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博士論文

Study of replication timing control by

internally located telomeric repeats and

the telomere-binding protein Taz1

in fission yeast

(分裂酵母染色体内部に存在するテロメア配列とテロメア 結合蛋白質 Taz1 による複製タイミング制御の研究)

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Doctoral Thesis

Study of replication timing control by internally located telomeric repeats and the telomere-binding protein Tazl in fission yeast

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Abstract

In eukaryotes, replication of chromosome DNA is coordinated by a replication-timing program that temporally regulates the firing of individual replication origins. However, the molecular mechanism underlying the program remains elusive. Here, I report that the telomere-binding protein, Taz1, plays a crucial role in the control of replication timing in fission yeast. A DNA element located proximal to a late origin in the chromosome arm represses initiation from the origin in early S phase. Systematic deletion and substitution experiments demonstrated that two tandem telomeric repeats are essential for this repression. The telomeric repeats recruit Taz1, a counterpart of human TRF1 and TRF2, to the locus. Genome-wide analysis revealed that Taz1 regulates about half of chromosomal late origins, including those in sub-telomeres. The Taz1-mediated mechanism prevents DDK-dependent Sld3 loading onto the origins. These results demonstrate that the replication-timing program in fission yeast utilizes the internal telomeric repeats and binding of Taz1. Furthermore, many of shelterin components and Rif1 are required to repress a wide range of late origins in arm regions and sub-telomeric regions, suggesting that telomere binding proteins other than Taz1 also involved in regulation of genome-wide control of replication timing. These results place telomere binding proteins at the interface between replication timing control including the site specific regulation by internally located telomeric repeats and telomere functions probably including metabolism and sub-nuclear localization.

General Introduction

Replication of eukaryotic chromosomes

DNA replication is fundamental and essential for inheritance of the genetic information through generations. For complete duplication of large eukaryotic chromosomes within the limited period of S phase, DNA replication initiates at a large number of chromosome loci known as replication origins. Cell biological studies show that DNA replication of large chromosome domain occurs in specific times during S phase in replication foci which occupy defined nuclear regions (Leonhardt et al., 2000). Replication timing control is important for the maintenance of proper cell cycle progression and genome stability, ensuring the efficient and complete duplication of chromosomes (Loipart et al., 2000; Pflumm and Botchan, 2001). Eukaryotic chromosomes are composed of chromatin structures, largely divided in euchromatin, where gene expression is active, and heterochromatin, where genes are silenced. In general, euchromatic regions tend to replicate in early S phase and heterochromatic regions replicate in late S phase (Fig.1A) (MacAlpine and Bell, 2005). Moreover, chromatin is organized within the nucleus in early G1 phase directing the localization of chromosomal domains to defined sub-nuclear positions. For example, heterochromatic domains, such as sub-telomere, which localize to the nuclear periphery or nucleoli, replicate in late S phase. In mammalian cells, the spatio-temporal program is established during a discrete time window in early G1 phase, the timing decision point (TDP) (Dimitrova and Gilbert, 1999). The fact that replication timings are changed coupled with alterations in histone modifications and gene expression during metazoan development suggest the importance of replication timing control (RTC) (hiratani et al., 2004, 2008; Lande-Diner et al., 2009).

Structure of chromosomes

Eukaryotic chromosomes consists arm region and several chromosomal loci with specialized chromatin structures, such as centromeres and telomeres. Telomere is the DNA-protein complex formed at the ends of eukaryotic chromosomes. Telomere

DNA consists of an array of short sequence repeats ending with a 3'-overhangs of single-stranded DNA. In mammal, the shelterin complex (TRF1, TRF2, POT1, RAP1, TIN2 and TPP1) binds to the telomere DNA in a sequence dependent manner. Telomere has two essential functions: the protection of the chromosome ends from degradation or fusion and maintenance of its length. To avoid cell-cycle arrest, telomere proteins, such as mammalian TRF1, TRF2 and POT1, are involved in attenuating checkpoint signaling regulated by ATM and ATR kinases at telomeres. To maintain telomere length, telomerase, telomere-specific reverse transcriptase, replenish telomere repeats since telomere becomes shorter at each round of replication. Thus, the Shelterin complex plays an important role in control of the telomere length. In general, centromere and telomere proximal regions (sub-telomere) form constitutive heterochromatin structures and are transcriptionally silenced. A core characteristic of heterochromatin is binding of heterochromatin protein 1 (HP1), a highly conserved family of chromosomal proteins. HP1 proteins (in fission yeast, Schizosaccharomyces pombe Swi6 and Chp2) specifically bind to di- and trimethylated H3K9 with its chromo-domain (CD) and recruit H3K9 metyltransferase, KMT1 (Clr4 in fission yeast, Su[var]3-9 in Drosophila, and Suv39H in mammals) to chromatin (Stewart et al., 2005). H3K9 methylation and HP1 proteins promote heterochromatic gene silencing by mechanisms that Chp2 recruits SHREC complex, containing Clr3 histone deacetylase, which mediates the deacetylation of H3K14 and transcriptional gene silencing (Sugiyama et al., 2007). The fission yeast chromosome contains three major heterochromatic loci: pericentromere, the silent mating-type locus and sub-telomeric region. In sub-telomeres, heterochromatin is maintained at least by two pathways. One is the RNAi (RNA interference) dependent pathway, which is commonly used at the heterochromatic loci including cenetromere and silent mating-type (MAT) locus (Hall et al., 2002; Volpe et al., 2002). The other is the Taz1, an ortholog of human TRF1 and TRF2, dependent pathway (Kanoh et al., 2005). Therefore, function and components of heterochromatin may differ between functional chromosomal loci since Taz1 is believed to localize specifically to telomere.

Structure of replication origins

The nucleotide sequences of replication origins greatly differ among organisms mainly due to the differences in DNA binding properties of ORC. In budding yeast, *Schizosaccharomyces cerevisiae*, replication origins are confined in less than 200 bp chromosome fragments that allow autonomous replication on plasmid (ARS activity). All the origins contain an 11-bp ARS consensus sequence (ACS) that is essential for initiation of replication. On the other hand, other eukaryotic cells have no such a consensus sequence in replication origins. In fission yeast, ARSs, comprising 500 bp-2 kb fragments, are located in intergenic regions. Since fission yeast ORC prefers AT rich sequence for its binding site, genome-wide locations of replication origins have been predicted by AT content and its length (Chuang and Kelly, 1999; Segurado et al., 2003; Takahashi et al., 2003). In multicellular organisms, no specific sequence or regions required for origin activity have been determined, although several chromosomal origins such as b-globin.

Cell cycle regulation of DNA replication

The initiation of replication in eukaryotes consists of several distinct steps that are regulated by cell cycle. Replication origins are recognized and bound by origin recognition complex (ORC), which is composed of six subunits Orc1-6. In G1 phase, ORC together with Cdc6 (Cdc18 in fission yeast) and Cdt1 promotes loading of a mini-chromosome maintenance (MCM) complex, composed of heterohexameric Mcm2-7, onto replication origins, resulting in a pre-replicative complex (pre-RC) (Bell and Dutta 2002). The activity of cyclin-dependent kinase (CDK), which inhibits this process, is low in late M and G1 phase, allowing the pre-RC formation in this period. At the beginning of S phase, activation of two conserved kinases, CDK and Dbf4-dependent kinase (DDK), promotes assembly of several other replication factors, including Sld3, Cdc45 and GINS, leading to unwinding of origin DNA and initiation of DNA synthesis (Fig. 1B)(Remus and Diffley 2009; Labib 2010; Tanaka and Araki 2010). The replisome including DNA polymerases and single-stranded DNA binding protein complex, Replication protein A (RPA), proceeds and synthesizes DNA

bidirectionally from replication origins. Replication origins do not fire simultaneously at the onset of S phase but do so at distinct time points during S phase. In budding yeast and fission yeast, pre-RCs are formed at all the origins, whereas specific origins are activated in early S phase (Raghuraman et al. 2001; Wyrick et al. 2001; Hayashi et al. 2007). Recent studies have suggested that DDK-dependent origin loading of Sld3 and Cdc45 is a key step determining the timing of initiation (Tanaka et al. 2011). These findings suggest that replication-timing program regulates activation of pre-RCs in these yeasts.

Regulation of replication origins

It is generally agreed that the status of chromatin has an impact on the timing of origin Replication origins in euchromatin domains, where genes are actively activation. transcribed, initiate early, while those in heterochromatin, where genes are repressed, replicate in late S phase (MacAlpine et al. 2004; Hiratani and Gilbert 2009). However, genome-wide identification of replication origins in fission yeast indicates that a subset of euchromatic origins do not fire in early S phase (Hayashi et al. 2007). Moreover, centromeric heterochromatin and the silent mating-type (mat) locus replicate in early S phase (Kim et al. 2003; Hayashi et al. 2009), and interestingly, Swi6 stimulates their early replication (Hayashi et al. 2009). On the other hands, sub-telomeric heterochromatin replicates very late in S phase in the presence or absence of Swi6 (Hayashi et al. 2009), suggesting that certain mechanism independent from the heterochromatin regulates replication timing. Although the checkpoint pathway represses late origins under depletion of nucleotides by hydroxyurea (HU) in budding yeast and fission yeast, it does not affect replication timing of the origins (Santocanale and Diffley 1998; Santocanale et al. 1999; Hayashi et al. 2007). Previous studies proposed that the replication program is related with the pattern of histone modifications, nucleosome organization and the nuclear positioning of chromosomal For example, deletion of histone deacetylase (HDAC), Rpd3, causes early loci. activation of nontelomeric late origins in budding yeast (Aparicio et al., 2004). Moreover, tethering of histone acetyltransferase (HAT) to a late origin advances its time of activation (Knott et al., 2009; Vogelauer et al., 2002). Similarly, histone hyperacetylation has been implicated to stimulate origin activation in *Drosophila* and human cells, suggesting that a similar mechanism may play a role in the regulation of origin activation in higher eukaryotes (Aggarwal and Calvi, 2004; Goren et al., 2008). In addition to a general correlation between these features of chromosome and origin activation, there exist other factors that affect replication timing of origins (See *Part* II).

Although lots of efforts have been concentrated on the dissection of trans factors whose deletion affect the genome-wide replication timing, the knowledge about the molecular mechanism which enables the specific regions to be recognized by the factors is limited. To understand this issue, it is necessary to identify the relation between cis-acting sequences regulating the replication timing of nearby origins involved in chromosome domains replicated at specific timing and trans factors associating to the sequences.

Introduction

It is well accepted that the time at which replication origin located in the eukaryotic chromosome initiates replication within S phase is a characteristic of each origin. However, what determines the activation timing of each origin is not well understood. Due to difficulties in analyzing pre-RC sites in metazoans, it is difficult to clarify the relation between individual pre-RC site and what determines its activation timing. I speculated that replication timing of origins may be an inherent property of the origin or affected by surrounding contents. Fission yeast is a suitable model organism to study the cis-acting sequences regulating the replication origin, since several hundreds loci distributed throughout the chromosomes have been identified as pre-RC sites or actual DNA synthesis sites in fission yeast (Feng et al., 2006; Hayashi et al., 2007; Heichinger et al., 2006). In common with other eukaryotes, initiation timing of fission yeast replication origins varies during S phase. Moreover, studying the regulation of replication origins in fission yeast may provide findings of general importance since structures of fission yeast chromosome and replication origin have similarities with those in higher eukaryotes. Although previous studies in yeasts have identified several chromosomal stretches and short cis-acting sequences that can force replication origins to fire later in S phase (Friedman et al., 1996; Sharma et al., 2001; Yompakdee and Huberman, 2004), little is currently known about the cis-acting sequences origins and trans factors associating to the sequences.

In this study, I investigated a representative fission yeast late origin *AT2088* in comparison with an early origin *ars2004*. To examine whether early/efficient and late/inefficient initiation of origins at chromosomal loci is owing to an inherent property of the origin or affected by surrounding contents, replication origin fragments that posses the ARS activity were translocated to other loci on chromosome. Effects on replication timing were examined by replication kinetics analysis using BrdU incorporation. Insertion of the late origin fragment, *AT2088*, to the vicinity of the early origin *ars2004* repressed the early activation of *ars2004*. Using systematic deletion and substitution experiments for the *AT2088* fragment, I identified the 17-bp

sequence containing two tandem copies of a telomeric repeat that is essential for the repression of replication origin. Mapping of telomeric repeats in the fission yeast genome allowed to identify 13 loci where the repeats exist within the same intergenic spaces with late origins in the chromosome arm. Disruption of the one neaby a late origin AT2035 caused early replication of the origin, suggesting that telomeric repeats are general determinant of late origins.

