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REPORT

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Mitogenomic analysis of *Montipora cactus* and *Anacropora matthai* (cnidaria; scleractinia; acroporidae) indicates an unequal rate of mitochondrial evolution among Acroporidae corals

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Abstract The complete nucleotide sequence of the mitochondrial (mt) genome was determined for specimens of the coral species *Montipora cactus* (Bernard 1897) and *Anacropora matthai* (Pillai 1973), representing two morphologically distinct genera of the family Acroporidae. These sequences were compared with the published mt genome sequence for the confamilial species, *Acropora tenuis* (Dana 1846). The size of the mt genome was 17,887 bp and 17,888 bp for *M. cactus* and *A. matthai*. Gene content and organization was found to be very similar among the three Acroporidae mt genomes with a group I intron occurring in the NADH dehyrogenase 5 (*nad5*) gene. The intergenic regions were also similar in length among the three corals. The control region located between the small ribosomal RNA (*ms*) and the cytochrome oxidase 3 (*cox3*) gene was significantly smaller in *M. cactus* and *A. matthai* (both 627 bp) than in *A. tenuis* (1086 bp). Only one set of repeated sequences was identified at the 3′-end of the control regions in *M. cactus* and *A. matthai*. A lack of the abundant repetitive elements which have been reported for *A. tenuis*, accounts for the relatively short control regions in *M. cactus* and *A. matthai*. Pairwise distances and relative rate analyses of 13 protein coding genes, the group I intron and the largest intergenic region, *igr3*, revealed significant differences in the rate of molecular evolution of the mt genome among the three species, with an extremely slow rate being seen between *Montipora* and *Anacropora*. It is concluded that rapid mt genome evolution is taking place in genus *Acropora* relative to the confamilial genera *Montipora* and *Anacropora* although all are within the relatively slow range thought to be typical of Anthozoa.

Keywords Mitochondrial genome · Acroporidae · Slow evolution · Unequal rate of evolution

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Introduction

Advances in nucleotide sequencing technology have enabled patterns of molecular evolution to be revealed based on genome-wide information. The mitochondrial (mt) genome has shown great potential for such studies. Animal mt genomes are usually intron-less, compact, closed circular DNAs, ranging in size from 14 to 40 kb (reviewed in Wolstenholme 1992). The gene content of animal mt genomes is usually conserved: 12 or 13 for proteins, one each for the small and large subunit ribosomal RNAs (*ms* and *rnl*), and 22 for transfer RNAs (*tRNA*). In addition, one non-coding sequence (control region in vertebrates or AT-rich region in insects) is known to contain elements controlling the initiation of replication and transcription. Variations in the length of this region are responsible for size variations observed between mt genomes (Wolstenholme 1992). In addition, mt gene organization can differ substantially across phylogenetic levels.

This general view of animal mt genome organization has been modified since complete mt sequences were obtained from the Anthozoa (Bridge et al. 1992; Wolstenholme et al. 1992; Beagley et al. 1995, 1996, 1998; Beaton et al. 1998; Pont-Kingdon et al. 1998; van Oppen et al. 1999a, 2002). The mt genomes of a sea anemone, *Metridium senile*, and a reef-building coral, *Acropora tenuis*, each contain only two *tRNA*s, namely $tRNA^{fmet}$ and $tRNA^{trp}$, and a group I intron, whereas only $tRNA^{fmet}$ is present in two octocorals, *Renilla kolikeri* and *Sacrophyton glaucum* (Beagley et al. 1996; van Oppen

et al. 1999b, 2002). An open reading frame (ORF) encoding a putative mismatch repair protein is also present in these two octocorals (Pont-Kingdon et al. 1998).

Despite the unique features of anthozoan mt genomes, their rate of molecular evolution has been shown to be slow in relation to that exhibited by other animals (van Oppen et al. 1999a; Chen and Yu 2000; reviewed in Shearer et al. 2002). Results from phylogenetic analyses of *Acropora* mt cytochrome b (*cytb*) and *ms* genes indicated that the rate of evolution in anthozoan mitochondrial genes is 10–20 times lower than the standard mitochondrial clock based on vertebrate sequences of 1–2% per million year (van Oppen et al. 1999a; Chen and Yu 2000). Shearer et al. (2002) reviewed DNA sequences of mt gene fragments commonly utilized in phylogenetic studies and concluded that slow evolution is probably a common feature not only in the anthozoans but also in other lower metazoans.

