The Genome of the Cauliflower Coral *Pocillopora verrucosa*

Carol Buitrago-López [1], Kiruthiga G. Mariappan[1], Anny Cárdenas [2], Hagen M. Gegner [1,3], and Christian R. Voolstra [1,2,*]

[1]Red Sea Research Center, Division of Biological BESE, King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia

[2]Department of Biology, University of Konstanz, Germany

[3]Centre for Organismal Studies (COS), University of Heidelberg, Germany

*Corresponding author: E-mail: christian.voolstra@uni-konstanz.de.

Accepted: 24 August 2020

Abstract

Climate change and ocean warming threaten the persistence of corals worldwide. Genomic resources are critical to study the evolutionary trajectory, adaptive potential, and genetic distinctiveness of coral species. Here, we provide a reference genome of the cauliflower coral *Pocillopora verrucosa*, a broadly prevalent reef-building coral with important ecological roles in the maintenance of reefs across the Red Sea, the Indian Ocean, and the Pacific Ocean. The genome has an assembly size of 380,505,698 bp with a scaffold N50 of 333,696 bp and a contig N50 of 75,704 bp. The annotation of the assembled genome returned 27,439 gene models of which 89.88% have evidence of transcription from RNA-Seq data and 97.87% show homology to known genes. A high proportion of the genome (41.22%) comprised repetitive elements in comparison to other cnidarian genomes, in particular in relation to the small genome size of *P. verrucosa*.

Key words: coral reef, genome assembly, reference genome, reference transcriptome, *Pocillopora verrucosa*.

Significance

The ongoing destruction of coral reefs worldwide heightens the need to better understand the genomic underpinnings of coral resilience. One critical resource to assist such efforts is the generation and provision of reference genomes to enable population genomics approaches and adaptive evolution studies. Here, we generated the genome of the common coral *Pocillopora verrucosa*, a broadly studied and ecologically important species. Our study demonstrates that reference genomes can be obtained utilizing improved assembly algorithms and the availability of highly assembled genomes from close-by species to fill critical gaps for species that lack genomic resources.

Introduction

Coral reefs are among the most biodiverse ecosystems on earth, providing habitat for about a third of all marine species (Spalding et al. 2001; Plaisance et al. 2011). Besides their ecological importance, coral reefs provide numerous goods and ecosystem services to millions of people (Moberg and Folke 1999; Cesar et al. 2003). The well-being of these ecosystems relies on the health of reef-building corals (order Scleractinia), which comprise the foundation species and main ecosystem architects of coral reefs. Despite their importance, corals are severely threatened by local (overfishing, pollution, industrialization) and global (climate change, ocean warming) anthropogenic impacts that continue to decrease coral cover at an alarming rate (IPCC 2018). Therefore, better knowledge on coral biology is critical to conceive strategies to mitigate coral reef demise.

The cauliflower coral *Pocillopora verrucosa* (Ellis and Solander 1786; NCBI Taxonomy ID: 203993; supplementary fig. S1, Supplementary Material online) is one of eight species currently described in the genus *Pocillopora* (Schmidt-Roach

et al. 2014) and belongs to the family Pocilloporidae together with the genera *Madracis*, *Seriatopora*, and *Stylophora*. *P. verrucosa* is widely distributed and is prevalent in the Red Sea, across the Indian Ocean, and across the Pacific Ocean, up to the Eastern Tropical Pacific, colonizing an extensive range of depths that cover shallow to mesophotic settings (Schmidt-Roach et al. 2014; De Palmas et al. 2018; Soto et al. 2018). *Pocillopora verrucosa* is an important reef framework builder and has an important ecological role as an early colonizer, aiding the recovery of reefs after natural disturbances (Pearson 1981; Bianchi et al. 2006). Despite the cosmopolitan distribution of *P. verrucosa*, which makes it a model for experimental and biological studies covering the fields of histology (Kruger and Schleyer 1998; Hirose et al. 2000), physiology (Ziegler et al. 2014; Sawall et al. 2015; Edmunds and Burgess 2016), phylogenetics (Flot et al. 2008, 2011; Pinzón et al. 2013; Schmidt-Roach et al. 2014), and population genetics (Combosch and Vollmer 2015; Robitzch et al. 2015), a reference genome is not available.