A recent discovery of fission yeast telomere binding proteins uncovered evolutionarily conserved elements of telomere functions between fission yeast and mammals. In fission yeast, Taz1 that binds directly to double stranded telomere DNA interacts with Rap1 and Rif1. Rap1 is a component of a Shelterin-like complex, in which Rap1 is linked with single-stranded telomere DNA binding protein, Pot1, via Poz1 (Miyoshi et al., 2008). Taz1, Rap1 and Poz1, components of the Shelterin-like complex, have inhibitory roles in recruitment or activation of telomerase (Chikashige and Hiraoka, 2001; Cooper et al., 1997; Miyoshi et al., 2008). Ccq1, another component of the Shelterin-like complex, is required for recruitment of telomerase and has a positive role in telomere elongation (Flory et al., 2004; Tomita and Cooper, 2008). On the other hand, Rif1 that associates with telomere by the interaction with Taz1 has a minor role in negative regulation of telomere length control (Kanoh and Ishikawa, 2001). In fission yeast, telomeric repeats in chromosome arm regions are essential for the repression of late origins. This finding raises the possibility that telomere binding proteins, which have been considered to act only at the chromosome ends, may function for regulation of replication in the internal chromosome regions.

In budding yeast, proximity to the telomeres confers late replication of some origins (Ferguson and Fangman, 1992). Telomeric DNA becomes shorter as a result of lagging strand synthesis, and shortened telomeres are elongated by telomerase. Interestingly, long telomeres cause a delay in the replication timing of telomere-proximal origins (Bianchi and Shore, 2007), suggesting the involvement of telomeric DNA and probably the telomere binding proteins. A recent study in fission yeast indicates that loss of rif1 rescues the growth of a null mutant of hsk1, the fission yeast homologue of Cdc7 kinase, and changes the replication timing program (Hayano et al., 2012). In mammalian cells including human and mouse, Rif1 is also a key factor that regulates replication timing program (Daniela Cornacchi et al., 2012; Satoshi Yamazaki et al., 2012). However, what enables the specific regions to be recognized by telomere binding proteins or other trans factors has not been elucidated.

Here, I demonstrate that Taz1 binding to the internal telomeric repeats plays an essential role in the control of replication timing in fission yeast. The telomeric repeats proximal to AT2088 and another late origin AT2035 recruit Taz1 to the loci and the recruitment of Taz1 was essential for timing control of these late origins. In the $taz 1\Delta$ strain, about half of previously identified late origins, including those in sub-telomeres, fire in early S phase. Remarkably, all of 13 origins associating internal telomeric repeats are regulated in a Taz1-dependent manner. These results indicate that Taz1, a well-defined telomere-binding protein, plays an essential role in replication timing control through binding to the telomeric repeats in the vicinity of internal late origins in fission yeast. Additionally, deletions of Rap1 and Poz1, which are components of the Shelterin-like complex, cause early replication of a number of late origins in chromosomal arm regions. Other telomere binding factor Rif1 causes early replication of almost all late origins in chromosomal arm regions and sub-telomeres including all the late origins that fire in $taz 1\Delta$. These results suggest that there are some pathways overlapping among telomere binding proteins for negative control of genome-wide replication origins.

Results

Identification of the DNA element that controls replication timing

To elucidate the mechanism that regulates timing of firing at individual replication origins, I compared two replication origins, ars2004 and AT2088/ARS745, which share properties of strong replication origins but differ in replication timing. Ars2004, located in the left arm of chromosome II (Fig. 2A), is a well characterized early origin (Okuno et al. 1999; Takahashi et al. 2003), where initiation factors assemble efficiently at the onset of S phase (Yamada et al. 2004; Yabuuchi et al. 2006). AT2088/ARS745 (Maundrell et al. 1988; Segurado et al. 2003) is a late/dormant origin located in the right arm of chromosome II (Fig. 2A). Despite the efficient formation of pre-RC at AT2088, 5-bromo-2'-deoxyuridine (BrdU), a heavy-density analogue of thymidine, was not incorporated in hydroxyurea (HU)-treated early S phase cells (Hayashi et al. 2007). Both origins are located in large intergenic regions flanked by divergent promoters, and contain long AT-rich regions that are essential for the replication origin activity. Moreover, they exhibit efficient ARS activity when the respective fragment is cloned on a plasmid (Fig. 2B). Since the previous study of early and late origins was carried out using HU-treated cells, where replication checkpoint was activated (Hayashi et al., 2007), I examined the replication timing of ars2004 and AT2088 in unperturbed S phase. Cells synchronously released from G2/M block by a temperature-sensitive cdc25-22 mutation were labeled for indicated periods with BrdU. The amounts of the heavy-light and light-light DNA, separated by CsCl density-gradient centrifugation, were determined by real-time PCR (qPCR) using primers amplifying ars2004 and AT2088, together with AT2024 (internal early origin control), AT2035 (late origin control), and TAS59, which is about 20 kb distant from the right end of chromosome II (Fig. 2A). Replication kinetics showed that ars2004 and AT2024 replicated about 10 min earlier than AT2035 and AT2088, while TAS59 replicated much later than the others (Fig. 2C). These results demonstrated that the replication timings of ars2004 and AT2088 differ in unperturbed S phase.

To investigate whether the replication timings of ars2004 and AT2088 are intrinsic to the origins, the intergenic fragment containing each origin was translocated into an ectopic chromosomal context. The 3.2-kb fragment containing ars2004 inserted at the AT2088 locus (ars2004/AT2088 Δ) replicated as early as the control early origin AT2024 (Fig. 3A). In contrast, the 3.6-kb fragment containing AT2088 inserted at the ars2004 locus (AT2088/ars2004 Δ) replicated late, as the control late origin AT2035 (Fig. 3B). Although the absolute times of replication vary between experiments, probably due to difference in period required for re-entry into the cell cycle from the G2/M block, I confirmed that the difference in $T_{1/2}$, time required for replication in half of cell population for an origin relative to that of the early origin control, AT2024, was maintained (Fig. 3C). The results of two-dimensional (2D) gel electrophoresis analysis indicated that replication initiated efficiently from the ars2004 placed at the AT2088 locus, as shown by the bubble arc (Fig. 3A), and that replication was rarely initiated from the AT2088 fragment at the ars2004 locus in early S phase (Fig. 3B). Moreover, the plasmids pARS2004 and pAT2088, carrying the corresponding fragments, replicated early and late in S phase, respectively (Fig. 4A, B). These results demonstrate that the replication timings are intrinsic to the ars2004 and AT2088 fragments.

If an element located in the AT2088 fragment forces the origin not to fire in early S phase, it might also repress another origin placed closely to the fragment. To test this possibility, the AT2088 fragment was inserted in the vicinity of *ars2004* on the chromosome (Fig. 5A), and the amounts of BrdU-incorporated DNA in HU-treated early S phase cells were analyzed for *ars2004* locus and other origins. In HU-treated wild-type cells without insertion, both *ars2004* and *AT2024* showed robust replication, while *AT2035* did not replicate efficiently (Fig. 5B). Although insertion of the *ura4*+ fragment alone did not cause significant change (Fig. 5B), insertion of *AT2088* fragment repressed the neighboring *ars2004* (Fig. 5B). This was due to decrease in initiation from *ars2004*, as shown by reduced amount of bubble arc in 2D-gel analysis (Fig. 5C). Furthermore, the *AT2088* fragment, when inserted at a site close to another early origin

ORI12 on chromosome I (Segurado et al. 2003), also repressed early replication of the origin (Fig. 6). These results showed that the *AT2088* fragment has the ability to control the replication timing of proximal origins. Accordingly, I named the activity as <u>replication timing control</u> (RTC) activity.

Identification of the essential sequence for replication timing control

To determine the minimum region of AT2088 that is required for RTC activity, AT2088 fragments lacking various regions were inserted next to ars2004 (Fig. 7A). The results presented in Fig. 7B show that a 634-bp fragment (L2312) of AT2088 is sufficient for repression of ars2004. Experiments using series of internal deletions in the 634-bp fragment revealed that a 32-bp fragment (2617-2648, N2617) is required for the RTC, and that the surrounding regions contribute to some extent (Fig. 7B). Base-substitutions of every 8 bp in the 32-bp region identified the 17-bp RTC essential sequence (from position 2624 to 2640) and 8-bp important sequence (from position 2641 to 2648) (Fig. 7D). Because RTC alters the replication timing of ectopically adjoined replication origins, its function is distinct from the replication origin activity of AT2088. The 3.6-kb intergenic fragment of AT2088 consists of two ARS fragments, each containing a highly AT-rich region (Fig. 7C; Fig. 8A). Disruption of the RTC essential sequence, located several hundred bp distant from the closer AT-rich region, did not affect the ARS activity (Fig. 8A), confirming that RTC is distinct from the origin activity.

I here examined whether the RTC controls replication timing at the original AT2088 locus. A 210-bp fragment containing the RTC essential sequence was deleted from the AT2088 locus ($AT2088\Delta 210$), and replication initiation was analyzed by 2D-gel electrophoresis. In contrast to a faint Y-arc from the AT2088 locus in HU-treated wild-type cells, a bubble arc, indicative of the initiation, was generated along with a strong transition Y-arc resulting from initiation from an asymmetrical position within the restriction fragment in $AT2088\Delta 210$ (Fig. 8B). These results indicate that the RTC is required for the control of replication timing at the native AT2088 locus.

Telomeric repeats are essential for repression of internal late replication origins

In fission yeast, telomeric repeats consist of GGTTAC followed by $A_{0.1}C_{0.1}G_{0.6}$ variations (Sugawara 1989; Cooper et al. 1997; Hiraoka et al. 1998). I found that the RTC essential sequence contains two tandem copies of a telomeric repeat, with a substitution of T for the last C (Fig. 9B). I examined whether the telomeric repeats are essential for control of replication timing at the native AT2088 locus. Base-substitution of the essential sequence (AT2088-S2632) promoted early replication specifically at AT2088 (Fig. 9B). Because the telomeric repeats in the RTC essential sequence contain an incomplete match to the consensus, I confirmed that two copies of telomere sequence, GGGTTACAGGTTACAGGG, replaced functionally consensus the incomplete sequence (Fig. 9B, AT2088-telF). Insertion of the consensus in the opposite direction also restored the RTC (Fig. 9B, AT2088-telR), suggesting that the telomeric repeats act as a discrete element, such as the protein-binding site. То explore the general role of telomeric repeats in the control of replication timing in fission yeast, I searched the fission yeast genome for two tandem telomeric sequences, GGTT A Y -N₍₁₋₃₎-GGTT A Y, where Y represents pyrimidine, using the "fuzznuc" program (Experimental Procedures). Such telomeric repeats are located at 26 loci, exclusively in the intergenic regions (Tables 1 and 2). Interestingly, 13 of them exist within the same intergenic spaces with late origins, which were identified in previous genome-wide study (Hayashi et al. 2007). To investigate whether the telomeric repeats have a general role in replication timing control, I disrupted the one located near AT2035 on chromosome II (Fig. 9C). Base-substitutions in the telomeric repeats caused robust early replication specifically at AT2035 (Fig. 9C, AT2035-S1959). These results strongly suggest that the telomeric repeats present near internal late origins play a general role in replication timing control.

Taz1 binds to the telomeric repeats near the internal late origins

At the ends of chromosomes, Taz1, a fission yeast orthologue of human TRF1 and TRF2, binds to two tandem copies of the telomeric repeat (Cooper et al. 1997; Spink et al. 2000). To elucidate the role of telomeric repeats located near the internal late

origins in the control of replication timing, I analyzed localization of 6Flag-tagged Taz1 at the internal chromosome regions using a chromatin immunoprecipitation (ChIP) assay. The experiments were accomplished by the support of Dr. Fukuura and Ami ChIP recovery of DNA for ade6, AT2035, AT2088 and Kishimoto. the telomere-proximal fragment (Tel-0.3) was determined by qPCR (Fig. 10). In wild-type cells, the recovery of *Tel-0.3* was about 50-fold higher than that of *ade6* (Fig. 10, left), indicating accumulation of Taz1 at the telomeres. Taz1 was also localized at the telomeric repeats near AT2035 and AT2088, as shown by recovery 3 and 4-fold higher than that of *ade6*, respectively (Fig. 10, right). Localization of Taz1 at AT2035 was impaired by AT2035-S1959 base-substitution, while the localization at AT2088 was not affected (Fig. 10, right). Moreover, AT2088-S2632 substitution abolished the Taz1 localization specifically at the AT2088 locus (Fig. 10, right). These results demonstrate that the telomeric repeats near AT2035 and AT2088 recruit Taz1 to the corresponding loci.

Taz1 plays an important role in global control of replication timing

I then asked whether Taz1 is required for replication timing control at late replication origins. BrdU incorporation was determined in the wild-type and $taz1\Delta$ strains for *AT2035* and *AT2088*, which are associated with telomeric repeats, as well as late origins *AT2080* and *ARS727*, which are not associated with telomeric repeats, and the sub-telomeric *TAS59*. In HU-treated wild-type cells, none of the late origins but the early origin *ars2004* replicated significantly (Fig. 11). In contrast, in HU-treated *taz1*\Delta cells, *AT2035* and *AT2080* or *ARS727* did not replicate significantly (Fig. 11). *TAS59*, which is located about 20-kb distant from the telomere, replicated more efficiently than ars2004 (Fig. 11). These results indicate that Taz1 is required for replication timing control of a subset of late origins that are associated with telomeric repeats.

