Development of a transcriptomic database for 14 species of scleractinian corals

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Abstract

Background: Scleractinian corals are important reef builders, but around the world they are under the threat of global climate change as well as local stressors. Molecular resources are critical for understanding a species’ stress responses and resilience to the changing environment, but such resources are unavailable for most scleractinian corals, especially those distributed in the South China Sea. We therefore aimed to provide transcriptome resources for 14 common species, including a few structure forming species, in the South China Sea.

Description: We sequenced the transcriptome of 14 species of scleractinian corals using high-throughput RNA-seq and conducted de novo assembly. For each species, we produced 7.4 to 12.0 gigabases of reads, and assembled them into 271 to 762 thousand contigs with a N50 value of 629 to 1427 bp. These contigs included 66 to 114 thousand unigenes with a predicted open reading frame, and 74.3 to 80.5% of the unigenes were functionally annotated. In the azooxanthelate species Tubastraea coccinea, 41.5% of the unigenes had at least a best-hit sequence from corals. In the other thirteen species, 20.2 to 48.9% of the annotated unigenes had best-hit sequences from corals, and 28.3 to 51.6% from symbiotic algae belonging to the family Symbiodinaceae. With these resources, we developed a transcriptome database (CoralTBase) which features online BLAST and keyword search for unigenes/functional terms through a user friendly Internet interface.

Short conclusion: We developed comprehensive transcriptome resources for 14 species of scleractinian corals and constructed a publicly accessible database (www.comp.hkbu.edu.hk/~db/CoralTBase). CoralTBase will facilitate not only functional studies using these corals to understand the molecular basis of stress responses and adaptation, but also comparative transcriptomic studies with other species of corals and more distantly related cnidarians.

Keywords: Coral, Coral reef, Database, Scleractinia, Symbiotic algae, Transcriptome

Background

Coral reefs are ecologically and economically important, but around the world they are threatened by global climate change such as ocean warming and acidification [1, 2], as well as local stressors such as poor fishing practices, pollution, coastal development, and unsustainable recreational activities [3–5]. Over the last several decades, coral reefs in many regions have degraded dramatically [6, 7]. A comprehensive assessment of 704 species of reef-building corals around the world placed 231 species (32.8%) in categories with elevated risk of extinction [8]. In Southeast Asia, around 50% of coral reefs are facing high or very high threat of degradation [9]. Along the northern coasts of the South China Sea, dramatic reduction in live coral cover and changes in dominant coral species have occurred over the last several decades in Hainan [10] and Guangdong [11] provinces.

Scleractinia, commonly called hard corals or stony corals due to their calcified skeleton, are often important reef builders. Around the world there are 1605 extant scleractinian species, which are classified into 304 genera and 40 families [12]. In recent years, it has been increasingly realized that developing molecular resources, especially transcriptome and genome sequences, can facilitate studies aiming to understand mechanisms underlying coral stress responses and resilience in the
changing environment [13, 14]. Nevertheless, our survey
in January 2019 showed that only a small fraction of
scleractinian species (i.e. 35 species representing 20
genera and 11 families) have transcriptome data deposited
in the National Center for Biotechnology Information
(NCBI) database and Reefgenomics (Additional file 1:Table S1). An analysis of the datasets with
collection site information shows that the geographic
distribution of such transcriptomic resources is biased:
6, 9, and 9 of the transcriptomes were produced based
on samples collected from the Great Barrier Reef, the
Caribbean Sea, and East Asia, respectively. Only 5 were
based on species distributed in the South China Sea,
which in total hosts 571 species of scleractinians [15]. In
addition, there were reports showing genetic differenti-
ation among coral populations in different regions [16–
19], therefore it is valuable to develop
population-specific transcriptomes.