Corals in the family Acroporidae play a major role in reef coral diversity in the Indo-Pacific region (Wallace 1999; Veron 2000). The family includes four extant genera: *Acropora*, *Anacropora*, *Astreopora*, and *Montipora*. Two of these, *Acropora* and *Montipora*, are the most diverse genera in the scleractinian corals. There is thus considerable interest in establishing the evolutionary relationships among the genera in the family (Fukami et al. 1999; Wallace 1999; van Oppen et al. 2001). Ridley (1884) proposed that *Anacropora* was recently derived from *Montipora*, based on skeletal morphology and microstructure, while Veron (1995) suggested that *Acropora* might have evolved from an *Anacropora*-like ancestor. A morphological phylogeny of the entire family, including the extinct genus *Dendracus* indicated a basal clade of *Montipora* and *Anacropora* with *Astreopora*, *Dendracus* and finally two subgenera of *Acropora* as the terminal clade (Wallace 1999). Molecular phylogenetic analysis using *cytb* and ATP synthetase (*atp6*) genes also indicated a close relationship between *Montipora* and *Anacropora* (Fukami et al. 1999). In the present study, we determined the complete mt genomes of *Montipora cactus* and *Anacropora matthai*, using the long PCR technique, and compared these to the mt genome of *A. tenuis* (van Oppen et al. 2002) from Genbank. We then examined the molecular evolution of the three genera based on these three genomes.

Materials and methods

Coral samples

Sperm was collected from a *M. cactus* colony during the 2002 spawning period at Chinwan Inner Bay, Penghu Islands (Hsieh et al. 2001). A tissue sample was collected from *A. matthai* (Museum of Tropical Queensland specimen G57868) at Walea Lighthouse, Bay of Tomini, Sulawesi, Indonesia, during the 1999 *Tethyana* expedition to Indonesia by the second author and preserved in 95% (v/w) ethanol.

DNA extraction, long PCR, cloning, and sequencing

Total DNA was extracted by the protocols described in Chen et al. (2002). Two fragments (9 kb each) covering the entire mt genomes of the *A. matthai* and *M. cactus* speci-

Table 1 Primers used in the long PCR and primer walking for DNA sequencing of the mt genomes of two Acroporidae corals

Primer	Oligonucleotide sequence (5′ → 3′)	Primer	Oligonucleotide sequence (5′ → 3′)
Monti16Slong-A[a]	GACTGCCAGGGGGAAACC TAGAGCAGACAC	Monti16Slong-B[a]	GACAGTGAGACCCTCGTGA CACCATTCATA
Monti12Slong-B[a]	GACACGCTCCTCTAATTAA AACAGTGAACAGCC	Monti12Slong-A[a]	CAGCAGACGCGGTGAAACT TAAGGGCTAGT
Ana16SAint1	ACGGATTGACTCGGATACT	Monti16SBint1	TGTGTTAGTTTGCGACAGTA
AnaND1Rint2	CTGTGATAAGCAATGGAACT	Monti16SBint2	TAGGACGTCATATGTGTA
Mito16SAint3	TGTCTTGATTATTGGAAC	Mito16SBint3	AGCTTAATCCATCTTAGT
Mito16SAint4	TCTATTGGGCTGATCATCA	Mito16SBint4	AAATCAGAATATCGTCTC
Mito16SAint5	TACGACCAGCTTATGTCT	Mito16SBint5	ATATAAACCTCTGGATGC
Mito16SAint6	CATGCATTATTGCGCAGA	Mito16SBint6	GATGATCGTCTCCTAACA
Mito16SAint7	AAGACTCCTGTGGACGATGT	Mito16SBint7	GAAGGCTAACGGTCTACT
Mito16SAint8	GTTGGTGGCGCTGTACTA	MO16BRint7	GTTAACTCGAGGTCTTAGTA
Mito16SAint9	GGACATGGAGAGGCTGAT	Mito16SBint8	CCCTCGTGAACACGTCTA
Mito12SBint1	CTCCGCATCATAGGCAAG	Mito16SBint9	CTACAAGTCGAGTAAGCA
Mito12SBint2	CCATGCGCCAACATCATA	Mito16SBint10	TTCTCTCGATCCGGTTGT
Mito12SBint3	AGAAGTAGGTCAAGCACT	Monti12SAin1	TTAATTAGAGGAGCGTGT
Mito12SBint4	CGGCAACGGCTACTTCTA	Mito12SAint2	TATGTCGTAACATAGTGA
Mito12SBint5	TTAGTCAAGGCGATCAGA	Mito12SAint3	TGAAGAGGGACGGTCCTA
Mito12SBint6	AATCAACTTGAAGCAACT	Mito12SAint4	TGGCTCCGGCTGTTGA
AN12SBint7	AAACAGATAGTCTCCTGGA	Mito12SAint5	GTTTATTGGTGGGGCTCA
AN12SBint8	AACCCACACAATAGAGCACA	Mito12SAint6	ATGGTTCCGACATCGGAT
Mito12SBint9	AATTCCACTGCAACATCT	Mito12SAint7	TATGGGTTTAACAATCGC