To investigate the role of Taz1 in global control of replication timing, I and other members of Prof. Masukata's laboratory analyzed the replication profile of all chromosomes. The experiments were accomplished by the support of Dr. Fukuura and Dr. Ogawa. The BrdU-labeled DNA prepared from HU-treated wild-type and $taz 1\Delta$ cells was subjected to sequencing by oligonucleotide ligation and detection (SOLiD) (Fig. 12; Supplemental Fig. S1). Comparison of the replication profiles in wild-type and $taz 1 \Delta$ cells revealed that 26 and 46, in chromosome arm regions and sub-telomeres, respectively, among 156 late/dormant origins fired in the HU-treated $taz 1 \Delta$ cells (Fig. 16; Supplemental Fig. S1; Supplemental Table S1). Genome-wide analysis of Taz1-localization showed that Taz1 was localized at 16 of 26 internally located late origins that fired in *taz1* Δ (Fig. 16; Supplemental Fig. S1; Supplemental Tables S1, S2). Notably, the entire sub-telomeric regions spanning 50-100 kb from the ends of chromosomes I and II, including 46 previously identified late origins, replicated robustly in $taz 1 \Delta$ cells, although Taz 1 was localized only in the vicinity of the telomere (Fig. 12; Supplemental Fig. S1). These results suggest that Taz1 plays an important role in the control of global replication timing in fission yeast.

Shelterin-like components and Rif1 contribute global control of replication timing

To elucidate the roles of Taz1 in regulation of DNA replication, I investigated involvement of other telomere binding proteins. I examined the replication efficiencies of early and late origins in HU-treated strains lacking each of $rap1^+$, $rif1^+$, $poz1^+$ or $ccq1^+$.

In *rap1* Δ strain, the replication efficiencies at late origins, *AT2088* and *AT2035* increased to a similar level with *ars2004*, whereas the non-ARS locus or *TAS59* did not replicate significantly (Fig. 11). In addition, *AT2080*, which was not activated in *taz1* Δ strain, showed robust replication. The results in *poz1* Δ are similar to *rap1* Δ (Fig. 11). In contrast, in *ccq1* Δ strain, *AT2088* and *AT2035* did not significantly replicate, as observed in wild type. However, the replication efficiency of the sub-telomeric origin *TAS59* increased to a higher level than other late origins in this mutant. In case of *rif1* Δ , not only the late origins *AT2088* and *AT2035* but *TAS59* replicated efficiently, as observed in *taz1* Δ (Fig. 11). In addition to the late origins activated in *taz1* Δ , two late origins *AT2080* and *ARS727* replicated more efficiently than *ars2004* in *rif1* Δ strain.

In summary, Rif1 represses a broader range of internal late origins than Taz1 regulates, while both of which are required for repression of the sub-telomeric origin *TAS59*. Rap1 and Poz1 are required for repression of the same set of internal late origins, but both of which do not repress *TAS59*. In contrast, Ccq1 may exclusively contribute repression for sub-telomeric origins.

Heterochromatin is not formed at internal late origins nearby telomere repeat

Taz1 interacts with various partners and participates in the functions such as telomere maintenance (Kanoh and Ishikawa, 2001; Miyoshi et al., 2008), establishment of telomere heterochromatin (Kanoh et al., 2005), localization of telomere at the nuclear periphery (Chikashige et al., 2009) and replication fork passage along telomere repeats (Miller et al., 2006). It has been shown that insertion of about 300 copies of telomere repeat at an internal chromosome locus promotes localization of Taz1 as well as K9-methylated histone H3 and Swi6 (Kanoh et al., 2005; Miyoshi et al., 2003). Because the highly condensed chromatin structure may prevent access of replication factors and delay activation of replication origin, I therefore tested whether heterochromatin is locally formed at late origins controlled by Taz1. To this end, I analyzed localization of Swi6 and K9-methylated histone H3 at the internal chromosome regions using a chromatin immunoprecipitation (ChIP) assay. ChIP recovery of DNA for TAS59, ars2004, AT2035 and AT2088 was determined by qPCR (Fig. 13). The Swi6-ChIP analysis revealed that the ars2004, AT2035 and AT2088 fragments were 3-fold less than TAS59 locus (Fig. 13A). Similarly, the localization of K9-methylated histone H3 was not detected at the internal late origins and ars2004 (Fig. 13B). Consistently, the late replicating property of AT2035 and AT2088 did not change in swi6 Δ or clr4 Δ , (Hayashi, unpublished), suggesting that heterochromatin does not play an important role in repression of the internal late origins that are controlled by Taz1.

The acetylation status of H3K9, K14 and H4K16 at AT2088 did not change when the RTC essential sequence was deleted

As describe above, previous studies suggest that histone acetylation and deacetylation can affect the activation timing of replication origins. The late origin AT2088 is located in the promoter region of the stress-inducible gene SPBC19C7.04c, which is Deletion of Clr6, the fission yeast homologue of Rpd3, repressed in normal S phase. causes derepression of this gene (Wiren et al., 2005). Moreover, several sites in histone H3 and H4 (H4 K12, K16 and H3 K9 and K14) in the promoter of this gene are deacetylated in the Clr6 dependent manner (Wiren et al., 2005). I examined whether the RTC controls histone acetylation at the original AT2088 locus. A 210-bp fragment containing the RTC essential sequence was deleted from the AT2088 locus $(AT2088\Delta 210)$, and a map of H3K9, K14 and H4K16 acetylation at the late origin AT2088 was created by ChIP assay (Fig. 14A). To compare WT and $AT2088\Delta 210$, I also analyzed telomere and the early origin ars2004. I could not detect significant difference in recovery of DNA with these three types acetylated histone between AT2088 and AT2088 Δ 210 (Fig. 14B, C and D). Then acetylation states of these sites may not be involved in origin regulation.

Taz1-mediated replication timing control prevents loading of Sld3 to late origins

Because pre-RCs are formed at both early and late replication origins, I assumed the process of pre-RC activation to be regulated by the Taz1-mediated mechanism. То elucidate the step that is regulated, I analyzed the localizations of a pre-RC component Mcm6, and Sld3, which is recruited to pre-RC in the most upstream step of origin activation process in S phase (Yabuuchi et al. 2006). Because Sld3 localization occurs only transiently under wild-type conditions, I employed the cold-sensitive nda4-108/mcm5 mutation that allows Sld3 loading but prevents initiation of replication (Yamada et al. 2004). In cdc25-22 nda4-108 sld3-flag cells carrying the native AT2088 (WT) released synchronously into S phase from G2/M, Mcm6 was efficiently localized at all the origins, but not in the non-origin (nonARS) region (Fig. 15A, left). Sld3 was preferentially enriched at the ars2004 but not at late origins or non-ARS (Fig. 15B, left). In AT2088-S2632 cells lacking the telomeric repeat near AT2088, localization of Sld3 increased specifically at AT2088 (Fig. 15B, middle), whereas Mcm6 localizations were not significantly different from those in the wild-type (Fig. 15A, middle). These results show that the telomeric repeat-dependent RTC activity represses Sld3 loading. I then examined whether Taz1 impacted localization of Mcm6 or Sld3. In $taz1\Delta$ strain, localization of Sld3 increased specifically at *AT2035*, *AT2088* and *TAS59*, but not at *AT2080* or *ARS727* (Fig. 15B, right), while Mcm6 was localized at the origins, similarly to those in wild-type (Fig. 15A, right). These results show that Taz1-mediated control of replication timing does not affect Mcm6 localization, but prevents Sld3 loading at specific late origins.

Discussion

A replication-timing program that regulates individual replication origins to fire at a pre-fixed time during S phase exists in all eukaryotes. In this study, I demonstrate that replication timing of replication origin is intrinsically determined by a proximal segment in fission yeast. The segment has the activity to repress initiation from nearby origins, even at ectopic sites, in early S phase, and two copies of the telomeric repeat are essential for this repression. This result provides novel insights into the mechanism of replication timing control, especially how chromosome regions are distinctly regulated.

The results presented here also shed light on the involvement of telomere binding proteins in the regulation of replication timing. A conserved telomere-binding protein, Taz1, binds to the internal telomeric repeats and plays an essential role in replication timing control. Genome-wide analysis revealed that about half of late origins are regulated by the Taz1-mediated mechanism. Remarkably, almost all origins in sub-telomeric regions about 100 kb long were found to be regulated by Taz1. Other shelterin components and Rif1 also affect a wide range of late origins in arm regions and sub-telomeric regions.

Replication timing control element consists of telomeric repeats

The results of replication kinetics analysis showed that late origins including AT2088 on chromosome arm regions replicated about 10 min later than early origins such as *ars2004* (Fig. 2C). The delay is due to the absence of initiation from late origins in early S phase, as shown by 2D gel electrophoresis (Fig. 8B). However, this is not due to the absence of a strong origin activity, because AT2088 fragment that contains previously identified ARS745 showed robust ARS activity when cloned on a plasmid (Fig. 2B). Interestingly, the pAT2088 plasmid replicated in late S phase (Fig. 4B), suggesting that the AT2088 fragment retains the replication timing control. It should be noted that insertion of the AT2088 fragment in proximal to early origins, *ars2004* and *ORI12*, on the chromosome caused repression of initiation from the origins in early

S phase (Fig. 5, 6). These results imply that the timing control activity present in AT2088 fragment is not specific to AT2088 but rather general to other origins. A 634 bp fragment that is sufficient for repression of ars2004 contains a 25 bp essential region and about 60 bp important region for origin repression (Fig. 7B). The essential sequence consists of two tandem copies of telomere repeat-like sequence and AG/TC motif. The results of linker substitution experiments show that both copies of telomere repeat are required. Although the telomere-like sequence differs from the telomere repeat consensus, $GGTTACA_{0.1}C_{0.1}G_{0.6}$, the RTC is restored by replacement of the consensus sequence (Fig. 9B, AT2088-telF). In addition, insertion of the consensus sequence in the opposite direction relative to the surrounding sequence is functional, suggesting the sequence has a distinct function such as the binding site for telomere binding protein (Fig. 9B, AT2088-telR). Since Taz1, an orthologue of human TRF1 and TRF2, has been reported to bind to two tandem copies of telomere repeat in vitro and in yeast one hybrid system, Taz1 and other telomere binding proteins may play an important role in regulating replication origin (Spink et al., 2000) (Cooper et al., 1997).

In addition to telomeric repeats, a flanking AAGAGAGA sequence has some importance for the RTC activity (Fig. 7D, and data not shown). A similar purine cluster is found flanking to the telomeric sequence near *AT2035* (Fig. 9C). A purine-rich sequence may either stimulate Taz1 binding or recruit a factor involved in repression of replication initiation. In addition, a region of about 60-bp (2557-2617) adjacent to the essential sequence contributes to origin repression to some extent (Fig. 7B). Since the region is included in the scaffold/matrix associating regions (SAR/MAR) (Amati and Gasser 1990), association with the nuclear scaffold may restrict the access of replication factors or increase local concentration of inhibitory factors.

Distribution and regulation of telomeric repeats in chromosome arm regions

Our results demonstrate that two tandem copies of a telomeric repeat located in the vicinity of two late origins, *AT2088* and *AT2035*, are essential for control of replication timing at these origins. Moreover, 13 telomeric repeats are associated with late origins,

suggesting that telomeric repeats are general determinant of replication timing. About half of the telomeric-repeat associated late origins (9 among 13), including *ori2081*, *ori2100 and AT2088/ori2114*, are flanked by the genes that are silenced in normal growth conditions and induced under various stresses or during meiosis (Table S2).

Since gene-expression at these loci might be regulated by the mechanisms involving specific transcription factors and histone modifications, control of replication timing may contribute to maintenance or alteration of histone modifications. Although the acetylation status of H3K9, K14 and H4K16 at *AT2088* did not change when the RTC essential sequence was deleted (Fig. 14), it is possible that replication timing influences other sites of histone acetylation status or other histone modifications. Therefore, further investigations of relations between replication timing and gene expression will be needed. In metazoan, histone acetylation status is distinctly regulated during replication in the early and late S phases, suggesting that change in replication timing can play a role in alteration of gene expression during development (Lande-Diner et al. 2009).

