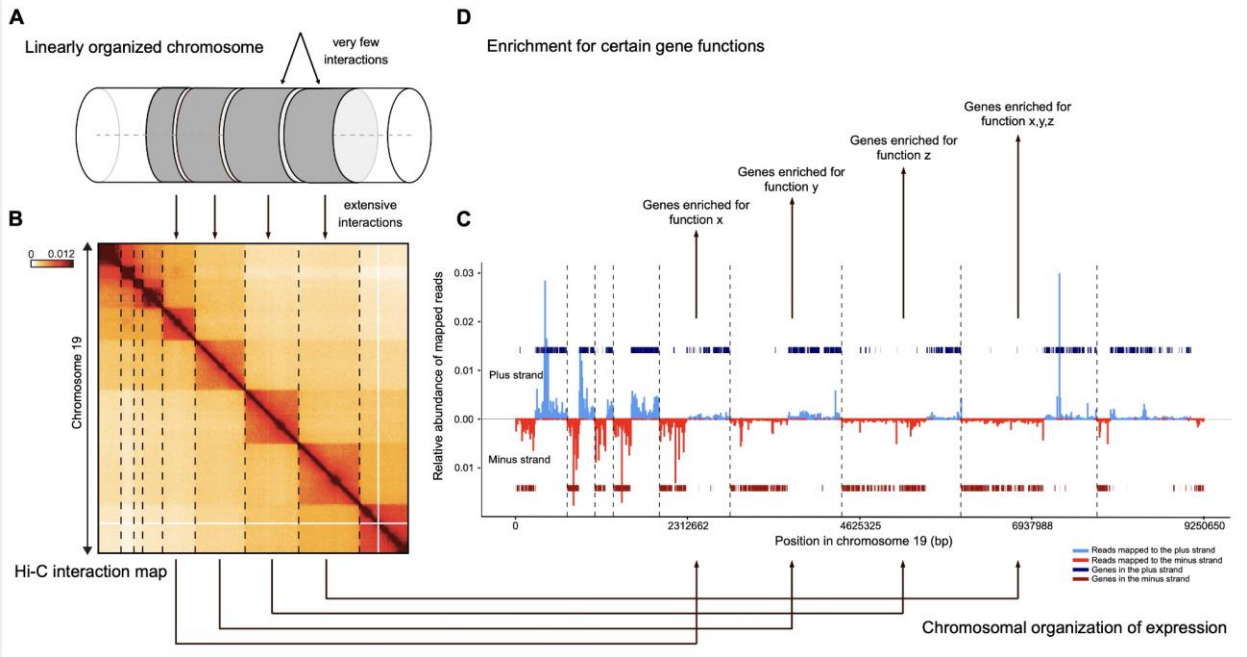

Figure 1. Structural and functional organization of Symbiodinium microadriaticum chromosomes. (A) Chromosomes fold as linear rods and each is composed of a series of structural domains separated by boundaries. **(B)** Hi-C interaction map for chromosome 19 (Smic1.0; bin size = 50 kb) with dotted lines indicating domain boundaries. **(C)** Domain boundaries (dotted lines) coincide with transcriptional domains, each composed of blocks of unidirectional genes that are co-expressed. **(D)** Some transcriptional domains are enriched for specific biological processes (for example, photosynthesis, nitrogen cycling, and stress response genes, indicated by x, y, z) and functionally related genes tend to co-occur at adjacent sites in the genome (although they are not always within one domain). Such level of structure-function correlation between chromatin domain formation, gene orientation, and gene expression is unprecedented. From an adaptation perspective, such a structural organization provides the opportunity for dynamic environmental adaptation through chromosome duplication or loss, which have been described for field and cultured specimens.

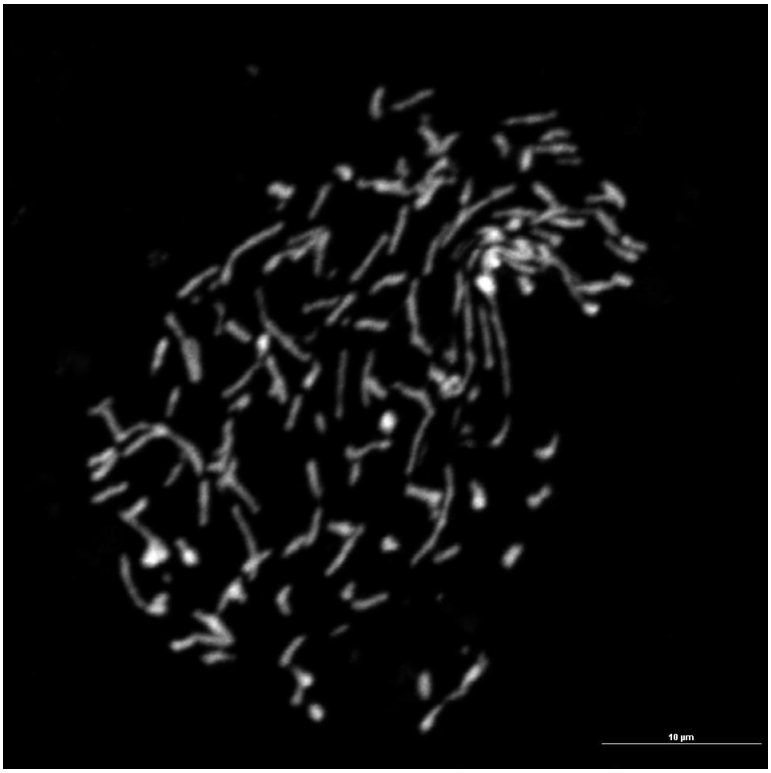

Figure 2. Interphase chromosomes spread on a slide and stained with DAPI. Chromosomes are condensed and rod-shaped and readily separate from each other during spreading. Photo credit: Ye Zhan.