Here, we report on the sequencing, assembly, and annotation of the genome of the cauliflower coral *P. verrucosa* from the Red Sea (supplementary fig. S1, Supplementary Material online), which we obtained through initial assembly of a high-throughput single paired-end short-read library and subsequent reference scaffolding to the available genome of *Pocillopora damicornis* (Cunning et al. 2018). The generated draft genome is ~380 Mb in size (scaffold N50 of 333 kb, contig N50 of 75 kb) and features a total of 27,439 predicted protein-coding genes. The genome of *P. verrucosa* will be of value for comparative studies (Voolstra et al. 2015, 2017; Bhattacharya et al. 2016; Cunning et al. 2018), as a genomic reference to enable population genomic approaches (e.g., RAD-Seq), and as a foundation for molecular biology studies (e.g., RNA-Seq).

Materials and Methods

Coral Sampling and Isolation of Genomic DNA

On April 26, 2018, a medium-size fragment (10 cm length) of a coral colony of *P. verrucosa* was collected at 6 m depth in the Red Sea Al Fahal forereef (22°15.100N, 38°57.386E) and transferred to the Coastal and Marine Resources Core Lab (CMOR) aquaria facilities in KAUST, Saudi Arabia (supplementary extended materials and methods, Supplementary Material online). The Saudi Coastguard Authority issued sailing permits to the site that included coral collection, following the Nagoya protocol. Coral genomic DNA (gDNA) was extracted using the Blood & Tissue kit (Qiagen, Hilden, Germany).

Pocillopora verrucosa Lineage Determination

Previous phylogenetic analyses have identified two genetic lineages (type 3 and type 7) within *P. verrucosa* in the Red Sea (Pinzón et al. 2013; Schmidt-Roach et al. 2014) with type 3 more commonly found than type 7. To determine the genetic lineage of our *P. verrucosa* specimen, we used the primers FATP6.1 (5′-TTTGGGSATTCGTTTAGCAG-3′) and RORF (5′-SCCAATATGTTAAACASCATGTCA-3′) (Flot et al. 2008) to amplify the mitochondrial open reading frame (mORF) region. Phylogenetic analysis showed that our *P. verrucosa* specimen clustered within the mitochondrial open reading frame lineage type 3 sequences (Pinzón et al. 2013), Clade 2 (Schmidt-Roach et al. 2014). Hence, the genome represents the most common Red Sea *P. verrucosa* lineage (supplementary fig. S2, file S1, and extended materials and methods, Supplementary Material online).

Physical Genome Size Estimation

We determined the physical genome size by measurement of the *P. verrucosa* nuclei size using chicken erythrocyte nuclei as a reference (DNA QC Particles kit, BD Biosciences, San Jose, CA; supplementary extended materials and methods and fig. S3, Supplementary Material online). The coral genome size estimation was based on the diploid DNA content of chicken erythrocytes of 2.5 pg±0.04 per cell and was calculated as follows: sample genome size [pg]=1.25 *x*/*y* (*x*, fluorescence intensity of unknown sample; *y*, fluorescence intensity of chicken erythrocyte nuclei). After calculating the mean DNA content per copy of genetic information (1C), the genome size was determined by considering that 1 pg DNA equals 978 Mb (Doležel et al. 2003).

Sequencing Library, Read Filtering, Genome Assembly, and Scaffolding

A single gDNA library was constructed using the NEBNext Ultra II DNA Library Prep Kit for Illumina according to the manufacturer's instructions (New England Biolabs, Ipswich, MA). The paired-end library was sequenced on the Illumina HiSeq2500 platform (rapid run—500 cycles) at the KAUST Bioscience Core Lab (BCL). The sequencing yielded 141,993,203 read pairs (>174× coverage assuming a genome size of ~400 Mb), which were trimmed, quality assessed, and filtered to remove unwanted sequences according to the pipeline detailed in the Supplement.