[a]Primers for long PCR amplification

mens were amplified using the long PCR technique (Cheng et al. 1994). Four pairs of primers Monti16Slong-A, 5′-GACTGCCAGGGGG AAACCTAGAGCAGACAC-3′, Monti12Slong-B, 5′-GACACGCTCCTCTAATT AAAACAGTGAACAGCC-3′, and Monti16Slong-B, 5′-GACAGTGAGACCCTCGT GACACCATTCATA-3′, Monti12Slong-A, 5′-CAGCAGACGCGGTGAA ACTTAAGGGCTAGT-3′ were designed on the basis of the partial sequences of *ms* and *rnl* genes available from the GenBank (Romano and Palumbi 1997; Chen and Yu 2000). Long PCRs were performed using the LA PCR Kit (Takara) under conditions recommended by the manufacturer. PCR was performed in a PC-9606 thermal sequencer (Corbett Research) using the following thermal cycle: 1 cycle at 94°C for 1 min. 30 cycles at 98°C (20 s), 68°C (15 min), and 1 cycle at 72°C for 10 min. The PCR products were electrophoresed in a 0.6% agarose (FMC Bioproduct) gel in 0.5X TAE buffer to assess the yield. PCR products were cloned using the pGEM-T system (Promega) under conditions recommended by the manufacturer. Nucleotide sequences were determined for complementary strands of two clones from each sample using an ABI 377 Genetic Analyzer. Primers used in this study are listed in Table 1. The sequences obtained were submitted to GenBank under the accession numbers AY903926 and AY903295 for *M. cactus* and *A. matthai*.

Sequence analyses

The DNA sequences were assembled using the software program, DNASTAR 5.05 (Madison, WI). The DNA sequences were compared with the mitochondrial DNA (mtDNA) sequences of *A. tenuis* (van Oppen et al. 2002). Pairwise genetic distances (p-distance) of 13 protein-coding genes, group I intron, and *igr3* were calculated using PAUP 4.0 b10 (Swofford 2002). Relative-rate test was performed using Tajima's relative-rate test (Tajima 1993) implemented in MEGA 2.1 (Kumar et al. 2001).

Results and discussion

Gene content and organization

The entire nucleotide sequences of the circular mtDNA molecules of *A. matthai* and *M. cactus* were 17,887 bp

Table 2 Length and position of all coding and non-coding regions in *M. cactus* and *A. matthai* mt genomes