We therefore aimed to provide comprehensive tran-
scriptomic resources for a set of common scleractinian
corals in the South China Sea. Based on samples col-
lected from Hong Kong, we sequenced and assembled
the transcriptomes for 14 species of scleractinians repre-
senting 8 families and 14 genera: Fungiidae (Lithophyllum
undulatum), Faviidae (Leptastrea purpurea), Merulin-
dae (Favites acuticollis, Platygrya carnosa, Hydnaphora
exesa, Dipsastrea rotuman), Acroporidae (Montipora
peltiformis, Acropora digitifera), Euphylliidae (Galaxea
fascicularis), Agariciidae (Pavona decussata), Poritidae
(Goniopora lobata, Porites lutea), Dendrophylliidae
(Turbinaria peltata, Tubastraea coccinea). These species
covered the most common species of scleractinian corals
in Hong Kong, including several species (i.e. A. digiti-
fera, P. carnosa, M. peltiformis and P. decussata) that are
important in forming reef structures [20]. Although a
transcriptome of P. carnosa from Hong Kong is already
available [21], its completeness is quite low, with only
73.42% complete BUSCOs (Benchmarking Universal
Single-Copy Orthologs). In recent years, the health of
some of these coral species has been affected by various
stressors including excessive bioerosion [22–24], skeletal
growth anomalies [25], bleaching [26], and recreational
activities [27, 28]. To facilitate easy access to the tran-
scriptome data, we constructed a relational database
with a user-friendly Internet interface.

Construction and content
Collection of coral samples
The following 14 species of stony corals were collected
from six sites in Hong Kong from June to July 2017 by
SCUBA diving (Fig. 1): P. decussata from Sharp Island
North; G. lobata, P. lutea, L. undulatum, L. purpurea
and G. fascicularis from Crescent Island; A. digitifera, T.
peltata, M. peltiformis, D. rotuman and F. acuticollis
from Bluff Island; H. exesa from Pak A; T. coccinea from
Basalt Island; and P. carnosa from Lai Chi Wo. For each
species, three small colonies (~ 2 cm²) were collected,
put in a cooler with dry ice immediately once they were
brought out of the sea surface, transported to Hong
Kong Baptist University where they were stored in a
freezer at –80 °C until use.

RNA extraction and RNA-seq
Total RNA was extracted from each sample using TRI-
zol reagent (Invitrogen, Carlsbad, CA, USA) following
the manufacturer’s protocol. After treatment with
RNase-free DNase I (ThermoFisher Scientific, Waltham,
MA, USA), the quality of RNA samples was determined
using 1% agarose gel electrophoresis and the quantity
was determined using a NanoDrop 2000c Spectropho-
tometer (ThermoFisher Scientific, Waltham, MA, USA).
RNA samples from three colonies for each species were
pooled, then sent to Beijing Genomics Institute (BGI),
Shenzhen for transcriptomic sequencing using an Illu-
mina X-TEN platform. Before the library preparation,
the concentration of the RNA samples was further ana-
lyzed using a Bioanalyzer 2100 (Agilent Technologies,
CA, USA). Oligo dT enrichment was used during the li-
brary construction with a NEBNext Poly(A) mRNA
Magnetic Isolation Module kit (New England Biolabs,
MA, USA). The library was prepared using a NEBNext
Ultra RNA Library Prep Kit for Illumina (New England
Biolabs, MA, USA). Sequencing was conducted under the
pair-end mode to produce reads 151 bp in length.
All sequences were cleaned to remove adaptors and
low-quality reads with a high proportion of N (>10%) or
high proportion of low-quality (Phred value Q ≤ 20)
nucleotide base (> 40%). The clean reads are deposited in
the Sequence Read Archive (SRA) of NCBI under acces-
sion number PRJNA512264.

Transcriptome assembly, completeness assessment, and
annotation
Clean reads of each species were assembled using Trini-
ty 2.5.1 [29] under the default settings. Transcript abun-
dance was estimated as transcripts per kilobase million
read (TPM) using RSEM 1.2.19 [30], and those without
expression or very low expression (TPM < 0.5) were
removed manually. Candidate open reading frames (ORFs)
and peptides were identified from the transcripts using
TransDecoder, and duplicate sequences with 100% simi-
arity in predicted peptides were removed using CD-HIT
[31]. For each species, the completeness of the assem-
bled transcriptome was assessed using BUSCO (bench-
marking universal single-copy orthologs) v1.1b [32] with
a set of 978 conserved single-copy metazoan genes as
the reference. Unigenes (i.e. the longest isoform for each
gene) were annotated using both Diamond v0.9.19.120
and InterProScan-5.13-52.0 [34]. Specifically, general sequence annotation was conducted using Diamond v0.9.19.120, which applied BLASTp search against NCBI’s non-redundant (nr) database with an E-value of $1 \times 10^{-5}$. To determine the protein domain structure and its functional features, Gene Ontology (GO) function, Kyoto Encyclopedia of Genes and Genomes (KEGG) and Reactome pathways for each unigene were classified using InterProScan-5.13-52.0 under default settings.