Roles of Taz1 in the control of replication timing

In this study, I demonstrated that two tandem copies of a telomeric repeat located in the vicinity of two late origins, *AT2088* and *AT2035*, are essential for control of replication timing at these origins. The results of ChIP analysis demonstrated that the telomeric repeats, which are the binding sites for a homo-dimeric Taz1 (Cooper et al. 1997; Spink et al. 2000), indeed recruit Taz1 to the internal chromosome loci (Fig. 10). Moreover, Taz1 is required for timing control of about half of late origins (72 among 156), including all the sub-telomeric origins (46 origins). Genome-wide analysis of Taz1 localization showed Taz1 binds to the vicinity of 16 among 26 internal late origins that are regulated in a Taz1-dependent manner (Fig. 12A, Fig. 16 and Table S1). Because 13 of 16 origins are associated with telomeric repeats (including 3 that are manually found), Taz1 plays a role in the control of replication timing through binding to telomeric repeats near these origins (Fig. 17A). On the other hand, Taz1-localization was not detected at 10 internal late origins that are activated in *taz1*

cells, leaving the possibility that Taz1 can participate in the control from a distance through certain mechanism. It is also remarkable that control of all the sub-telomeric late origins are dependent on Taz1, despite the absence of Taz1-localization at individual origins except for the vicinity of the telomeres (Fig. 12B; Supplemental Fig. S1; Supplemental Table S1) (Kanoh et al. 2005). It is likely that Taz1 that binds to the telomere may play a role in control of sub-telomeric origins. Because the number of telomere-bound Taz1 varies depending on the length of individual telomere, Taz1 monitors the telomere length and impacts the timing of sub-telomeric replication. This is consistent with the observations that shortened telomeres induce early firing of sub-telomeric replication origins in budding yeast, in which Rap1 plays a role of Taz1 (Bianchi and Shore 2007; Shore and Bianchi 2009; Lian et al. 2011). Timing of replication fork passage through the telomere is important for stable association of the telomerase and elongation of the telomere (Dionne and Wellinger 1998; Marcand et al. 2000; Gallardo et al. 2011). Thus, Taz1 is likely to play crucial roles in the feedback loop of replication mediated maintenance of telomere length, in addition to its role in passage of the replication forks through the telomeres (Miller et al. 2006).

Roles of shelterin components and Rif1 in the control of replication timing

This study also revealed the unexpected function of other shelterin components and Rif1 in genome-wide regulation of DNA replication. Recently, the observation that Rif1, another telomere binding protein in fission yeast, is involved in global control of replication timing has been reported (Hayano et al. 2012). Genome-wide analysis of replication in *taz1* Δ as well as *rif1* Δ revealed that all the 72 late origins that fire in *taz1* Δ are also activated in *rif1* Δ (Fig. 16; Supplemental Fig. S1; Supplemental Table S1). Moreover, 47 late origins that do not fire in *taz1* Δ , including *AT2080* and *ARS727/AT2013*, are activated in *rif1* Δ (Fig. 16; Supplemental Fig. S1; Supplemental Table S1). These observations suggest that there are at least Taz1-dependent and Taz1-independent pathways for timing control and both require Rif1. It is likely that Rif1 acts downstream of Taz1. It has been reported that the *ARS727* fragment cloned on a plasmid forces late replication of a concurrently cloned early origin, and that several copies of the late consensus sequence (LCS), A/G-G/T-G/T-GGGGGGA-A/T, are required for the repression (Yompakdee and Huberman 2004). The LCS might be involved in Taz1-independent Rif1-dependent pathway (Hayano et al. 2012).

Recent studies revealed that mammlian Rif1 also affects spatio-temporal program of DNA replication (Yamazaki et al., 2012; Cornaccia et al., 2012). Interestingly, Human rif1 associates with the nuclear scaffold structures at late M to early G1 phase and colocalizes with the mid-S replication foci. Mouse Rif1 accumulates at sites and is cleared from chromatin prior to its replication in mid S phase. These results suggest the hypothesis that Rif1 may be a crucial factor for generating chromatin architecture and establish accessibility of different origin clusters for limiting replication factors. I speculate that Taz1 recruits Rif1 to Taz1-dependent late origins and tethers the sites at the nuclear scaffold to form proper chromatin structures and/or recruit some factors enriched at the nuclear scaffold for limiting access of replication factors (Fig. 17B). Supporting this hypothesis, the Scaffold/matrix associating region (SAR/MAR) adjacent to the telomeric repeats at AT2088 contributes to repress the activation of AT2088. The telomeric repeats and other cis-elements on chromosome arm regions may enable the specific regions to be replicated at the specific time in S phase.

In contrast to Taz1 and Rif1 which repress late origins located in both chromosome arm regions and sub-telomeric regions, Rap1 and Poz1 are not required for repression of sub-telomeric origins. Since Rap1 is directly connected to Poz1 and binds to Taz1 independently of Rif1, Rap1 and Poz1 may posses same or similar functions in the control of replication timing (Baumann and Cech, 2001; Miyoshi et al., 2008). In *rap1* Δ or *poz1* Δ mutant, terminal telomere repeats extensively elongates as long as 3-5 kb and 1-2 kb (Kanoh and Ishikawa, 2001; Miller et al., 2005), respectively, compared with 300 bp in wild type cells, resulting in accumulation of Taz1 as well as the associating Rif1 to the elongated telomeres. This may cause decrease in Taz1 and Rif1 bound to internal chromosomes, leading to de-repression of late origins specifically in arm regions (Fig. 18A). On the other hand, deletion of the telomerase recruiter, Ccq1, leads telomere shortening (Flory et al., 2004; Tomita and Cooper,

2008). Then, the amount of Rif1 at telomere ends may be reduced in $ccq1\Delta$ cells, leading to partial de-repression of sub-telomeric origins (Fig. 18A). Alternatively, it is also possible that Rif1 anchored to telomeres represses replication origins, and Shelterin-like complex acts as a mediator for Rif1 and exists at both telomeres and internal late origins. The telomeres of mitotically dividing fission yeast are localized at the nuclear periphery in two to four clusters (Alfredsson-Timmins et al., 2007; Funabiki et al., 1993). In this model, Shelterin-like complex bound to chromosome arm regions may localize late origins into telomere clusters, and Rif1 repress the origins (Fig. 18B).

Taz1-dependent pathway regulates DDK-dependent Sld3 loading in initiation of replication

In Taz1-dependent control of replication timing described here, Taz1 that binds in the vicinity of late origin impacts the process of initiation. The effects diminish by distance, because an early origin 20 kb from the Taz1 binding site is not inhibited (Supplemental Fig. S1; Supplemental Table S1). These characteristics suggest that a catalytic reaction or a semi-diffusible factor may be involved in the interference with the process of replication initiation. The heterochromatin formation does not play a significant role, because Swi6 and H3K9 methylation are not detected around the late origin *AT2088* (Fig. 13). Checkpoint pathways, which are proficient in $taz1\Delta$ (Miller and Cooper 2003), may not play a major role in the Taz1-dependent timing control. Therefore, the Taz1-dependent regulation seems to involve a novel mechanism that affects the initiation process.

In this study, I showed that loading of Sld3 onto pre-RC is prevented at late origins by a Taz1-mediated control of replication timing. In fission yeast, loading of Sld3 onto replication origins is dependent on pre-RC and DDK, and prerequisite for CDK-dependent assembly of other replication factors (Yabuuchi et al. 2006; Fukuura et al. 2011). A recent *in vitro* study in budding yeast has shown that origin association of Sld3 is dependent on DDK and distinct from those require CDK (Heller et al. 2011). Moreover, in vivo study in budding yeast suggest that origin association of low-abundance Sld3, Sld7 and Cdc45, which is dependent on DDK, is crucial for temporal order of origin firing (Tanaka et al. 2011). The following evidence in fission yeast further emphasizes the importance of DDK recruitment in replication timing control; Swi6/HP1-dependent recruitment of Dfp1, a regulatory subunit of DDK, stimulates early activation of origins in peri-centromeric heterochromatin and the silent mat locus (Hayashi et al. 2009). Furthermore, tethering of Dfp1 to the late origin ARS727, which is Taz1-independent and Rif1-dependent, causes early firing of the origin (Patel et al. 2008). Because DDK preferentially phosphorylates subunits of chromatin-bound Mcm2-7 complex (Francis et al. 2009), both Taz1-dependent and independent regulation may interfere with the access of DDK, or phosphorylation of chromatin-bound Mcm2-7 complex by DDK (Francis et al. 2009). Although recruitment of DDK and loading of Sld3 occur in S phase, a process that occurs in G1 phase may impact the reactions. Correlation of the origin association timing of ORC and MCM in G1 phase with initiation timing has been reported in fission yeast (Wu and Nurse 2009). In mammalian cells, it has been proposed that a replication timing program is established during a discrete window of time in G1 phase, the timing decision point (TDP) (Dimitrova and Gilbert 1999). It is possible that an early event such as chromatin modifications around individual replication origins could affect the recruitment of DDK and subsequent loading of replication factors at the origins in S phase.

Our results show that fission yeast utilizes a set of telomeric sequences and telomere binding proteins for regulation of replication timing. Recent studies revealed novel genome-wide functions of telomere binding proteins in mammals. Mouse Rap1 binds to two tandem copies of the telomere repeat outside telomeric regions and regulates expression of the genes located in vicinity of the repeats (Martinez et al. 2010). In addition, mammalian Rap1 has also been identified as a regulator of the NF-κB signaling pathway that mediates the transcriptional responses to various stresses (Teo et al. 2010). Since telomeric sequences and telomere binding proteins are highly conserved among eukaryotes, it would be interesting to investigate whether they could be involved in regulation of DNA replication in other organisms.

Materials and Methods

Strains and Media

Strains and media used in this study are described in Supplementary Information and listed in Supplemental Table S3. Media used for fission yeast cultivation were YE medium as a complete medium and EMM medium as a selection medium (Moreno et al, 1991). All solid media contained 2.0% agar. Transformation of *S. pombe* was performed by the lithium acetate method (Forsburg, 2003), and geneticin (G418) was used for selection of transformants at a final concentration of 100 μ g/ml. *E. coli* DH10B was used for plasmid construction. The medium used for *E. coli* cultivation was L-medium (1% Bacto Peptone, 0.5% Bacto Yeast Extract, 1% NaCl), and ampicillin and methicillin were added at a final concentration of 30 μ g/ml for plasmid selection.

Construction of fission yeast strains

The origin-exchanged strains were constructed as described below. To construct a strain carrying the *ars2004* fragment at the *AT2088* locus, two segments, d1 and d2, near the ends of the intergenic region between *SPBC19C7.04c* and *SPBC19C7.05* were PCR-amplified using pair-wise primers, AT-3 with AT-4, and AT-5 with AT-6, and cloned into modified pBluescript II (pBS-EHB), where the *Hin*dIII-*Not*I fragment was replaced with *Eco*RI-*Hin*dIII-*Bam*HI recognition sequences, resulting in pTZ1. The 1.8-kb *ura4*⁺ fragment was inserted at the *Hin*dIII site between the d1 and d2 inserts of pTZ1 to make pTZ2. The *Bam*HI fragment of pTZ2 carrying the *ura4*⁺ gene flanked by the d1 and d2 fragments was used for transformation of HM83 (h^+ *ura4-D18*). HM1172 carrying *ura4*⁺ at the *AT2088* locus was selected by PCR among the Ura⁺ transformants. A 3.2-kb *Not*I-*Xba*I fragment of pARS2004 lacking an internal *Bam*HI site (Okuno et al., 1999) was inserted into the *Not*I-*Xba*I sites between d1 and d2 was co-transformed with pREP1 into HM1178. Among transformants grown on EMM plates (EMM containing 150 µg/ml uracil) and 5'FOA plates (EMM containing 500

 μ g/ml 2'-deoxy-5'-fluorouridine and 150 μ g/ml uracil), HM1281 carrying *ars2004* in place of *ura4*⁺ at the *AT2088* locus was selected by PCR. HM1285 carrying *cdc25-22 Pnmt1-TK* was constructed by standard genetic crossing.

To construct a strain carrying the *AT2088* fragment in place of *ars2004*, a 232-bp e1 fragment and a 235-bp e2 fragment located at each end of the *ars2004* fragment were amplified using pair-wise primers AT-7 with AT-8, and AT-9 with AT-10 and cloned at the *Eco*RI-*Hin*dIII and *Hin*dIII-*Bam*HI sites, respectively, of modified pBluescript II to form pTZ4. A 3.6-kb *AT2088* fragment amplified using primers AT-1 and AT-2 was inserted at the *Hin*dIII site between e1 and e2 of pTZ4, to form pTZ4. The *Bam*HI fragment carrying e1-*AT2088*-e2 was used for transformation of HM198, in which the essential region at the *ars2004* locus was replaced by *ura4*⁺ (Takahashi et al, 2001). Ura⁻ transformants were selected on 5'FOA plates, and HM1346 carrying *AT2088* integration in place of *ura4*⁺ at the *ars2004* locus was identified by PCR. HM1389 carrying *cdc25-22 Pnmt1-TK A2088::ura4* was obtained by standard genetic crosses.