Region[a]	Length, bp/(Position)		
	M. cactus	*A. matthai*	*A. tenuis*
trnM	71 (1–71)	71 (1–71)	71 (1–71)
rnl	2266 (72–2337)	2261 (72–2332)	2261 (72–2332)
igr1	102 (2338–2439)	102 (2333–2434)	102 (2333–2434)
nad5 5′	720 (2440–3159)	720 (2435–3154)	720 (2435–3154)
intron 5′	321 (3160–3480)	322 (3155–3476)	323 (3155–3477)
nad1	984 (3481–4464)	984 (3477–4460)	984 (3478–4461)
igr2	106 (4465–4570)	106 (4461–4566)	108 (4462–4569)
cytb	1158 (4571–5728)	1158 (4567–5724)	1155 (4570–5724)
igr3	534 (5729–6262)	534 (5725–6258)	521 (5725–6245)
nad2	1098 (6263–7360)	1098 (6259–7356)	1098 (6246–7343)
igr4	32 (7361–7392)	32 (7357–7388)	32 (7344–7375)
nad6	594 (7393–7986)	594 (7389–7982)	594 (7376–7969)
igr5	70 (7987–8056)	73 (7983–8055)	68 (7970–8037)
atp6	699 (8057–8755)	699 (8056–8754)	699 (8038–8736)
igr6	179 (8756–8934)	180 (8755–8934)	151 (8737–8887)
nad4	1476 (8935–10,410)	1476 (8935–10,410)	1476 (8888–10,363)
igr7	28 (10,411–10,438)	28 (10,411–10,438)	52 (10,364–10,415)
ms	1172 (10,439–11,610)	1174 (10,439–11,612)	1176 (10,416–11,591)
control region	627 (11,611–12,237)	627 (11,613–12,239)	1086 (11,592–12,677)
cox3	789 (12,238–13,026)	789 (12,240–13,028)	789 (12,678–13,466)
igr8	55 (13,027–13,081)	55 (13,029–13,083)	56 (13,467–13,522)
cox2	744 (13,081–13,825)	744 (13,084–13,827)	744 (13,523–14,266)
igr9	35 (13,826–13,860)	35 (13,828–13,862)	32 (14,267–14,298)
nad4L	300 (13,861–14,160)	300 (13,863–14,162)	300 (14,299–14,598)
igr10	31 (14,161–14,191)	31 (14,163–14,193)	32 (14,599–14,630)
nad3	357 (14,192–14,548)	357 (14,194–14,550)	357 (14,631–14,987)
intron 3′	96 (14,549–14,644)	96 (14,551–14,646)	95 (14,988–15,082)
nad5 3′	1116 (14,645–15,760)	1116 (14,647–15,762)	1116 (15,083–16,198)
igr11	29 (15,761–15,7896)	28 (15,763–15,790)	30 (16,199–16,228)
trnW	70 (15,790–15,859)	70 (15,791–15,860)	70 (16,229–16,298)
igr12	32 (15,860–15,891)	32 (15,861–15,892)	32 (16,299–16,330)
atp8	219 (15,892–16,110)	219 (15,893–16,111)	219 (16,331–16,549)
cox1	1602 (16,092–17,693)	1602 (16,093–17,694)	1602 (16,531–18,132)
igr13	194 (17,694–17,887)	194 (17,695–17,888)	206 (18,133–18,338)

[a]Abbreviations of mt genes and regions referred to be van Oppen et al. (2002)

Table 3 Nucleotide content and length of the mt genomes in three Acroporidae corals as well as *M. senile* and *S. glaucum*

Taxa	A (%)	T (%)	G (%)	C (%)	Length (bp)
A. matthai	24.9	36.7	24.2	14.2	17,888
M. cactus	24.8	36.8	24.2	14.2	17,887
A. tenuis	25.1	37.0	24.2	13.7	18,338
M. senile	38.0	24.5	20.5	17.0	17,433
S. glaucum	29.6	34.7	19.4	16.3	18,453

and 17,888 bp in length (Table 2). These are compared with *M. senile* (17,433 bp), *A. tenuis* (18,338 bp), *Sarcophyton glaucum* (18,453 bp), and *Renilla kolikeri* (18,911 bp), (Table 3; Beagley et al. 1995, 1998; Beaton et al. 1998; van Oppen et al. 2002). Gene content and organization of the mt genomes of *M. cactus* and *A. matthai* (Fig. 1) are identical to those seen in *A. tenuis* with 13 protein genes, two rRNAs (*rnl*, *ms*), 2 tRNAs (*trnM*, *trnW*), a putative control region, and a group I intron spanning within the *nad5* gene in the genome (van Oppen et al. 2002). The complex repetitive elements occurring in the putative control region in *A. tenuis* (van Oppen et al. 2002) account for the size differences in the mt genomes among the three Acroporidae.

Nucleotide composition and codon usage

The nucleotide composition was 61.6% A + T in the mt genome of both *M. cactus* and *A. matthai*. This is similar to the A+T% reported for *A. tenuis*, *M. senile*, *R. kolikeri*, and *S. glaucum* (Table 3) but lower than that in ther invertebrates (reviewed in Wolstenholme 1992). As shown in *A. tenuis*, the least used nucleotide is cytosine (14.2% in both species) and the most used one is thymine (36.7% in *A. matthai* and 36.8% in *M. cactus*). A similar nucleotide composition was reported for *M. senile* and two octocorals (Beagley et al. 1995, 1998; Beaton et al. 1998). In *A. matthai* and *M. cactus*, the start codons are GTG and ATG as in the mt genome of *A. tenuis*. The termination codons are TGA and TAA which also occur in the third position in other cnidarians. Two tRNAs, *trnM* and *trnW*, are highly conserved in terms of size and composition in the mt genomes of all the three Acroporidae.