For each of the 14 species, RNA-seq produced 7.4 to 12 Gb clean reads (Table 1). Transcriptome assembly produced 271,569 to 762,693 contigs with an N50 of 629 to 1610. These contigs contained 259,788 to 495,155 predicted proteins. After removing unigenes with low expression level (TPM < 0.5) and the identical sequences, there were 66,342 to 113,634 unigenes left in the sequenced stony corals for use in downstream analyses.

The transcriptomes were assessed for the presence of the 978 core metazoan BUSCOs, which showed that they contained 86.09 to 94.58% complete BUSCOs, and 2.76–9.00% partial BUSCOs (Table 1). These metrics are comparable with those of recently published coral transcriptomes [35, 36], indicating the high completeness of our transcriptome assemblies.

**Proportion of sequences from coral and symbiotic algae**

Unigenes from each species were annotated by BLAST search against NCBI nr database and InterProscan. For each species, 51,685 to 86,253 unigenes were
Table 1 Summary of transcriptome assembly results for 14 species of corals

| Species  | G. lobata | P. lutea | L. undulatum | L. purpurea | G. fascicularis | A. digitifera | T. pettai | M. peltiformis | D. rotumana | F. acuticollis | H. exesa | T. coccinea | P. decussata | P. carnosa |
|----------|-----------|----------|--------------|-------------|----------------|---------------|----------|----------------|-------------|---------------|----------|--------------|-------------|-----------|
| Sequences |           |          |              |             |                |               |          |                |             |               |          |              |             |           |
| No. clean reads (×10⁶) | 53.5 | 52.9 | 57.3 | 546 | 57.2 | 568 | 57.1 | 58.0 | 57.4 | 57.1 | 52.1 | 80.1 | 496 | 716 |
| No. clean bases (×10⁶) | 8020.5 | 7931.8 | 89528 | 81904 | 85759 | 85250 | 86571 | 86927 | 86084 | 85706 | 78149 | 12011.7 | 74466 | 10703.7 |
| Q20 (%) | 94.43% | 95.03% | 94.69% | 95.02% | 95.09% | 94.78% | 94.96% | 95.17% | 95.25% | 94.86% | 97.20% | 94.55% | 97.78% |          |
| GC (%) | 48.59% | 46.62% | 47.16% | 48.40% | 45.46% | 47.21% | 49.68% | 44.41% | 47.00% | 44.99% | 47.06% | 44.82% | 48.36% | 48.68% |
| Assembly |           |          |              |             |                |               |          |                |             |               |          |              |             |           |
| Contigs | 343,691 | 361,384 | 329,100 | 312,242 | 371,569 | 563,805 | 314,269 | 583,587 | 389,239 | 677,268 | 529,492 | 762,693 | 329,657 |
| GC% | 46 | 45 | 46 | 45 | 46 | 46 | 45 | 47 | 45 | 47 | 46 | 44 | 47 |
| N50 (bp) | 1252 | 1181 | 1427 | 979 | 1473 | 1610 | 1072 | 1292 | 629 | 1337 | 946 | 1053 | 1077 |
| No. peptides | 298,424 | 277,066 | 293,531 | 468,029 | 289,072 | 281,219 | 435,029 | 259,788 | 364,047 | 306,486 | 495,155 | 316,983 | 452,102 |
| No. unigenes | 78,532 | 74,781 | 70,872 | 114,375 | 70,841 | 67,587 | 98,266 | 66,651 | 93,470 | 75,250 | 107,504 | 70,018 | 107,565 |
| Retained unigenes | 78,193 | 74,484 | 70,535 | 113,634 | 70,576 | 67,367 | 97,609 | 66,342 | 93,004 | 74,923 | 106,640 | 69,464 | 104,573 |
| Completeness assessment |           |          |              |             |                |               |          |                |             |               |          |              |             |           |