The filtered paired-end reads were assembled with DISCOVAR de novo (Weisenfeld et al. 2014). To assess the level of heterozygosity, the filtered paired-end reads were used to obtain k-mer counts of lengths 25 and 31 using the software jellyfish version 2.2.6 (Marçais and Kingsford 2011) (details available in the Supplement). Based on k-mer distributions of lengths 31 and 25, the obtained heterozygosity rate was 1.21% and 1.32% (supplementary table S1, Supplementary Material online), respectively. This is in line with the high heterozygosity rates (1–2%) reported for other coral genomes (Bellis et al. 2016; Helmkampf et al. 2019; Robbins et al. 2019). Consequently, we applied a hierarchical

filtering strategy as follows: 1) Circular scaffolds as well as contigs of mitochondrial origin were identified and removed, 2) contigs containing potential sequences from dinoflagellate, bacterial, or viral origin were identified with BLASTN (Altschul et al. 1990; Camacho et al. 2009) applying a 90% identity cutoff over 50% query length and removed (Voolstra et al. 2017). After that, the assembly was scaffolded using a reference-based approach employing CSAR (Chen et al. 2018) and the available genome of the closely related species *P. damicornis* (Cunning et al. 2018). Gaps were filled with GapFiller version 1.11 (Boetzer and Pirovano 2012) using the filtered reads of the paired-end sequencing library (see above). As a final filtering step 3), the scaffolded assembly was processed with the Haplomerger2 pipeline v20180514 (Huang et al. 2017) to further improve the assembly.

Basic summary statistics of the initial DISCOVAR de novo assembly as well as the putative haploid final genome assembly were estimated by QUAST version 5.0.2 (Gurevich et al. 2013) (supplementary table S2, Supplementary Material online). QUAST version 5.0.2 was also used to estimate genome statistics for the genomes of *P. damicornis* (Cunning et al. 2018) and *Stylophora pistillata* (Voolstra et al. 2017). Both genomes were downloaded from the reefgenomics.org database (Liew et al. 2016) at http://pdam.reefgenomics.org/ and http://spis.reefgenomics.org, respectively.

Genome Assembly Completeness Analysis

Completeness of the *P. verrucosa* genome was assessed by searching for 978 universal metazoan Single-Copy Orthologs (metazoa_odb9) using BUSCO version 3 in mode 'genome'. For comparative purposes, we performed the same genome completeness assessment for the genomes of *P. damicornis* and *S. pistillata* (supplementary table S3, Supplementary Material online).

Annotation of Repetitive Elements

Repetitive elements in the genome assembly of *P. verrucosa* were identified de novo using RepeatScout version 1.0.5 (Price et al. 2005) with an l-mer size of 16 bp and default settings (supplementary extended materials and methods and table S4, Supplementary Material online).

Reference Transcriptome Sequencing and Assembly

An RNA-Seq library was generated from 500 ng of total RNA using the TruSeq Stranded mRNA Library prep Kit (Illumina, San Diego, CA) as per the manufacturer's instructions (further details in the Supplement). The constructed library (median size 340 bp) was indexed and paired-end sequenced on the Illumina HiSeq4000 platform (300 cycles) at the KAUST BCL. RNA sequencing yielded 121,056,948 read pairs (i.e., 242 mio. paired-end reads), which were trimmed and further processed as detailed in the Supplement.

Gene Model Prediction

Coral transcripts from the reference transcriptome ($n = 49{,}384$, supplementary extended materials and methods, Supplementary Material online) were mapped to the genome assembly and filtered by PASA version 2.3.3 (Haas et al. 2008) to create a training set for AUGUSTUS version 2.5.5 (Stanke and Morgenstern 2005).

Protein Set Annotation

The final set of predicted proteins was generated by selecting the longest isoform per gene. The protein sequences were annotated following a hierarchical approach using the UniProt (SwissProt and TrEMBL) and the NCBI "nr" databases sensu Baumgarten et al. (2015). This approach led to the annotation of 19,427 proteins in SwissProt, 7,145 proteins in TrEMBL, and 283 proteins using the NCBI "nr" database; 584 proteins had no hits in either of the reference databases (supplementary extended materials and methods and file S2, Supplementary Material online).