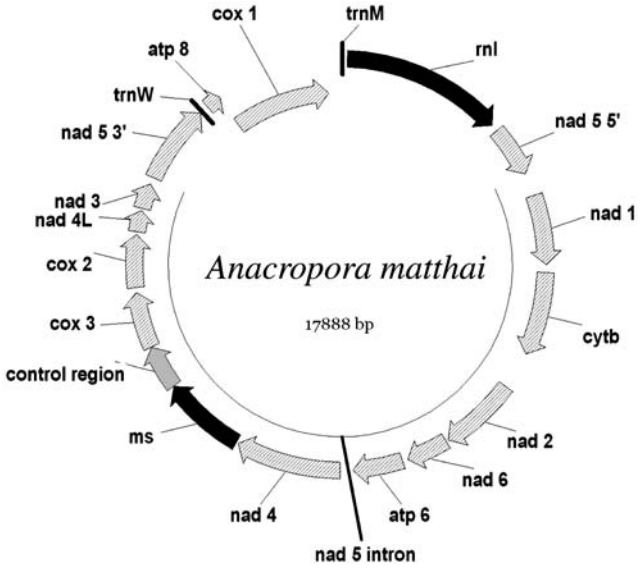

Fig. 1 Gene map of the *A. matthai* mt genome. The abbreviations of mt genes and regions referred to by van Oppen et al. (2002). The filled portions indicate the two ribosomal encoding genes. Protein-coding genes are indicated by the shaded portions. The large grey part represents the putative control region. Arrows indicate the direction of transcription. *nad5* intron is also indicated

Intergenic spacers, putative control region, and nad5 group I intron

As documented in other published cnidarian mt genomes, the genes in the mt genome of the two Acroporidae studied here are not as closely packed as seen in higher animals (Beagley et al. 1995, 1998; Beaton et al. 1998; van Oppen et al. 2002). Thirteen intergenic regions (*igr*) are identified among the junctions of protein-coding genes in the mt genomes of each species with lengths ranging from 28 bp (*igr7*) to 534 bp (*igr3*) (Table 1). Pairwise distance of *igr3* (ranging from 1.12 to 8.87%) showed significant matches of intergenic spacers to those of *A. tenuis*, which indicate that the *igrs* are conserved among the three Acroporidae corals (Table 4). No match was found either between any of the Acroporidae and *M. senile*, or between Acroporidae and octocorals (see also van Oppen et al. 2002).

The *rns cox3* intergenic spacer has been suggested to act as a control region for the mt genome of *A. tenuis* (van Oppen et al. 1999b, 2002). The *A. tenuis* mt control region has typical features commonly associated with control regions in the higher animals, including repetitive sequences, conserved sequences blocks (CSB), and secondary structure associated with the initiation of heavy-strand replication (Rand and Harrison 1989; Zhang et al. 1995; Lavrov et al. 2000; Chen et al. 2004). These complex repetitive elements also accounted for variation in length in phylogenetic comparisons among the *Acropora* species (van Oppen et al. 2001). In contrast, only two copies of a 22-bp repeated fragment (5′-TAAAAAAGTT TTGMTAATTG TG-3′) were identified at the 3′-end of control region of the mt genome in *A. matthai* and *M. cactus* (Fig. 2). Lack of other repetitive elements probably accounted for the shorter putative control re-