For construction of a strain carrying the *AT2088* fragment inserted next to *ars2004*, two fragments, f1 and f2, left of *ars2004* were amplified using pair-wise primers, AT-11 with AT-12, and AT-13 with AT-14, respectively. The f1 and f2 fragments digested by *Eco*RI-*Not*I and *Not*I-*Bam*HI, respectively, were cloned into modified pBluescript II forming pTZ5. The *ura4*⁺ fragment was inserted at the *Hind*III site between the f1 and f2 segments of pTZ5, making pTZ6. A 3.6-kb *AT2088* fragment amplified using primers AT-15 and AT16 was inserted into the *Not*I site setoff pTZ6, resulting in pTZ7. An *Eco*RI fragment of pTZ7 carrying f1-*ura4*⁺-*AT2088*-f2 was used for transformation of the EOY15 strain, and a transformant carrying the insertion of *AT2088* next to *ars2004* was identified by PCR. HM1800, a derivative carrying *cdc25-22 Pnmt1-TK*, was obtained by standard genetic crossing.

For construction of a strain carrying the AT2088 fragment inserted next to the ORI12 locus, the ura4-AT2088 fragment was amplified by two-step PCR amplification. The first PCR amplified two fragments containing the left regions of ORI12 with part

of the *ura4* gene and AT2088, using the primer sets AT-33 with AT-34, and AT-35 with AT-36. The second PCR amplified the ura4-AT2088 fragment from pTZ7 using the first PCR products and AT-33 with AT-36 as primers. The second PCR products were used for transformation of HM2836, which has cdc25-22, nmt1-TK, ade6::ade6⁺-Padh1-hENT and auxotrophy for uracil. The transformants were selected on EMM plates.

To construct a series of deletion derivatives of *AT2088* that were inserted next to *ars2004* on the chromosome, fragments were PCR-amplified using the primers listed in Table 2, and the products digested by *Not*I alone or by *Not*I and *Pst*I, were cloned into pTZ6. The plasmids carrying the truncated *AT2088* fragments were digested by *Eco*RI and used for transformation of HM2836.

For introduction of a deletion $AT2088 \Delta 210$ into the chromosomal AT2088 locus, the AT2088A210 fragment amplified using the pair-wise primers AT-1 with M2527-R and M2637-F with AT-2 was inserted into the HindIII site in pBS-EHB. For introduction of base substitutions AT2088-telF and AT2088-telR into the AT2088 locus, the AT2088-telF/R fragments amplified using the pair-wise primers AT-45 with S2617-R and telF/R with AT-46 were inserted into the EcoRI-BamHI site in pBS-EHB. The altered AT2088 fragments were excised by digestion with HindIII or EcoRI and used for transformation of HM4035, which has AT2088::ura4, cdc25-22, nmt1-TK, ade6::ade6+-Padh1-hENT. For introduction of a base substitution AT2088-S2632 AT2088 into the locus, а NotI fragment of the plasmid carrying f1-*ura4*⁺-*AT2088-S2632*-f2 was used for transformation of HM4035. The transformants were selected on **EMM** plates containing 500 µg/ml 2'-deoxy-5'-fluorouridine (5'FOA) and 150 µg/ml uracil.

For construction of strains carrying base substitutions in the *AT2035* locus, two segments near the right end of the intergenic region flanked by *sds23* were amplified using the primer sets AT-37 with AT-38 and AT-39 with AT-40. The products were used as primers together with the primers AT-37 with AT-40 for PCR amplification of the *ura4*⁺ gene from pTZ7, and the products were used for transformation of HM2836 to obtain *AT2035-ura* (HM4159) carrying *ura4*⁺ inserted at the *AT2035* locus.

Fragments carrying base substitutions *AT2035-S1956* and *AT2035-S1985* were amplified using the primer sets AT-41 with AT-42 and AT-41 with AT-43, respectively, from strain HM4159 used as the template. The respective products were used as primers for the second PCR reactions in the presence of primers AT-41 and AT-44 from HM4159, and the PCR products were used for transformation of HM2836.

Epitope tagging of Taz1

For epitope tagging of Taz1, the upstream part of $taz1^+$ was amplified by PCR using the primers TazlupF and TazlupR, and the product was digested by HindIII and EcoRI, and then cloned into the HindIII-EcoRI sites of pBluescript II KS(+) to generate pJS1. The EcoRI-BamHI fragment containing kanMX6 was introduced into the *Eco*RI-*Bam*HI site of pJS1 to create pJS2. The promoter region of $taz1^+$ was amplified by PCR using the primers Taz1proF and Taz1proR, and the product was digested by BamHI and SpeI and cloned into the BamHI and SpeI sites of pBluescript II KS+ to generate pJS3. The fragment, which was generated by digestion of pJS3 with BamHI and SpeI, was cloned into the BamHI-SpeI site of pJS2 to generate pJS4. The N-terminal fragment of $taz1^+$ amplified by PCR using the primers Taz1NF and Taz1NR was digested by BamHI and SpeI and cloned into the HindIII-EcoRI sites of pBluescript II KS+ to generate pJS5. pJS5 was then digested by NdeI and SpeI, and the product containing the N-terminal fragment of $taz l^+$ was introduced into the NdeI-SpeI site of pJS4 to create pJS6. The NdeI fragment containing six tandem copies of FLAG-epitopes (6Flag) was cloned into the NdeI site of pJS6, resulting in pJS7, and the sequences were confirmed. The Sall-SpeI fragment of pJS7 was used for transformation of HM4045 (h^{-} 972E). Transformants were selected on YE-geneticin (100 µg/ml) plates, and insertion of the 6flag-tag at the N-terminal of $taz l^+$ was confirmed by genomic sequencing. The resulting strain showed normal replication profiles, and the telomere lengths were maintained as those in wild-type strain, suggesting that the Flag-tagged Taz1 was functional.

Construction of ARS plasmids and ARS assay

A 3.2-kb fragment containing *ars2004* had been cloned into pYC11, a derivative of pBluescriptII SK(-) carrying the *LEU2* marker gene (pXN289) (Okuno et al, 1997). A 3.6-kb intergenic fragment between *SPBC19C7.04c* and *SPBC19C7.05* containing *AT2088* was PCR-amplified using the primers AT-1 with AT-2 and cloned at the *Hin*dIII site of pYC11, resulting in pAT2088. To analyze the ARS activity, derivatives of pYC11 plasmids were introduced into HM123 (h^{-} leu1-32) by the electroporation method, and Leu⁺ transformants were selected on EMM plates for 4 days at 30 °C.

Construction of ARS plasmids and ARS assay

To obtain the deletion mutants of telomere binding proteins $taz1^+$ (JK702), $rap1^+$ (JK774), $rif1^+$ (JK690), $poz1^+$ (TM2374) and $ccq1^+$ (TM2370) were gifted from Dr. J. Kanoh (JK702, JK774 and JK690) and Dr. F. Ishikawa (TM2374 and TM2370). The deletion mutants carrying cdc25-22 *Pnmt1-TK* were obtained by standard genetic crosses.

Strain	Genotype
EOY15	<i>h- ura</i> 4- <i>D</i> 18
HM83	h^+ ura4-D18
HM198	h^+ ura4-D18 leu1-32 ars2004::ura4 ⁺
HM668	h- cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺
HM1172	h^{+} ura4-D18 ura4-D18:: ura4 ⁺ nmt1-TK ⁺
HM1235	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺
HM1281	h- ura4-D18 leu1-32 AT2088::ars2004 pREP1
HM1285	h ⁺ cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088::ars2004
HM1346	h ⁺ ura4-D18 leu1-32 ars2004::AT2088
HM1389	h? cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ars2004::AT2088 AT2088:: ura4 ⁺
HM1415	<i>h?</i> cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ars2004::ura4 ⁺
	AT2088::AT2088-ars2004-ura4 ⁺
HM1800	<i>h</i> ? cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088-ars2004
	AT2088::ura4 ⁺
HM1847	h? cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ars2004::ura4 ⁺ ars2004 AT2088::ura4 ⁺
HM1864	h- cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ade6::ade6 ⁺ adh1-hENT ⁺
HM1921	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088R1630-ars2004
HM1922	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088R2017-ars2004
HM1923	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088R2527-ars2004
HM1924	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088R2947-ars2004
HM1926	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L476-ars2004
HM1930	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L1519-ars2004
HM2418	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L1519R2947-ars2004
HM2484	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L1/0/R294/-ars2004
HM2485	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L210/R294/-ars2004
HM2487	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L2312R294/-ars2004
HM2419	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L2508R294/-ars2004
HM2488	h- cdc25-22 ura4-DS/E:nmt1-1K ars2004::ura4 A12088L2681R294/-ars2004
HM2595	h- $cdc25$ - 22 $ura4$ - $D18$:: $ura4$ $nmt1$ - IK $adeb$:: $adeb$: $adh1$ - $hEN1$ $taz1$:: $kanMXb$
HM2037	<i>n-cac25-22 ura4-D18:: ura4 nm11-1K naa4-108 sla5-5F lag::kanMX0</i>
HM2830	$h = cac_{2}^{2} - 22$ ura4-DS/E:nmi1-1K ade0::ade0 adn1-nEN1
HWI2635	n- cac2J-22 ura4-DS/E:nmu1-1K ars2004::ura4 A12060-ars2004 ada6::ada6 ⁺ adb1 hENT ⁺
HM2854	$h = cdc^{25} 22 = uraA DS/F : nmt 1 TK^{+} = arc^{200} A : uraA^{+} AT20881 2312B2047 arc^{200} A$
11112034	ade6:ade6 ⁺ adh1_hFNT ⁺
HM2857	$h_{-} = cdc^{25-22} = ura4-DS/F \cdot nmt1-TK^{+} = ars^{2004} \cdot ura4^{+}AT^{2088}M^{2433} \cdot ars^{2004}$
11112037	ade6::ade6 ⁺ adh1-hENT ⁺
HM2875	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088L2412R2947-ars2004
	$ade6::ade6^+adh1-hENT^+$
HM2877	<i>h</i> - <i>cdc</i> 25-22 <i>ura</i> 4- <i>DS</i> / <i>E</i> : <i>nmt</i> 1- <i>TK</i> ⁺ <i>ars</i> 2004:: <i>ura</i> 4 ⁺ <i>AT</i> 2088 <i>M</i> 2527- <i>ars</i> 2004
	ade6::ade6 ⁺ adh1-hENT ⁺
HM2878	<i>h</i> - <i>cdc</i> 25-22 <i>ura</i> 4- <i>DS</i> / <i>E</i> : <i>nmt</i> 1- <i>TK</i> ⁺ <i>ars</i> 2004:: <i>ura</i> 4 ⁺ <i>AT</i> 2088 <i>M</i> 2637- <i>ars</i> 2004
	ade6::ade6 ⁺ adh1-hENT ⁺
HM2881	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088M2737-ars2004
	ade6::ade6 ⁺ adh1-hENT ⁺
HM2882	h - $cdc25-22$ $ura4-DS/E:nmt1-TK^+$ $ars2004::ura4^+AT2088R2849-ars2004$
111 (2007	$ade6::ade6^{\dagger}adh1-hEN1^{\dagger}$
HM2895	<i>h</i> - $cdc25-22$ ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ade6:: $ade6^+adh1-hENT^+$ rif1:: ura4
HM2901	h- cdc25-22 ura4-D18:: ura4 nmt1-TK ade6::ade6 adh1-hENT rap1:: ura4
HM2926	<i>h- cac25-22 ura4-DS/E:nmt1-1K' ars2004::ura4</i> *AT2088N2527-ars2004
LIM2027	aaeo::aaeo aani-nENI
ПWI2927	n- cuc23-22 uru4-D3/E.mm11-1K urs2004::uru4'A12088N233/-ars2004 ada6::ada6+adb1 hENT+