| Complete (%) | 895 (91.51%) | 907 (92.74%) | 898 (91.82%) | 911 (93.15%) | 895 (91.51%) | 874 (89.37%) | 880 (89.98%) | 897 (91.72%) | 842 (86.09%) | 899 (92.90%) | 906 (92.64%) | 869 (88.5%) | 895 (91.31%) |
| Partial (%) | 40 (4.09%) | 30 (3.07%) | 33 (3.37%) | 44 (4.50%) | 30 (3.07%) | 27 (2.76%) | 57 (5.83%) | 22 (2.25%) | 88 (9.00%) | 38 (3.89%) | 47 (4.80%) | 36 (3.68%) | 49 (5.01%) |
| Missing (%) | 43 (4.40%) | 41 (4.19%) | 47 (4.81%) | 23 (2.35%) | 53 (5.42%) | 77 (7.87%) | 41 (4.19%) | 59 (6.03%) | 48 (4.91%) | 41 (4.19%) | 25 (2.56%) | 17 (1.74%) | 55 (5.62%) |
| Unigene annotation |           |          |              |             |                |               |          |                |             |               |          |              |             |           |
| Total number | 61,440 | 58,120 | 56,529 | 86,253 | 54,862 | 54,249 | 73,723 | 51,685 | 71,551 | 57,922 | 79,394 | 53,035 | 63,291 |
| Annotated by nr database | 58,935 | 55,932 | 54,422 | 82,138 | 52,919 | 52,195 | 69,753 | 49,930 | 68,939 | 55,943 | 75,512 | 50,544 | 60,674 |
| Annotated by Interproscan | 39,253 | 36,023 | 35,383 | 58,466 | 33,451 | 33,469 | 50,410 | 31,360 | 42,071 | 36,407 | 55,404 | 39,467 | 39,111 |
| With GO | 31,308 | 28,816 | 28,188 | 47,479 | 26,694 | 26,827 | 40,852 | 25,142 | 33,095 | 29,274 | 45,268 | 32,664 | 30,913 |
| With KEGG & REACTOME | 7899 | 6664 | 6222 | 12,720 | 6040 | 5935 | 10,877 | 5888 | 8339 | 7217 | 13,102 | 9157 | 6608 |
| No. coral genes | 19,610 | 22,621 | 22,673 | 20913 | 21,254 | 19,806 | 16,253 | 20,569 | 27,993 | 22,226 | 15,287 | 21,993 | 29,689 |
| No. algal genes | 26,022 | 26,197 | 26,019 | 24,784 | 25,861 | 26,399 | 23,829 | 23,888 | 30,427 | 23,861 | 21,415 | 154 | 26,056 |

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successfully annotated, which accounted for 74.3 to 80.5% of the total unigenes (Table 1). Consistent with the expectation that members of the genus *Tubastrea* are azooxanthellate, 43.5% of the annotated *T. coccinea* unigenes had best hits from corals; only 0.3% of the annotated unigenes had best hit sequences from *Cladocentrum* (formerly *Symbiodinium* clade C [37]), which likely came from the environmental water or reef inhabitants that had symbiotic algae. Among the annotated unigenes from the 13 zooxanthellate species, 20.2 to 48.9% unigenes had best-hit sequences from corals, and 28.3 to 51.6% from symbiotic algae. Among the unigenes, 45.8 to 61.6% were successfully annotated with GO terms, and 9.8 to 17.3% with KEGG and Reactome.

**The identities of symbiotic algae**

To determine the identities of symbiotic algae in the corals, we searched our coral transcriptome data for several gene fragments in two ways. First, we conducted local BLAST against the GeoSymbio database [38] to search for ITS2 genes, after adding the ITS2 Symbiodiniaceae sequences reported from several species of corals in Hong Kong [39]. Our query returned subclade C1 as the best hit sequence in 10 of 13 sequenced corals that have symbionts (i.e. *G. lobata*, *P. lutea*, *L. undulatum*, *L. purpurea*, *A. digitifera*, *T. peltata*, *F. acuticollis*, *H. exesa*, *P. decussata*, *P. carnosa*) (Additional file 1: Table S2A). Subclade C15 was the best hit for *Porites lutea*. However, there was no ITS2 BLAST result for the symbionts of *G. fascicularis*, *M. peltiformis* and *D. rotuma*, probably because the Oligo dT enrichment procedure used in the library construction had removed all of the ribosomal RNA sequences including ITS2 in these three species.