Results and Discussion

Genome Size Estimation

We estimated the genome size of *P. verrucosa* using FACS of propidium-iodide-stained nuclei in addition to a k-mer based approach. The physical estimate yielded a genome size of ~407 Mb (supplementary fig. S3, Supplementary Material online) showing a good agreement with the k-mer based estimate, which obtained a size of 406 and 418 Mb for k-mers 25 and 31, respectively (supplementary table S1, Supplementary Material online). This genome size is larger than the estimated genome size of *P. damicornis* (349 Mb assessed using k-mer counts, Cunning et al. 2018) and smaller than that of *S. pistillata* (434 Mb assessed using FACS, Voolstra et al. 2017), which are the two other coral species in the family Pocilloporidae with published genomes.

Genome Assembly and Statistics

We obtained 141,993,203 paired-end read pairs (2×250 bp) from a single gDNA library. About 88% of read pairs were kept after filtering and used for a de novo genome assembly. Read coverage was estimated to be 153× based on the physical genome size estimate (407 Mb), which was reported to be in the optimal range for DISCOVAR de novo genome assemblies (Love et al. 2016). After assembly, we applied a filtering strategy to remove nonnuclear and noncoral contigs before scaffolding using the reference genome of the closely related coral *P. damicornis*. To address the issue of high levels of heterozygosity, we applied the Haplomerger2 pipeline to consolidate incompletely merged loci/alleles and produce a haploid reference genome assembly with a total length of ~380 Mb assembled in 25,605 contigs and 18,268 scaffolds

Table 1
Summary Statistics of the *Pocillopora verrucosa* Genome Assembly

Genome Assembly Statistics	Length		Number	
	Contig	Scaffold	Contig	Scaffold
Total (bp)	379,998,154	380,505,698	25,605	18,268
Max (bp)	571,091	2,095,917	—	—
≥5,000 (bp)	353,178,732	358,580,702	8,537	3,932
N50 (bp)	75,704	333,696	1,401	326
N75 (bp)	30,836	125,371	3,336	766
N's per 100 kb	7.89	134.40		

with a corresponding contig N50 of 75,704 bp and scaffold N50 of 333,696 bp, respectively (table 1). The assembly statistics of the scaffolded haploid genome compare well to the genome assemblies of the available genomes in the family Pocilloporiadae, namely *P. damicornis* (contig N50 = 25,987 bp, scaffold N50 = 326,133 bp) and *S. pistillata* (contig N50 = 20,518 bp, scaffold N50 = 457,453 bp).

To compare the assembly before and after reference genome scaffolding, we computed basic statistics of the DISCOVAR de novo assembly and of the final reference scaffolded and filtered assembly (after DISCOVAR assembly) (supplementary table S2, Supplementary Material online). As expected, the scaffolded haploid genome was a substantial improvement over the de novo assembly, highlighting the utility of having genomes of closely related species available for the generation of reference genomes from so far unconsidered species.

Genome assembly completeness was assessed by searching for 978 universal metazoan single-copy orthologs using BUSCO. We could identify 902 (92.22%) complete metazoan single-copy orthologs (of which 3.17% were duplicated), 18 orthologs (1.84%) were present but fragmented, and 58 orthologs (5.93%) were missing. Comparison to *P. damicornis* and *S. pistillata* showed that *P. damicornis* had 862 (88.14%) and *S. pistillata* had 861 (88.03%) complete metazoan single-copy orthologs (supplementary table S3, Supplementary Material online). The number of fragmented universal metazoan single-copy orthologs is comparable among the three pocilloporid species, whereas the number of missing single-copy orthologs is smaller in *P. verrucosa* (58, 5.93%) than in *P. damicornis* (87, 8.90%) and *S. pistillata* (89, 9.10%).

Genomic Repeats

The identification and annotation of repetitive elements showed that 41.22% of the genome comprised repetitive elements. Out of the 15,905 repeat motifs identified, we could annotate 4,915 motifs, which were further classified in six groups encompassing 63 superfamilies/clades (supplementary table S4, Supplementary Material online). Transposable elements (TEs), such as DNA transposons, LTR retrotransposons, and non-LTR retrotransposons (among others) comprised the largest portion of the *P. verrucosa* genome (17.22%), followed by unclassified interspersed repeats (13.47%) and simple repeats (10.28%). Given that unclassified interspersed repeats comprise putative species-specific TEs, we considered them TEs for the purpose of comparison between *P. verrucosa* and *S. pistillata*, as previously done for other coral genomes (Ying et al. 2018). Overall, we found a slightly higher proportion of TEs in *P. verrucosa* (30.69% of genome size) in comparison to *S. pistillata* (28.43% of genome size), despite the smaller assembly size of *P. verrucosa*. This was unexpected given the known positive correlation between TEs and genome size (Kidwell 2002; Hua-Van et al. 2005; Biscotti et al. 2015), although some margin of error exists.