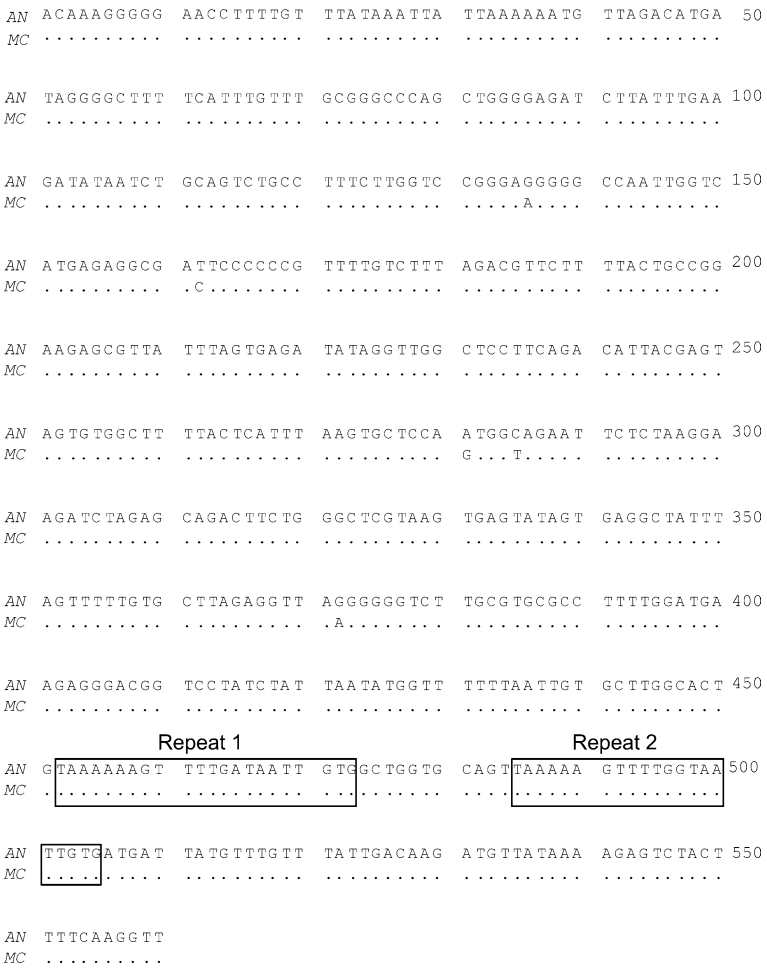

Fig. 2 Alignment of the mitochondrial putative control region in *A. matthai* (AN) and *M. cactus* (MC). Repeats are marked by boxes

gion of *A. matthai* and *M. cactus* (627 bp) when compared with the same region of *A. tenuis* (1086 bp). Surprisingly, the core sequence of the 22-bp repeat (5′-AAAGTT-TTGG-3′) shows a complete match with the *A. tenuis* mt control region at positions 606 to 615 (data not shown), indicating a significant functional role for this region, although more comparative data are needed to test this proposal.

Group I intron reported for the mt genomes of *A. tenuis* and *M. senile* (Beagley et al. 1996; van Oppen et al. 1999b) was observed in the same position of the *nad5* gene in both *A. matthai* and *M. cactus*. The size of group I intron is similar among the three Acroporidae (Table 1). Alignment of these group I introns indicated p-distances of 0.96 between *Anacropora* and *Montipora*, and of 6.01 between these two genera and *Acropora* (Table 4). Our data supports the hypothesis of van Oppen et al. (2002) that the *nad5* group I intron was acquired by a common ancestor prior to divergence of the Scleractinia and Actinaria.

Pairwise distances and relative rate tests

Pairwise distances of the 13 protein-coding genes, *nad5* group I intron, and the largest integenic spacer, *igr3*, demonstrated an extremely slow rate of evolution of the mt genomes between *A. matthai* and *M. cactus* (Table 4). These two species share three identical genes, *atp8*, *nad3*, and *nad4L*. The most divergent mt region between the two is *igr3* with a p-distance of 1.12. These rates are 3 to 8 times slower than those seen in *A. tenuis*. Tajima's relative-rate tests also strongly suggested that an unequal evolution rate occurred among the mt genomes of the three genera that has been studied (Table 4). From the p-distance comparisons and relative-rate tests, we conclude: first, the short p-distances in the 15-pair comparisons of mt regions indicate a close affinity between the genera *Anacropora* and *Montipora*. Molecular phylogenetic analyses of the three independent loci, including *igr3*, nuclear ribosomal internal transcribed spacer (ITS), and an intron spanning between exons 2 and 3 of the calmodulin gene (CaM-II), also indicated a close relationship between *Montipora* and *Anacropora* (Chang 2004). These results support both the morphological phylogeny of Wallace (1999) and the molecular phylogeny using mt *cytb* and *atp6* genes by Fukami et al. (1999). Secondly, the rate of mt genome evolution is unequal among the genera within the Acroporidae. This represents either an acceleration in *Acropora* or a slowing-down in *Anacropora* and *Montipora* after separation from their common ancestor.