Second, we conducted local BLAST against several Symbiodiniaceae markers (chloroplast 23S rRNA genes, 18S rRNA, ITS1, 5.8S rRNA and 28S rRNA) that have been used to identify symbiotic algal types. The accession numbers of sequences of these other markers used in local BLAST are listed in Additional file 1: Table S3. To improve the accuracy of the BLAST results, the e-value threshold was set as 1e−100 and the identity larger than 98%. Our query returned *Symbiodinium* clade C (i.e. *Cladocentrum* [37]) as the best-hit taxon for most of our transcriptomes, with some annotations also contained the subclade information (Additional file 1: Table S2B). Specifically, for the three species whose symbiont type could not be identified based on ITS2, both subclade C1 and C3 were the best hit for *G. fascicularis* and *D. rotuma* (based on 5.8S rRNA, ITS2, 28S rRNA and chloroplast 23S rRNA) and subclade C1 for *M. peltiformis* (based on 5.8S rRNA, ITS2, 28S rRNA). For the azooxanthellate coral *Tubastrea coccinea*, BLAST returned only one sequence from Symbiodiniaceae but its very low expression level (TMP = 0.56) indicated that the sequences were contaminants from the environment.

**Database structure**

CoralTBase, a relational database, was constructed using a method described previously [21, 40] to provide access to the 14 assembled coral transcriptomes through the Internet. Users can search data from one species or multiple species at the same time. The database, constructed using MySQL v5.6.34, is hosted on an Apache HTTP server. The data include DNA and protein sequences of all unigenes, which are linked with their corresponding NCBI nr, GO and KEGG and Reactome annotations by unigene ID. The database contains two relation tables (“GO_relation” and “KEGG_and_Reactome_relation”) and five entity tables (“NCBI annotation”, “Proteins”, “DNAs”, “GO” and “KEGG and Reactome”). A stand-alone web server, powered by ViroBLAST [41], was incorporated in the database to allow for BLAST search.

**Utility and discussion**

**Layout of CoralTBase**

CoralTBase can be accessed at www.comp.hkbu.edu.hk/~db/CoralTBase. Users can search the data from one or multiple species in several ways by BLAST or by a number of other query terms (Fig. 2). BLAST supports queries using DNA/protein sequence or fasta-format file against NCBI nr database (Fig. 2d). The output is a list of gene or protein sequences that match the query sequence with an E-value and similarity score (Fig. 2e). The returned DNA or protein sequence contains an attribute “Unigene ID” as well as its corresponding annotation. General Annotation Search allows users to query gene annotation (i.e. NCBI annotation) by gene name (e.g. ammonium transporter 2, Fig. 2f and g) or sequence ID. GO Annotation Search is the search method according to the GO class ID (Fig. 2b). A successful search will return a table that contains the matched GO class ID, and the unigene ID. KEGG and Reactome Annotation Search will return a table containing the KEGG or Reactome pathway and the matched unigenes (Fig. 2c). The DNA and protein sequences of all unigenes for each species can be downloaded from the Downloads area.

We used the host genes in the transcriptome of *A. digitifera* as an example to show the potential utility of the resource. We prepared a figure showing the GO annotations of the host genes (Additional file 3: Figure S1a). For the same species, we also plot the Wnt pathway (Additional file 3: Figure S1b). The Wnt pathway plays important roles in biomineralization and osteogenesis in vertebrates [42, 43] and has been reported in the transcriptome of the stony coral *Stylophora pistillata* [44]. We found that all Wnt genes in the KEGG pathway
for *A. digitifera* can be found in our transcriptome obtained in this study. Moreover, we found a few more genes (in red boxes) in the Wnt signaling pathway from our transcriptome, which is currently not present in the KEGG networks for *A. digitifera*. This example indicates that the transcriptome obtained in this study has a high coverage and it will be useful for further analysis of coral biology.