S. pombe strains used in this study. (Supplemental Table S3)

HM2930	<i>h</i> - <i>cdc25-22 ura4-DS/E:nmt1-TK</i> ⁺ <i>ars2004::ura4</i> ⁺ <i>AT2088N2587-ars2004</i>
	ade6::ade6 ⁺ adh1-hEN1 ⁺
HM2932	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088N2617-ars2004
11112022	$\frac{1}{1000}$
HM2933	n- cac23-22 ura4-DS/E:nm11-1K ars2004::ura4 A12088N2649-ars2004 ade6::ade6 ⁺ adh1-hENT ⁺
HM2936	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088N2677-ars2004
11112/00	ade6::ade6 ⁺ adh1-hENT ⁺
HM2939	<i>h</i> - <i>cdc</i> 25-22 <i>ura</i> 4- <i>DS</i> / <i>E</i> : <i>nmt</i> 1- <i>TK</i> ⁺ <i>ars</i> 2004:: <i>ura</i> 4 ⁺ <i>AT</i> 2088 <i>N</i> 2707- <i>ars</i> 2004
	ade6::ade6 ⁺ adh1-hENT ⁺
HM3085	<i>h</i> - <i>cdc</i> 25-22 <i>ura</i> 4- <i>DS</i> / <i>E</i> : <i>nmt</i> 1- <i>TK</i> ⁺ <i>ars</i> 2004:: <i>ura</i> 4 ⁺ <i>AT</i> 2088X2617- <i>ars</i> 2004
	ade6::ade6 ⁺ adh1-hENT ⁺
HM3190	h - $cdc25-22$ $ura4-DS/E:nmt1-TK^+$ $ars2004::ura4^+AT2088S2617-ars2004$
	ade6::ade6 ⁺ adh1-hENT ⁺
HM3191	h - $cdc25-22$ $ura4-DS/E:nmt1-TK^+$ $ars2004::ura4^+AT2088S2624-ars2004$
	ade6::ade6 ⁺ adh1-hENT ⁺
HM3192	h - $cdc25-22$ $ura4-DS/E:nmt1-TK^{*}$ $ars2004::ura4^{*}AT2088S2632-ars2004$
XXX 42.42.0	ade6::ade6 ⁺ adh1-hEN1 ⁺
HM3429	h- cdc25-22 ura4-D18:: ura4 ⁺ nmt1-TK ⁺ ade6::ade6 ⁺ adh1-hEN1 ⁺
	tazI-3Flag::kanMXb
HM3663	h^{+} cdc25-22 ura4-D18:: ura4 nmt1-1K poz1:: nyg
HM3007	$n cac_{25-22} \text{ ura4-D18:: ura4 nmi1-1K} aaeo::aaeo \ aan1-nEN1 ccq1:: nyg$
HM3707	n- cuc25-22 ura4-D16:: ura4 nmu1-1K A12086::A1208652052 ada6.uada6 ⁺ adh1 hENT ⁺ ta - 1.3ElagutanMY6
11112007	dae0aae0 aan1-nEN1 aa1-5F aagkanninA0
HWI300 /	n- cac25-22 uru4-D5/E.nmu1-1K ar52004uru4 A12000uru4 ade6ade6 ⁺ adb1 hENT ⁺ nYN280
HM3888	$h = cdc^{25} 22$ $\mu rad DS/F mmt 1 TK^{+} = ars^{200} A \cdot \mu rad^{+} = AT^{2088} \cdot \mu rad^{+}$
11113000	ade6:ade6+adh1-hENT+ pYC11+AT2088
HM4034	h^{-} cdc25-22 ura4-DS/E:nmt1-TK ⁺ ars2004::ura4 ⁺ AT2088S2641-ars2004
	ade6::ade6 ⁺ adh1-hENT ⁺
HM4035	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ AT2088::ura4 ⁺ ade6::ade6 ⁺ adh1-hENT ⁺
HM4037	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ AT2088::AT2088-telF ade6::ade6 ⁺ adh1-hENT ⁺
HM4040	h- cdc25-22 ura4-DS/E:nmt1-TK ⁺ AT2088::AT2088-telR ade6::ade6 ⁺ adh1-hENT ⁺
HM4041	<i>h</i> - <i>cdc</i> 25-22 <i>ura</i> 4- <i>D</i> 18:: <i>ura</i> 4 ⁺ <i>nmt</i> 1- <i>TK</i> ⁺ <i>AT</i> 2088:: <i>AT</i> 2088S2632
	ade6::ade6 ⁺ adh1-hENT ⁺
HM4155	h - $cdc25$ -22 $ura4$ - $D18$:: $ura4^+nmt1$ - TK^+ $nda4$ -108 $sld3$ - $5Flag$:: $kanMX6$
	AT2088::AT2088S2632
HM4159	<i>h</i> - <i>cdc</i> 25-22 <i>ura</i> 4- <i>DS</i> / <i>E</i> : <i>nmt</i> 1- <i>TK</i> ⁺ <i>ade</i> 6:: <i>ade</i> 6 ⁺ <i>adh</i> 1- <i>hENT</i> ⁺ <i>AT</i> 2035:: <i>AT</i> 2035- <i>ura</i> 4
	control
HM4211	h - $cdc25-22$ $ura4-DS/E:nmt1-TK^{\dagger}$ $ade6::ade6^{\dagger}adh1-hEN1^{\dagger}$
10//010	A12035::A12035-S1950-ura4
HMI4212	n- cac25-22 ura4-D5/E:nmt1-1K adeb::adeb`adh1-hENT AT2025::AT2025 \$1085 ura4
<u>НМ/265</u>	A12033A12033-S1903-WW4 $h = cdc^{2}5.22$ wrad D18 wrad mmt 1 TK ⁺ mdad 108 sld2 5ElaskanMV6
11114203	n- cuc25-22 uru4-D16 uru4 nmi1-1K nuu4-106 su3-51 lug::kunMX0 taz1::natMX6
JK690	h- ura4-D18 leu1-32 rif1:: ura4
JK702	h - ura4 - D18 leu1 - 32 taz1:: ura4
JK774	h- ura4-D18 leu1-32 rap1:: ura4
TM2370	h- ura4-D18 leu1-32 cca1:: Hyg
TM2374	h- ura4-D18 leu1-32 poz1:: Hyg
	$\mathbf{I} = \mathbf{V} \mathbf{O}$
Oligonucleotide sequences of primers (Supplemental table S4)

Primers for construction of strains and plasmids AT-1: 5'- AAAAAGCTTGAGAAGGAGTTGTTTG-3' AT-2: 5'- AAAAAGCTTCTGATGCAAATATAGGC-3' AT-3: 5'- AAAGAATTCGGATCCTTGAGAAGGAGTTGTTTG-3' AT-4: 5'- AAAAAGCTTGCGGCCGCGTTGTGTCAGATTTGATAC -3' AT-5: 5'- AAAAAGCTTCTAGATTATCTTCATCAACCTGC-3' AT-6: 5'- AAAGGATCCACTGATGCAAATATAGGC-3' AT-7: 5'- AAAGAATTCGGATCCGAAGATTCGCGAGGCACC -3' AT-8: 5'- AAAAAGCTTCTGGCGAGCTATCTGTG-3' AT-9: 5'- AAAAAGCTTCCAAATCAACACACCCTAAC-3' AT-10: 5'- AAAGGATCCGAATTCGTTAGATGTCTGTACAGG-3' AT-11: 5'-AAAGAATTCGATGAATGCAGTGACC-3' AT-12: 5'-AAAGCGGCCGCAAGCTTGCCTTCTTTCCCAGTCC-3' AT-13: 5'-AAAGCGGCCGCGAAGATTCGCGAGGCACC-3' AT-14: 5'-AAAGGATCCGAATTCTGGCGAGCTATCTGTG-3' AT-15: 5'-AAAGCGGCCGCTTGAGAAGGAGTTGTTTG-3' AT-16: 5'-AAAGCGGCCGCACTGATGCAAATATAGGC-3' AT-17: 5'-GAAGAGGAGAATGAGCTTTACG-3' AT-18: 5'-CCGTGATGATGATGGTGGTGAGATTGATAATTAACAAGCTCTTCC-3' AT-19: 5'-CGCCTCGACATCATCTGCCCCTCCGGATAGAGTTTGTTCA-3' AT-20: 5'-GGACAATTAACGCTTGAC-3' AT-21: 5'-CCGGTCCGACTATAATCAT-3' AT-22: AT-23: 5'-CGCCTCGACATCATCTGCCCGCATCTCTGCCCAAATTC-3' AT-24: 5'-GTTGATTTACTCTGCTACATCAAAG-3' AT-25: 5'-CAATCAATGACGGAAGCCA-3' AT-26: 5'- CCGTGATGATGATGGTGGTGAGCAATTCTAGATAAAATAGCTCTCTG-3' AT-27: 5'-CGCCTCGACATCATCTGCCCTTATTCAACTCATGGGTACAGG-3' AT-28: 5'-GATTTTGGACGCCAAACT-3' AT-29: 5'-AAACTGCAGGAAGGGTTACAGGTTACAGGGTCTCTCTTTAGACAAAGCTA AAAATC -3' AT-30: 5'- AAGGATCCGAATTCACTGATGCAAATATAGGCAAA -3' AT-31: 5'-AAACTGCAGGAACCCTGTAACCTGTAACCCTCTCTCTTTAGACAAAGCTA AAAATC -3' AT-32: 5'-AAGAATTCTTGAGAAGGAGTTGTTTGTTTAC -3' AT-33: 5'-CACTTGAATAGATTAGCATTGTCC-3' AT-34: 5'-TGCCTTCTTTTCCCAGTCCCTATTCACTTGCCGCGTAAAC-3' AT-35: 5'-GCCTATATTTGCATCAGTGCTAGAATAACCTATGGTCTGTTTAAATCG-3' AT-36: 5'-AAAGCCTTCATAGCAAAGT-3' AT-37: 5'-GCAATGGTAATGATGATCATCTG-3' AT-38: 5'-CAAATGCATACATATAGCCAGCATCTACCCAATCTTGA-3' AT-39: 5'-AGCCAATGAAAGATGTATGTAGATCGCAACGTTGAATTATGTAT-3' AT-40: 5'-TTGTAGATGCAGTGTAGGTC-3'

AT-41: 5'-CTAGATGAGCGTCTATTTGTGTC-3'

AT-42:

5'- TCACTCCGGGGAAGAGGTTCCTGCAGGACGTAAAAAGACTCATGTGC-3' AT-43:

5'-GTTTCAATATTGAGTAAATGGTCCGCCTGCAGGCACTCCGGGGAAGAGG-3'

AT-44: 5'-CATAAAGTGGGAAAGTGGGGCAG -3'

AT-45: 5'- AAGAATTCTTGAGAAGGAGTTGTTTGTTTAC-3'

AT-46: 5'- AAGGATCCGAATTCACTGATGCAAATATAGGCAAA-3'

Primers for construction of AT2088 truncated fragments

L476-F: 5'-GGAATTCGCGGCCGCGTCTCATTTGAACTGATCC-3' L1519-F: 5'-GGAATTCGCGGCCGCATTCATGTTGTTCCACTACG-3' R2947-R: 5'-AGGAATTCGCGGCCGCGAATGTATGGACGACACAC-3' R2527-R: 5'-AGGAATTCGCGGCCGCTATCCCTTGTTATGGAGAG-3' R2017-R: 5'-GGAATTCGCGGCCGCTGTGTGTGCCTCCTTTGAAC-3' R1630-R: 5'-AGGAATTCGCGGCCGCTACACGCATGAGACAGTCG-3' L1707-F: 5'-AAGGAATTCGCGGCCGCAAGGTTGCTATAGAGTC-3' L2107-F: 5'-AGGAATTCGCGGCCGCGACGATGTTGTTTCACGCA-3' L2312-F: 5'-AGGAATTCGCGGCCGCGTGTGCGCCATGAAAGTGG-3' L2508-F: 5'-AGGAATTCGCGGCCGCTCTACGTTTTAGTTGTAATATCTG-3' L2681-F: 5'-AGGAATTCGCGGCCGCTCTCCATAACAAGGGATA-3' L2432-F: 5'-GAATTCGCGGCCGCATTCGCACATGTATCTC-3' M2433-R: 5'-AACTGCAGGAAAAATACAATACAGCTCAAG-3' M2433-F: 5'-AACTGCAGAAATATATTGAAACATCTTTGTATC-3' M2527-R: 5'-AACTGCAGTATCCCTTGTTATGGAGAG-3' M2527-F: 5'-AACTGCAGAACCTCTCTCTTTAGACAAAG-3' M2637-R: 5'-AACTGCAGACGAGGTTATATTTGAAATGTAC-3' M2637-F: 5'-AACTGCAGTGAATTACAAAAGTTTTTTGGTT-3' M2737-R: 5'-AACTGCAGAAAGAAGAAGAAATATGAAAGGAGTA-3' M2737-F: 5'-AACTGCAGTTCGTCCGCCTTTTCC-3' N2527-R: M2627-R N2527-F: 5'-AACTGCAGTTAATATTCAATTCTGTACG-3' N2557-R: 5'-AACTGCAGTTTAAGATACAAAGATGTTTC-3' N2557-F: 5'-AACTGCAGATAACAAAAACTATGACT-3' N2587-R: 5'-AACTGCAGCTTGAAACGTACAGAATTG-3' N2587-F: 5'-AACTGCAGTTTCAAATATAACCTCGT-3' N2617-R: 5'-AACTGCAGTACATTTTAAAGTCATAGTT-3' N2617-F: 5'-AACTGCAGTAGACAAAGCTAAAAATC-3' N2649-R: 5'-AACTGCAGAGAGAGGGTTACGAGGTT-3' N2649-F: 5'-AACTGCAGTACACAGCGTGGAATTTGG-3' N2677-R: 5'-AACTGCAGAGCGTAAATAGATTTTTAGC-3' N2677-F: 5'-AACTGCAGATAAAATACTCCTTTCATAT-3' N2707-R: 5'-AACTGCAGAAGTTTAAGACCCAAATTCC-3' N2707-F: F9.1 S2617-R: N2617-R S2617-F: 5'-ACCTGCAGGAATATAACCTCGTAACCTCT-3' S2624-R: 5'-ACCTGCAGGTGAAATGTACATTTTAAAGT-3'