Table 4 Pairwise distances and Tajima's relative-rate tests (X^2 -test) of 13 mt protein-coding genes, *igr3*, and the group I intron among three Acroporidae corals.

Region	p-distance			X^2 -test		
	MC vs. AN	MC vs. AT	AN vs. AT	(MC,AN)AT	(MC,AT)AN	(AN,AT)MC
atp6	0.72	4.01	3.86	$0.2^{n.s.}$	17.29**	19.59**
atp8	0	4.11	4.11	$0^{n.s.}$	9*	9*
cox1	0.38	4.56	4.18	$6^{n.s.}$	50.95**	67**
cox2	0.27	4.17	4.17	$0^{n.s.}$	27.13**	27.13**
cox3	0.38	5.7	5.58	$0.33^{n.s.}$	37.36**	40.09**
cytb	0.52	5.54	5.88	$2.67^{n.s.}$	60.06**	49.47**
nad1	0.41	4.65	4.65	$0^{n.s.}$	32.4**	32.4**
nad2	0.91	5.65	5.01	$5.44^{n.s.}$	33.2**	50.07**
nad3	0	4.76	4.76	$0^{n.s.}$	17**	17**
nad4	0.41	3.79	3.79	$0^{n.s.}$	44.64**	44.64**
nad4L	0	3.33	3.33	$0^{n.s.}$	10*	10*
nad5	0.5	4.64	4.46	$1^{n.s.}$	65.67**	71.43**
nad6	0.51	4.71	4.88	$0.33^{n.s.}$	24.14**	21.55**
igr3	1.12	8.87	8.87	$0^{n.s.}$	34.78**	34.78**
Group I intron	0.96	6.01	6.01	$0^{n.s.}$	17.64**	17.64**

Abbreviations: *AN*, *A. matthai*; *AT*, *A. tenuis*; *MC*, *M. cactus*. *n.s.*, not significant; * $p < 0.05$; ** $p < 0.001$

Studies conducted on *Acropora* suggest that there is a potential for cross-species introgression among species of this genus (Marquez et al. 2002a, b; van Oppen et al. 2001; Vollmer and Palumbi 2002), which should slow down rates of molecular evolution at species level rather than increasing them. However, phylogenetic analysis (neighbor-joining tree) of the Family Acroporidae using *cytb* gene showed a significantly shorter tree length of *Montipora*/*Anacropora* lineage (0.00712 ±0.00383) than that of the *Acropora* lineage (0.03258 ±0.00712) (Fukami et al. 1999; Chen et al. unpublished data). In addition, analysis of nuclear ribosomal genes and spacers suggested that highly heterogeneous rate of divergence is observed only in the lineage of *Acropora*, not in *Montipora*/*Anacropora*, among all the scleractinian corals available so far (Chen et al. 2004; Wei et al. unpublished data). These preliminary evidences based on the gene fragment analyses imply that the molecular evolutionary rate of *Acropora* genomes, both mitochondrial and nuclear, are accelerated after divergence from the common ancestor of *Montipora*, *Anacropora*, and *Acropora*.

Conclusions

Complete DNA sequences are presented for the mt genomes of *A. matthai* and *M. cactus*. Only one other complete scleractinian mt genome has been reported to date (*A. tenuis*, van Oppen et al. 2002). We found that gene content, organization, features of intergenic spacers, and a group I intron were conserved among these three mt genomes of the family Acroporidae. However, the putative control regions in *A. matthai* and *M. cactus* were significantly shorter than that reported for *A. tenuis* (van Oppen et al. 2002) and this was attributed to the presence of a significantly smaller number of distinct repetitive elements in those two species. A highly conserved short fragment identified at the 3′-end repeats of *A. matthai* and *M. cactus* mt control region was homologous that in *A. tenuis*, implying a functional role for this region. From p-distances and relative-rate tests, we concluded that more rapid mt evolution may be taking place within the genus *Acropora* than in *Montipora* and *Anacropora*, although all accord with the slower than usual rate of evolution proposed to be a general characteristic of the anthozoan mt genome (van Oppen et al. 1999a; Shearer et al. 2002). Further sequencing of species in these genera, as well as in *Astreopora*, is required to test this hypothesis.

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