At the moment, we can only speculate on the significance of the increased TE content in the genome of *P. verrucosa* in comparison to *S. pistillata*. TE expansion can denote signatures of genus radiation (Wong et al. 2019), and TE activity has been associated with response to environmental stress and phenotypic plasticity in plants (Negi et al. 2016), arguably of relevance for corals in the context of climate change and ocean warming. From this perspective, an increased TE content in *P. verrucosa* fits with the species' broad geographical and depth distribution, and arguably, broad physiological plasticity (Ziegler et al. 2014; Sawall et al. 2015; Voolstra and Ziegler 2020; Ziegler et al. 2019).

At large, however, the proportion of TEs in the genomes of both pocilloporid species were in line with expectation following Kidwell (2002), which predicts 28.29% and 29.71% for *P. verrucosa* and *S. pistillata*, respectively. Of note, a direct comparison with *P. damicornis* was not possible, due to the lack of high-identity repetitive content, which evaded assembly (Cunning et al. 2018).

Transcriptome Assembly, Gene Models, and Protein Annotation

RNA sequencing yielded 121,056,948 read pairs (i.e., 242 mio. paired-end reads) that produced 49,384 coral transcripts available for gene model prediction. Based on BUSCO , we found a high number of complete single-copy orthologs (893 of 978, 91.31%), whereas some orthologs were complete but duplicated (33, 3.37%). Consequently, the number of fragmented (28, 2.86%) and missing (24, 2.45%) single-copy orthologs was rather small, indicating that the reference transcriptome assembly is largely complete.

We identified a final set of 27,439 protein-coding genes with a mean CDS of 1,849.67 bp (table 2). Of these, 96.60% ($n = 26,506$) have complete ORFs and 89.88% ($n = 24,662$) are corroborated by RNA-Seq evidence. Despite largely similar gene statistics (table 2), the proportion of intronless gene models in *P. verrucosa* (10.62%) was comparable to that of

Table 2
Genomic Gene Sets of *Pocillopora verrucosa* (Present Study) in Comparison to the Other Pocilloporid Genomes of *Pocillopora damicornis* and *Stylophora pistillata*

	P. verrucosa	*P. damicornis*	*S. pistillata*
Genes			
Number of protein-encoding genes	27,439	26,077	25,769
Mean gene length (bp)	7,566.63	5,859.80	8,378.20
Genes with annotation (%)	97.87	N/A	88.91
Genes with annotation to SwissProt (%)	70.80	59.70	67.93
Exons			
Mean number of exons per gene	7.54	7.17	7.85
Mean exon length (bp)	316.92	244.86	265.66
Mean coding region (CDS) length (bp)	1,849.67	1,365.30	1,833.33
Introns			
Percentage of genes with introns (%)	89.38	87.74	96.59
Mean number of introns per gene	7.37	7.03	7.09
Mean intron length (bp)	784.93	665.17	918.25

P. damicornis (12.26%), but three times higher than in *S. pistillata* (3.41%). Intronless genes are commonly thought to arise from horizontal gene transfer events of sequences of bacterial origin or through reverse transcription (Baumgarten et al. 2015). As such, the higher number of intronless genes in both *Pocillopora* genomes may indicate extensive horizontal gene transfer or increased TE element activity, as genes encoding for reverse transcriptases are most commonly found as components of retrotransposons in eukaryotes (Lescot et al. 2016).

The majority of the 27,439 protein-coding genes were annotated (supplementary file S2, Supplementary Material online): in total, 97.87% ($n = 26,855$) had an annotation, the large majority of which (70.80%, $n = 19,427$) retrieved hits from the SwissProt database, followed by 7,145 proteins (26.04%) with hits in TrEMBL, and 283 proteins (1.03%) that showed similarity to proteins from the NCBI "nr" database. Only a small percentage of proteins (2.13%, $n = 584$) had no hits to either database.