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Figure 1

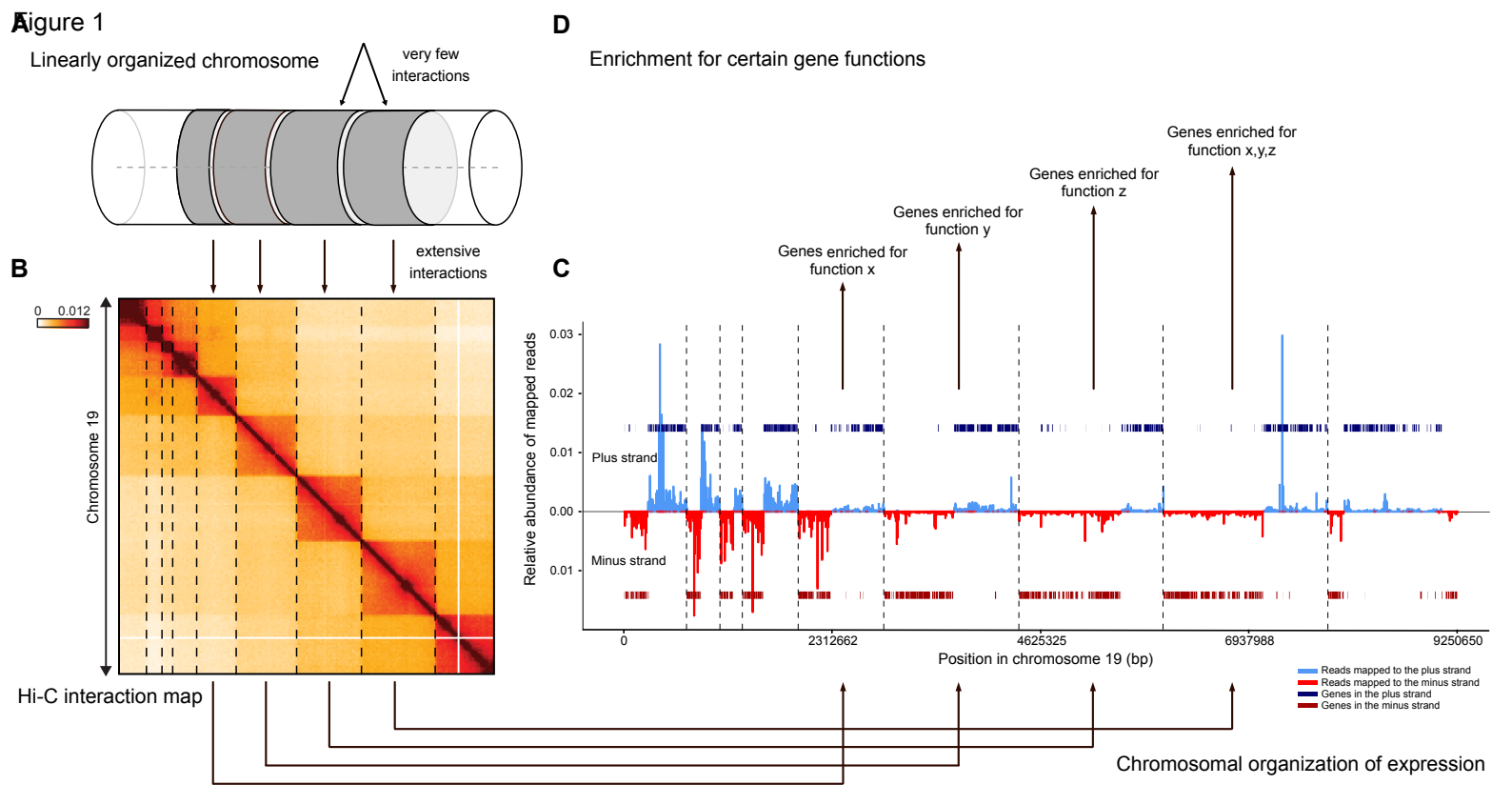
A
Linearly organized chromosome
very few interactions
extensive interactions
B
0
0.012
Chromosome 19
Hi-C interaction map
C
Genes enriched for function x
Genes enriched for function y
Genes enriched for function z
Genes enriched for function x,y,z
Relative abundance of mapped reads
0.03
0.02
0.01
0.00
0.01
Plus strand
Minus strand
0
2312662
4625325
6937988
9250650
Position in chromosome 19 (bp)
Reads mapped to the plus strand
Reads mapped to the minus strand
Genes in the plus strand
Genes in the minus strand
D
Enrichment for certain gene functions
Chromosomal organization of expression

Figure 2

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