S2624-F: 5'-ACCTGCAGGCTCGTAACCTCTCTCTTTAG-3'

S2632-R: 5'-ACCTGCAGGGTTATATTTGAAATGTACATTTT-3' S2632-F: 5'-ACCTGCAGGCTCTCTCTTTAGACAAAGCT-3' S2641-R: 5'- AAACCTGCAGGGGTTACGAGGTTATATTTGAAATG-3' S2641-F: 5'- AAACCTGCAGGTAGACAAAGCTAAAAATCTATTTACGC-3' Tel-F: 5'- AAACTGCAGGAACCCTGTAACCTGTAACCCTCTCTCTTTAGACAAAGC'

5'-AAACTGCAGGAACCCTGTAACCTGTAACCCTCTCTCTTTAGACAAAGCTA AAAATC-3'

Tel-R:

5'-AAACTGCAGGAAGGGTTACAGGTTACAGGGTCTCTCTTTAGACAAAGCT AAAAATC-3'

Primers for Southern hybridization probes AT2046-F: 5'-GGATATGATACTGCGGTTGG-3' *AT2046*-R: 5'-CCACTCTGTTGGGGTATC-3' *AT2047*-F: 5'-GCACTGCTGGCACCAAC-3' *AT2047*-R: 5'-GAGACAAGAAGCCTGG-3'

Primers for detection of replication efficiencies AT2024-F: 5'-GATGATTCGAGCTCTGCT-3' AT2024-R: 5'-GCTCTTTAATCTCTCACTCC-3' RT-AT2024-F: 5'-GCGACGGAGATGTCCAGAAA-3' RT-AT2024-R: 5'-TGCACATGCACAATACACACCTT-3' RT-AT2035-F: 5'-TGGTACGTCGAGTGAGACACAAT-3' RT-AT2035-R: 5'-AAAGACTCATGTGCTGTGGGAAT-3' RT-ars2004-F: 5'-AAAATGCCAACCCGTATTGAC-3' RT-ars2004-R: 5'-ATAACATACCAACCCTTACAAC-3' RT-AT2088(-1.2 kb)-F: 5'-TCCTCACTTCCTTAAAAACAGATTAAGAAATA-3' RT-AT2088(-1.2 kb)-R: 5'-CGCAAAATAACATCGTAGTGGAAC-3' RT-TAS59-F: 5'-CAGAAGAGACTACAGAGGCGGTTT-3' RT-TAS59-R: 5'-GGATGCCTTATCTGCGACCA-3' RT-AT2080-F: 5'-CGAACAACAGGCTTGGTTAGAA -3' RT-AT2080-R: 5'- GAAGTACGGACTTGTTTCGATTCC -3' RT-ARS727-F: 5'-TTGCTTTACCCATGATACCCTTT-3' RT-ARS727-R: 5'-CCGCGCATACCGAATGTA-3'

Primers for Taz1-ChIP analysis

RT-tel0.3kb-F: 5'-TATTTCTTTATTCAACTTACCGCACTTC-3' RT-tel0.3kb-R: 5'-CAGTAGTGCAGTGTATTATGATAATTAAATGG-3' RT-*AT2035*-F: 5'-TGGTACGTCGAGTGAGACACAAT-3' RT-*AT2035*-R: 5'-AAAGACTCATGTGCTGTGGGGAAT-3' RT-*AT2088*-core element-F: 5'-TCAATTCTGTACGTTTCAAGCAAAT-3' RT-*AT2088*-core element-R: 5'-CCCAAATTCCACGCTGTGTA-3' RT-*ade6*-F: 5'- TGATGGAGGACGTGAGCACATTGA-3' RT-*ade6*-R: 5'- TTGAATGCATCGCAGAGTTGCAGG-3'

Primers for Swi6 and H3K9Me-ChIP analysis

RT-*AT2035*-F: 5'-TGGTACGTCGAGTGAGACACAAT-3' RT-*AT2035*-R: 5'-AAAGACTCATGTGCTGTGGGAAT-3' RT-*AT2088*-core element-F: 5'-TCAATTCTGTACGTTTCAAGCAAAT-3' RT-*AT2088*-core element-R: 5'-CCCAAATTCCACGCTGTGTA-3' RT-*ars2004*-F: 5'-AAAATGCCAACCCGTATTGAC-3' RT-*ars2004*-R: 5'-ATAACATACCAACCCTTACAAC-3' RT-*TAS59*-F: 5'-CAGAAGAGACTACAGAGGCGGTTT-3' RT-*TAS59*-R: 5'-GGATGCCTTATCTGCGACCA-3

Primers for H3K9Ac, K14Ac and H4K16Ac-ChIP analysis RT-tel0.3kb-F: 5'-TATTTCTTTATTCAACTTACCGCACTTC-3' RT-tel0.3kb-R: 5'-CAGTAGTGCAGTGTATTATGATAATTAAATGG-3' RT-ars2004-F: 5'-AAAATGCCAACCCGTATTGAC-3' RT-ars2004-R: 5'-ATAACATACCAACCCTTACAAC-3' RT-AT2088 0.7kb-F: 5'-GGAGTAAGGATGGAAATGTGGAA-3' RT-AT2088 0.7kb-R: 5'-CATGATCGACGACCTATAAGTTGCT-3 RT-AT2088 1.1kb-F: 5'-GAGAAGTTTTGTAATTCCAATGCCA -3' RT-AT2088 1.1kb-R: 5'-ATAACCGCACCAAAATACCCATATC -3 RT-AT2088 1.5kb-F: 5'-TCCTCACTTCCTTAAAAACAGATTAAGAAATA -3' RT-AT2088 1.5kb-R: 5'-CGCAAAATAACATCGTAGTGGAAC -3 RT-AT2088 1.7kb-F: 5'-TGCTGTCAGAGGCTTACACTAAC -3' RT-AT2088 1.7kb-R: 5'-GAAAATATCCAAGTCATGTTCATTGC -3 RT-AT2088 2.1kb-F: 5'-TCTTAACGTTACTTGGAAGCCATATGTAAA -3' RT-AT2088 2.1kb-R: 5'-CCACTTTCATGGCGCACA -3 RT-AT2088 3.0kb-F: 5'-AGCAGCTAGTTCATTCGTATATCAATTT -3' RT-AT2088 3.0kb-R: 5'-GAATGTATGGACGACACACATGTTCGAAA -3

Primers for Mcm6 and Sld3-ChIP analyses

RT-*ars2004*-F: 5'-AAAATGCCAACCCGTATTGAC-3' RT-*ars2004*-R: 5'-ATAACATACCAACCCTTACAAC-3' RT-*AT2035*-1F: 5'-CACTAAGCTACTGGCAGTTTGTACG-3' RT-*AT2035*-1R: 5'-GGTAAAACACCCACGTGCG-3' RT-*AT2088*(-1.2 kb)-F: 5'-TCCTCACTTCCTTAAAAACAGATTAAGAAATA-3' RT-*AT2088*(-1.2 kb)-R: 5'-CGCAAAATAACATCGTAGTGGAAC-3'

BrdU incorporation and replication timing analysis

Fission yeast strains carrying P_{nmt1} -TK cdc25-22 were cultured in EMM medium lacking thiamine to induce transcription of the TK gene at 25°C for 18 h to 5 x 10₆ cells/ml. Cells arrested at the G2/M boundary by cdc25-22 mutation at 36°C for 3 h were released at 25°C and cultured for indicated periods in the presence of 200 [M 5-bromo-2'-deoxyuridine (BrdU). Preparation of cellular DNA and separation of BrdU-labeled DNA by CsCl density gradient centrifugation were carried out as described previously (Hayashi et al., 2007). For replication kinetics analysis, the amount of DNA in the HL and LL densities was determined by real-time PCR using the primer sets listed in Supplemental Table S4. Replication (%) at each time point was calculated with the equation 100 x (1/2HL)/(1/2HL+LL). To determine replication (%) of specific loci in early S phase, 10 mM hydroxyurea (HU) was added upon release from G2/M block.

Chromatin immunoprecipitation

ChIP assay was performed essentially as described previously (Hayashi et al., 2009), except for the following modifications. For Taz1-ChIP, approximately 2.5 x 108 *flag-taz1* cells grown at 30°C were disrupted with glass beads in 0.4 ml of lysis buffer (50 mM Tris-HCl [pH 8.0], 280 mM NaCl, 1 mM EDTA, 1% Triton X-100, 0.1% sodium deoxycholate, 1 mM phenylmethylsulfonyl fluoride, supplemented with proteinase inhibitor cocktail [Sigma-Aldrich]). The soluble extracts diluted with lysis buffer to adjust the TritonX-100 to 0.3% were used for immunoprecipitation with magnetic beads (Dynal) conjugated with mouse monoclonal anti-FLAG M2 (1:400; Sigma-Aldrich). For Mcm6- and Sld3-ChIP, cdc25-22 sld3-flag nda4-108/mcm5 cells grown at 28°C were synchronized at the G2/M boundary at 36°C for 3 h and released at 20°C, which is the restrictive temperature for the nda4-108 (Yamada et al. 2004). Cell extracts were used for ChIP assays with mouse anti-Flag and rabbit anti-Mcm6 antibodies. For Sld3- and H3K9diMe, H3K9Ac, H3K14Ac and H4K16Ac-ChIP, cdc25-22 cells grown at 25°C were synchronized at the G2/M boundary at 36°C for 3 h and released at 25°C and cultured for 40 min. Cell extracts were used for ChIP assays with rabbit anti-Swi6 (Living Colors Full-length A.v. Polyclonal Antibody, Clontech) and anti-H3K9diMe, H3K9Ac, H3K14Ac and H4K16Ac (a gift from Dr. H Kimura) antibodies. DNA prepared from whole-cell extracts or immunoprecipitated fractions was quantified by qPCR using SYBR green I in the 7300 PCR system (Applied Biosystems).

Two-dimensional gel electrophoresis

Neutral-neutral 2D gel electrophoresis was carried out as described (Hayashi et al., 2007). For Southern blotting probes, relevant origin fragments, as described below, were used after random prime labeling with ³²P-dCTP using the Megaprime DNA

labeling system (GE Healthcare). For detection of *ars2004*, a 940-bp *NotI- Hind*III fragment from p940 was labeled for probe to prevent cross-hybridization between the translocated *ars2004* and *ars2004* partially substituted with *ura4*⁺ at the native locus. The *ars2004* probe was used to detect a 6.5-kb *Eco*T22I fragment and a 6-kb *Fba1-Nco1* fragment (for re-hybridization after *AT2088* detection) in HM668 and a 5.1-kb *FbaI-NcoI* fragment in HM1285 and a 7.4-kb *StyI* fragment in HM1800. The 3.6-kb *Hin*dIII fragment from pAT2088 was used to detect a 5.5-kb *FbaI-NcoI* fragment in HM1285 and a 7.4-kb *StyI* fragment in HM1800. The 3.6-kb *Hin*dIII fragment from pAT2088 was used to detect a 5.5-kb *FbaI-NcoI* fragment in HM1668 and a 7.4-kb *Eco*T22I fragment in HM1389 both containing *AT2088*. Fragments of 1.7 kb and 2 kb amplified by PCR using primers *AT2046*-F with *AT2046*-R, and *AT2047*-F with *AT2047*-R, were labeled to detect a 5.5-kb *Eco*T22I fragment containing *AT2046* in HM1389 (for re-hybridization after detection of the translocated *AT2088*) and a 7.4-kb *StyI* fragment containing *AT2047* in HM668 and HM1800, respectively. Radioactive signals were detected with a BAS2500 system (Fuji Film) and measured using Image Gauge software.

Nucleotide pattern search

For search of two copies of telomere-like sequence, the pattern of GGTTAYN(1,3)GGTTAY was searched using the EMBOS "fuzznuc" program, which was obtained at

http://emboss.sourceforge.net/apps/release/6.3/emboss/apps/fuzznuc.html.

SOLiD analysis

BrdU-labeled DNA prepared at 120 min after G2/M release from HU-treated wild-type, $taz1\Delta$ and $rif1\Delta$ strains and separated by CsCl density gradient centrifugation, and those obtained by FLAG-Taz1-IP were used for SOLiD deep sequencing analysis, which was performed according to the manufacturer's standard protocol (Applied Biosystems).

Accession numbers

Sequecne data have been deposited to the Sequence Read Archive

(http://www.ncbi.nlm.nih.gov/Traces/sra/) with the accession number SRP011412.

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Figure 1. Introduction

(A) General correlations between features of chromosomes and activation of replication origin. (B) Activation of replication origin occurs in a step-wise manner. When cells enter S phase, Sld3 is recruited to pre-RCs in a DDK dependent manner. Then, GINS is recruited in a CDK dependent manner followed by Cdc45 loading. MCM is activated and double strand DNA is unwound. Finally, RPA assembles to single strand DNA and replication initiates.