Toward Generation of Model Species Reference Genomes

In this study, we present the first genome assembly for the coral species *P. verrucosa*. This is an important resource to advance the understanding of coral reef ecology and evolution, particularly because *P. verrucosa* is a common and globally distributed reef builder. As demonstrated above, we have assembled >90% of the *P. verrucosa* genome with a contig and scaffold N50 and gene completeness on par with the available genomes of *P. damicornis* and *S. pistillata*. We have accomplished this through utilization of an available genome of a closely related species used for scaffolding after initial assembly based on the sequencing of only a single genomic library, with overlapping paired-end reads. We recognize the challenge of assembling a coral genome particularly with regard to their high heterozygosity. We hope that the *P. verrucosa* genome assembly will be useful for a number of studies ranging from comparative genomics to genetic variants identification (e.g., SNPs and microsatellites).

Supplementary Material

Supplementary data are available at *Genome Biology and Evolution* online.

Acknowledgments

We would like to thank the Coastal & Marine Resources Core Lab (CMOR) for the aquaria facilities as well as the Bioscience Core Lab (BCL) at KAUST for sequencing. Further, we would like to thank Larissa Morales for support with R code for the repetitive elements analysis and Yi Jin Liew for his support to analyze gff3 files of *Stylophora pistillata* and assistance with hosting data on reefgenomics.org. In addition, we thank Sebastian Schmidt-Roach for confirming coral species identification based on skeletal morphology. Research reported in this publication was supported by King Abdullah University of Science and Technology (KAUST), the University of Konstanz, and the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) project number 433042944.

Author Contributions

Conceptualization: C.B.L. and C.R.V. Data curation: C.B.L., K.G.M., A.C., and C.R.V. Formal analysis: C.B.L. and K.G.M. Funding acquisition: C.R.V. Investigation: C.B.L., K.G.M., A.C., and C.R.V. Project administration: C.R.V. Resources: C.B.L., H.M.G., and C.R.V. Supervision: C.R.V. Validation: C.B.L. and C.R.V. Writing—original draft preparation: C.B.L. and C.R.V. Writing—review and editing: C.B.L., A.C., H.M.G., and C.R.V.

Data Availability

The reference genome of *Pocillopora verrucosa* (Pver_genome_assembly_v1.0.fasta) together with the structural and functional annotation of genes (Pver_genome_assembly_v1.0.gff3, Pver_genes_names_v1.0.fna, and Pver_proteins_names_v1.0.faa) as well as the transcriptome (Pver_transcriptome_v1.0.fasta) used for gene calling are available at http://pver.reefgenomics.org/ (last accessed September 8, 2020) (Liew et al. 2016). Detailed annotation of the gene models can be found in the supplementary information (supplementary file S2, Supplementary Material online) as well as the classification of repeat elements identified in the genome (supplementary table S4, Supplementary Material online). Raw sequence data determined for the *P. verrucosa* reference genome project are available under NCBI BioProject PRJNA551401 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA551401; last accessed September 8, 2020). The code to reproduce the analyses described herein is available at https://github.com/Carol-Symbiomics/Pocillopora-verrucosa-genome (last accessed September 8, 2020).

Literature Cited

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990. Basic local alignment search tool. J Mol Biol. 215(3):403–410.

Baumgarten S, et al. 2015. The genome of *Aiptasia*, a sea anemone model for coral symbiosis. Proc Natl Acad Sci U S A. 112(38):11893–11898.

Bellis ES, Howe DK, Denver DR. 2016. Genome-wide polymorphism and signatures of selection in the symbiotic sea anemone *Aiptasia*. BMC Genomics 17(1):160.

Bhattacharya D, et al. 2016. Comparative genomics explains the evolutionary success of reef-forming corals. Elife 5:9983.

Bianchi CN, et al. 2006. Dynamics and pattern of coral recolonization following the 1998 bleaching event in the reefs of the Maldives. Proc 10th Int Coral Reef Symp. 1:30–37.

Biscotti MA, Olmo E, Heslop-Harrison J(P). 2015. Repetitive DNA in eukaryotic genomes. Chromosome Res. 23(3):415–420.