We obtained 132 one-to-one homologous genes from 18 species including all species we sequenced as well as four species whose data were downloaded from the GenBank. Based on these homologous genes we constructed a phylogenetic tree to show their evolutionary relationships (Fig. 3), using a method detailed in Additional file 3: Methods. We also provided the sequences alignment in Additional file 2: Alignment.

**Potential applications and expansion**

The resources produced in this study can be used to understand basic coral biology such as stress responses, development, reproduction, symbiosis and calcification. They can also be used as a transcriptomic reference for
Tag-seq, which is more cost-effective and accurate than traditional RNA-seq at quantifying gene expression [45]. Such studies can be conducted to understand the molecular mechanisms underlying various responses to stressors, such as high temperature, low salinity and disease development [46–48]. In a broader taxonomic context, these resources can be used in comparative genomic studies aiming to understand the evolution of early development [49], biomineralization [50], and immunity [51]. In the future, CoralTBase can be expanded to include more scleractinian and non-scleractinian species. For the species that have been included in the database, the transcriptome can be updated with data from more developmental stages or from different populations.

Conclusions
This work has generated high-throughput transcriptome data for 14 species of scleractinian corals. It has increased the number of scleractinian corals around the world with transcriptome dataset from 35 species to 45 species, 20 genera to 26 genera and 11 families to 13 families. For some species with published transcriptome database already, our new data are either more comprehensive (i.e. Platygyra cariosa) or are based on specimens collected from different geographical areas and therefore represent different populations (i.e. A. digitifera, G. fascicularis and P. lutea). We have also organized the transcriptome data into a relational database to facilitate easy access by the public.

Additional files

**Additional file 1:** Table S1. Information on published transcriptome datasets from Scleractinia. Table S2. Symbiotic algae types determined by BLAST coral transcriptomes against the ITS2 and rRNA genes (i.e. 18S, 28S 23S rRNA) from GenBank database. Table S3. The accession numbers of sequences in the GenBank database used for symbiotic algae clade identification. (XLSX 179 kb)

**Additional file 2:** Alignment. The alignment of one-to-one homologous genes of 18 stony coral species. (FASTA 3031 kb)

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Fig. 3 Phylogenetic tree of Scleractinia constructed based on one-to-one orthologous genes of 18 species. An image of the skeleton of each coral species is shown on the right of the species name. Numbers on main branches are bootstrap values in ML analysis. The transcriptomes of the stony coral Pocillopora damicornis, Pseudodiploria strigosa, Stylophora pistillata were downloaded from NCBI GenBank TSA database. Heliopora coerulea belongs to the order Helioporacea was used as the outgroup.
Competing interests

Kong (Cap. 170).

Ethics approval and consent to participate

initiated the project, contributed resources and revised the manuscript. All analyzed transcriptome data and drafted the manuscript. QC and JX

JYX and YHY identified and collected coral samples. YZ extracted coral RNA, contributions'

Authors

transcriptomes are available at the following website: www.comp.hkbu.edu.hk/~db/CoralTBase.

Acknowledgements

We thank Dr. Alice Y.S. Law at Hong Kong Baptist University for technical support.

Funding

This project was supported by Shenzhen Science and Technology Innovation Committee (JCYJ20170307161325613), Environment and Conservation Fund (2017–03) and General Research Fund of Hong Kong (12102018).

Availability of data and materials

All clean reads are deposited in the NCBI Sequence Read Archive (SRA) under the project number PRJNA512264. The assembled and annotated transcriptomic database for the brain coral Platygyra carnosus. Mar Biotechnol. 2013;15:244–61. 64.

Authors’ contributions

JYX and YHY identified and collected coral samples. YZ extracted coral RNA, designed and constructed the database website. JWQ, JX, BX and BL initiated the project, contributed resources and revised the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Our research adheres to the Wild Animals Protection Ordinance of Hong Kong (Cap. 170).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 19 February 2019 Accepted: 29 April 2019

Published online: 17 May 2019

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