Boetzer M, Pirovano W. 2012. Toward almost closed genomes with GapFiller. Genome Biol. 13(6):R56.

Camacho C, et al. 2009. BLAST+: architecture and applications. BMC Bioinformatics 10(1):421.

Cesar H, Burke L, Pet-soede L. 2003. The economics of worldwide coral reef degradation. Cesar Environ Econ Consult Arnhem WWF-Netherlands. 14:23.

Chen K-T, et al. 2018. CSAR: a contig scaffolding tool using algebraic rearrangements. Bioinformatics 34(1):109–111.

Combosch DJ, Vollmer SV. 2015. Trans-Pacific RAD-Seq population genomics confirms introgressive hybridization in Eastern Pacific *Pocillopora* corals. Mol Phylogenet Evol. 88:154–162.

Cunning R, Bay RA, Gillette P, Baker AC, Traylor-Knowles N. 2018. Comparative analysis of the *Pocillopora damicornis* genome highlights role of immune system in coral evolution. Sci Rep. 8:1–10.

De Palmas S, Soto D, Denis V, Ho MJ, Chen CA. 2018. Molecular assessment of *Pocillopora verrucosa* (Scleractinia; Pocilloporidae) distribution along a depth gradient in Ludao, Taiwan. PeerJ. 6:e5797.

Doležel J, Bartoš J, Voglmayr H, Greilhuber J. 2003. Nuclear DNA content and genome size of trout and human. Cytom A. 51A:127–128.

Edmunds PJ, Burgess SC. 2016. Size-dependent physiological responses of the branching coral *Pocillopora verrucosa* to elevated temperature and PCO2. J Exp Biol. 219(24):3896–3906.

Flot J-F, et al. 2011. Incongruence between morphotypes and genetically delimited species in the coral genus *Stylophora*: phenotypic plasticity, morphological convergence, morphological stasis or interspecific hybridization? BMC Ecol. 11(1):22.

Flot JF, Magalon H, Cruaud C, Couloux A, Tillier S. 2008. Patterns of genetic structure among Hawaiian corals of the genus *Pocillopora* yield clusters of individuals that are compatible with morphology. Comptes Rendus Biol. 331(3):239–247.

Gurevich A, Saveliev V, Vyahhi N, Tesler G. 2013. QUAST: quality assessment tool for genome assemblies. Bioinformatics 29(8):1072–1075.

Haas BJ, et al. 2008. Automated eukaryotic gene structure annotation using EVidenceModeler and the Program to Assemble Spliced Alignments. Genome Biol. 9(1):R7.

Helmkampf M, Bellinger MR, Geib SM, Sim SB, Takabayashi M. 2019. Draft genome of the rice coral *Montipora capitata* obtained from linked-read sequencing. Genome Biol Evol. 11(7):2045–2054.

Hirose M, Kinzie R. A, Hidaka M. 2000. Early development of Zooxanthella-containing eggs of the corals *Pocillopora verrucosa* and *P. Eydouxi* with special reference to the distribution of Zooxanthellae. Biol. Bull. 199(1):68–75.

Hua-Van A, Le Rouzic A, Maisonhaute C, Capy P. 2005. Abundance, distribution and dynamics of retrotransposable elements and transposons: similarities and differences. Cytogenet Genome Res. 110(1-4):426–440.

Huang S, Kang M, Xu A. 2017. HaploMerger2: rebuilding both haploid sub-assemblies from high-heterozygosity diploid genome assembly. Bioinformatics 33(16):2577–2579.

IPCC. Forthcoming 2018. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T, editors].

Kidwell MG. 2002. Transposable elements and the evolution of genome size in eukaryotes. Genetica 115(1):49–63.

Kruger A, Schleyer MH. 1998. Sexual reproduction in the coral *Pocillopora verrucosa* (Cnidaria: Scleractinia) in KwaZulu-Natal, South Africa. Mar Biol. 132(4):703–710.

Lescot M, et al. 2016. Reverse transcriptase genes are highly abundant and transcriptionally active in marine plankton assemblages. ISME J. 10(5):1134–1146.

Liew YJ, Aranda M, Voolstra CR. 2016. Reefgenomics.Org - a repository for marine genomics data. Database 2016:baw152. doi:10.1093/database/baw152

Love RR, Weisenfeld NI, Jaffe DB, Besansky NJ, Neafsey DE. 2016. Evaluation of DISCOVAR de novo using a mosquito sample for cost-effective short-read genome assembly. BMC Genomics 17(1):187.

Marçais G, Kingsford C. 2011. A fast, lock-free approach for efficient parallel counting of occurrences of k-mers. Bioinformatics 27(6):764–770.

Moberg FF, Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecol Econ. 29(2):215–233.

Negi P, Rai AN, Suprasanna P. 2016. Moving through the stressed genome: emerging regulatory roles for transposons in plant stress response. Front Plant Sci. 7:1448.

Pearson RG. 1981. Recovery and recolonization of coral reefs. Mar Ecol Prog Ser. 4:105–122.

Pinzón JH, et al. 2013. Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). J Biogeogr. 40(8):1595–1608.

Plaisance L, Caley MJ, Brainard RE, Knowlton N. 2011. The diversity of coral reefs: what are we missing? PLoS One 6(10):e25026.

Price AL, Jones NC, Pevzner PA. 2005. De novo identification of repeat families in large genomes. Bioinformatics 21(Suppl 1):i351–i358.

Robbins SJ, et al. 2019. A genomic view of the reef-building coral *Porites lutea* and its microbial symbionts. Nat Microbiol. 4(12):2090–2100.

Robitzch V, Banguera-Hinestroza E, Sawall Y, Al-Sofyani A, Voolstra CR. 2015. Absence of genetic differentiation in the coral *Pocillopora verrucosa* along environmental gradients of the Saudi Arabian Red Sea. Front Mar Sci. 2:5.

Sawall Y, et al. 2015. Extensive phenotypic plasticity of a Red Sea coral over a strong latitudinal temperature gradient suggests limited acclimatization potential to warming. Sci Rep. 5:8940.

Schmidt-Roach S, Miller KJ, Lundgren P, Andreakis N. 2014. With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. Zool J Linn Soc. 170(1):1–33.

Soto D, De Palmas S, Ho MJ, Denis V, Chen CA. 2018. Spatial variation in the morphological traits of *Pocillopora verrucosa* along a depth gradient in Taiwan. PLoS One 13(8):e0202586.

Spalding MD, Ravilious C, Green EP. 2001. World Atlas of Coral Reefs. Prepared at the UNEP World Conservation Monitoring Centre. Berkeley: University of California Press.

Stanke M, Morgenstern B. 2005. AUGUSTUS: a web server for gene prediction in eukaryotes that allows user-defined constraints. Nucleic Acids Res. 33(Web Server):W465–W467.

Voolstra CR, et al. 2015. The ReFuGe 2020 Consortium—using "omics" approaches to explore the adaptability and resilience of coral holobionts to environmental change. Front Mar Sci. 2(68).

Voolstra CR, et al. 2017. Comparative analysis of the genomes of *Stylophora pistillata* and *Acropora digitifera* provides evidence for extensive differences between species of corals. Sci Rep. 7:1–14.

Voolstra CR, Ziegler M. 2020. Adapting with microbial help: microbiome flexibility facilitates rapid responses to environmental change. BioEssays 42(7):2000004.

Weisenfeld NI, et al. 2014. Comprehensive variation discovery in single human genomes. Nat Genet. 46(12):1350–1355.

Wong WY, et al. 2019. Expansion of a single transposable element family is associated with genome-size increase and radiation in the genus *Hydra*. Proc Natl Acad Sci U S A. 116(46):22915–22917.

Ying H, et al. 2018. Comparative genomics reveals the distinct evolutionary trajectories of the robust and complex coral lineages. Genome Biol. 19(1):175.

Ziegler M, et al. 2019. Coral bacterial community structure responds to environmental change in a host-specific manner. Nat Commun. 10:3092.

Ziegler M, Roder CM, Buchel C, Voolstra CR. 2014. Limits to physiological plasticity of the coral *Pocillopora verrucosa* from the central Red Sea. Coral Reefs. 33(4):1115–1129.

Associate editor: Sujal Phadke