В

С



Figure 2. Replication timings of origins in fission yeast

(A) The locations of early and late replication origins on S. pombe chromosome II are presented schematically. Positions of early origins, AT2024 (gray) and ars2004 (red), cen2, late origins, AT2035 (green) and AT2088 (blue), and a sub-telomeric origin TAS59 (purple) are shown. For the ars2004 and AT2088 loci, locations of the genes with the direction of transcription (arrow) and fragments (red: 3.2-kb ars2004, blue: 3.6-kb AT2088) used for translocation are presented. Relevant restriction fragments (E, EcoT22I; F, Fbal: N, Ncol) analyzed by two-dimensional (2D) gel electrophoresis are shown below theomaps. (B) Derivatives of the pYC11 (LEU2) plasmid carrying 23.2kb ars2004 and a 3.6-kb AT2088 were introduced into HM123 (h leuT-32). Transformants formed 40n minimal media plates after 4 days at 30FC are presented. (C) Replication kinetics of early and late origins. Fission yeast cdc25-22 nmt1-TK+ cells arrested at G2/M boundary at 36°C for 3 h were released at 25°C in the presence of BrdU (200 mM). At the indicated time points, the replicated heavy-light (HL) DNA was separated from light-light (LL) DNA using CsCl density gradient centrifugation and the amount of DNA of AT2024 (black), AT2035 (green), ars2004 (red), AT2088 (blue) and TAS59 (purple) in the LL and HL densities were determined by aPCR. Replication The route of biologically independent kinetics of each origin are presented. experiments are shown in Supplementary Fig. Sle



Figure 3. Replication timings of ars2004 and AT2088 origin fragments are maintained at ectopic loci.

Replication kinetics of *ars2004* (red) inserted at the *AT2088* locus (A) and *AT2088* at the *ars2004* locus (B) were obtained as described in Fig. 2C. Right panels show the results of 2D gel analysis of *ars2004* (*FbaI-NcoI* fragment) at the *AT2088* locus (A) and *AT2088* (*Eco*T22I fragment) at the *ars2004* locus (B) prepared at 90 min after G2/M release in the presence of HU (10 mM). The membrane was re-hybridized with the early origin *AT2046* probe (B). An arrowhead indicates the bubble arc. (C) Comparison of time required for replication in half of cell population (T1/2). T1/2 (min) for each origin was obtained from the results presented in Figs. 2C, 3A, 3B and unpublished data. The difference in T1/2 between an origin and *AT2024* (early origin control) was presented. *AT2035* and *AT2088* replicate 6-12 min later than *ars2004* and *AT2024*, regardless of their locations on the chromosome.



Figure 4. Replication timings of ars2004 and AT2088 origin fragments cloned on plasmids.

Replication kinetics of *ars2004* (red) cloned on a plasmid pXN289 (A; pARS2004) and *AT2088* (blue) cloned on the pXN289 (B; pAT2088) were obtained as described in Fig. 2C.



Figure 5. Repression of early initiation from ars2004 origin by the adjoining AT2088 fragment.

(A) Schematic presentation of the ars2004 locus carrying the ura4+-AT2088 or ura4+ insertion. (B) cdc25-22 nmt1-TK+ derivatives with or without insertion of ura4+-AT2088 or ura4+ alone next to the ars2004 locus were released from G2/M block and labeled with BrdU for 120 min in the presence of HU (10 mM). Replication (%) in the presence of HU was determined for ars2004 (red) as well as the control early and late origins, AT2024 (gray) and AT2035 (green), respectively. Mean \pm s.d. obtained from multiple measurements in qPCR is presented. (C) The replication intermediates of ars2004 (StyI fragment) and a control early origin AT2047 (StyI fragment) prepared at 90 min after G2/ M release of the HU-treated AT2088-ars2004 cells were analyzed by 2D gel electrophoresis. An arrowhead shows the bubble arc.



Figure 6. Repression of early replication origin ORI12 by insertion of the AT2088 fragment.

The position of *ORI12* on chromosome I and a physical map of the *ORI12* locus with insertions of $ura4^+$ -AT2088 and $ura4^+$ alone are schematically presented. For BrdU assay, cells were cultured for 120 min in the presence of HU after G2/M release. The replication efficiencies of AT2035 (green), ars2004 (red) and ORI12 (orange) were determined as described in Fig 5.





Figure 7. Identification of the essential sequence for replication timing control.

(A) The structure of ars2004 locus with the insertion of AT2088 fragment is presented schematically. (B) Cells carrying insertion of various portions of AT2088 fragment (blue horizontal bars) next to the ars2004 locus were synchronously released from G2/M and labeled with BrdU in the presence of HU (10 mM) for 120 min (top panel), 90 min (middle panel) or 80 min (bottom panel). Replication (%) of the ars2004 and that of the internal control origin AT2024 were determined as mean \pm s.d. from multiple qPCR measurements, as described in Fig. 5. To compare the effects of insertions on early replication of ars2004, relative replication of ars2004 to that of AT2024 was obtained, and the ratio of relative replication (ars2004/AT2024) with insertion to value without insertion was determined (red horizontal bars). (C) The profile of AT content of every 100-bp window in a 3.6-kb AT2088 region is presented together with two AT-rich regions (>75%, shaded rectangles), the pre-RC site (arrowhead) (Hayashi et al., 2007) and locations of two ARS fragments, AT2088A (Fig. 8) and ars745 (Maundrell et al., 1988). The regions sufficient (gray) and essential (red) for replication timing control are shown above the AT content profile. (D) The 3.6-kb AT2088 fragment with base substitutions in the essential region from position 2617 to 2648, as determined in (B), was inserted next to the ars2004 and the effects of base-substitutions on repression of early replication of ars2004 were analyzed as described in (B). The nucleotide sequence of the complementary strand of 2617-2648 is presented together with base-substitutions (lower case letter). The RTC essential sequence is indicated.



Figure 8. ARS assay for fragments of AT2088.

(A) The ARS activity of pYC11 (*LEU2*) derivatives carrying fragments of *AT2088*, shown by black bars, was examined by high-frequency transformation of HM123 (*h*⁻ *leu1-32*) as described in Fig. 2B. The locations of two ARS fragments, *AT2088A* and *ars745* (Maundrell et al., 1988), are indicated above the AT-content profile. (B) Replication intermediates in the HU-treated wild-type (left panels) and *AT2088*/210 cells (right panels) lacking the 210-bp (2527-2736) sequence were analyzed by 2D gel electrophoresis for *ars2004* (*Eco*T22I fragment) and *AT2088* (*FbaI-NcoI* fragment) at 90 min after G2/M release. Arrowheads indicate the bubble arcs.



Telomeric repeats are essential for repression of late replication origins. Figure 9. (A) The positions of AT2035 (green), AT2088 (blue) and Tel-0.3 (purple) on chromosome, II and *ade6* (gray) on chromosome III are presented schematically. (B) (left) The nucleotide sequences of the relevant regions of AT2088 (2624-2648, complementary strand) containing two copies of telomere-like repeats (blue underlining) <u>TAT2088-S2632</u> carrying base substitutions (red), AT2088-telF and 1stelR with two telometic repeats (blue underlining) in either orientation, respectively, are presented together with the consensus sequence of fission yeast telomeres (Cooper et al. 1997). (right) Replication (%) of the AP2088 (blue), ars2004 (red) and AT2035 (green) Were measured in the type and strains carrying base substitutions in AT2088 at 120 min described in Fig 5. Mean \pm s.d. obtained from multiple measurements in qPCR is presented. (C) Replication of the AT2035 was examined as described in (B). The nucleotide sequences of the region (1954-1993, complementary strand) containing telomere-like repeats (blue underlining) and base substitutions (red) in AT2035-S1959 and AT2035-S1985 are presented.





Figure 10. Telomeric repeats recruit Taz1 to the internally located late origin

Flag-Taz1 was immunoprecipitated from asynchronously cultured wild-type, AT2035-S1959 and AT2088-S2632 cells. IP recovery of the chromosome locus against the total cellular DNA was measured by qPCR for ade6+ (gray), AT2035 (green), AT2088 (blue) and Tel-0.3 (purple). Bars indicate the mean of IP-recovery (%) with standard error (SE) obtained from three biologically independent experiments. (right) The results except for those of Tel-0.3 are presented for better comparison of Taz1 localization at the internal sites.



Figure 11. Taz1 and other telomere binding proteins are required for repression of a subset of late replication origins.

Replication (%) of AT2035 (green), ars2004 (red), AT2088 (blue), ARS727 (orange) and TAS59 (purple) was determined in HU-treated wild-type and cells lacking $taz1^+$, $rap1^+$, $rif1^+$, $poz1^+$ and $ccq1^+$ at 120 min after release from G2/M. Mean \pm s.d. obtained from multiple measurements in qPCR is presented. Replication (%) of ARS727 was not examined in $poz1\Delta$ and $ccq1\Delta$ cells.





Figure 12. Replication profiles and Taz1 binding of late origins associated with the telomeric repeats.

(A) BrdU-incorporation profiles of 6 late origins associated with the telomeric repeats in wild-type (top) and $taz1\Delta$ (middle) are presented together with profiles of Taz1-ChIP-seq (bottom). The sequence read from the HL density DNA prepared from 120 min sample after G2/M release in HU-treated wild-type (top) and $taz1\Delta$ (middle) was compared with the sequence read from the total cellular DNA of the respective cells and the relevant enrichment was plotted over the chromosome region (Supplementary Fig. S1). Flag-Taz1 was immunoprecipitated as described in Fig. II-1 and the relevant enrichment, the sequence read from ChIP in *flag-taz1* cells versus the sequence read from ChIP in non-tag strain, was plotted (bottom). The positions of late origins and telomeric repeats are shown by blue arrows and purple triangles, respectively. The results covering the entire genome are presented in Supplementary Fig. S1 and summarized in Supplementary Table S1. (B) Replication profile of the sub-telomere 2R is presented. Blue arrows show late origins.



Figure 13. Heterochromatin is not formed at late origin AT2088 and AT2035

Localizations of Swi6 (A) and K9 di-methyled histone (B) at replication origins were analyzed by ChIP assay. Cells, carrying the cdc25-22 mutation, were synchronously released from the G2/M boundary and incubated at 25°C for 40 min. DNA of the indicated loci recovered by immunoprecipitation with Swi6 (A) and K9 di-methyled histone was measured by qPCR for AT2035 (green), ars2004 (red), AT2088 (blue) and TAS59 (purple). Mean \pm s.d. obtained from multiple measurements in qPCR is presented.





Figure 14. Change of replication timing doesn't affect the acetylation status of H3K9, H3K14 and H4K16 at the AT2088 locus.

(A) The ARS activity of pYC11 (*LEU2*) derivatives carrying fragments of *AT2088*, shown by black bars, was examined by high-frequency transformation of HM123 (*h*⁻ *leu1-32*) as described in Fig. 2B. The locations of two ARS fragments, *AT2088A* and *ars745* (Maundrell et al., 1988), are indicated above the AT-content profile. (B~D) Effects of early firing on histone acetylation states at L1. Fission yeast *cdc25-22* cells (WT), or *cdc25-22 AT2088* Δ 210 mutant cells (*AT2088* Δ 210) were arrested at G2/M boundary by incubating at 36°C for 3 hr and then incubated at 25°C for 40 min (G1). Cells were fixed with formaldehyde and the DNA fragments cross-linked to specific sites (H3K9,14 and H4K16) acetylated histones were immunoprecipitated with anti-AcH3K9 (B), anti-AcH3K14 (C) or anti-AcH4K16 (D) antibody (Hiroshi Kimura, Osaka Univ). DNA recovered was quantified by Real-Time PCR analysis. Mean ± s.d. obtained from multiple measurements in qPCR is presented.





Figure 15. Recruitment of Sld3 to a subset of late origins in $taz 1\Delta$.

Localizations of Mcm6 (A) and Sld3-5Flag (B) at replication origins were analyzed by ChIP assay. Wild-type, AT2088-S2632 and $taz1\Delta$ strains, carrying the nda4-108/mcm5 and cdc25-22 mutations, were synchronously released from the G2/M boundary and incubated at 20°C for 120 min, causing arrest before initiation of replication due to the nda4-108 mutation (Yamada et al., 2004). DNA of the indicated loci recovered by immunoprecipitation with Mcm6 or Sld3-5Flag was measured by qPCR for non-ARS (white), AT2035 (green), ars2004 (red), AT2080 (yellow), AT2088 (blue), ARS727 (orange) and TAS59 (purple). Mean \pm s.d. obtained from multiple measurements in qPCR is presented.





A Venn diagram shows 72 late origins activated in $taz I\Delta$ (purple) that contain 46 subtelomeric and 26 internal origins (white), including 16 internal origins where Taz1 was localized (blue). Interestingly, all of 72 late origins activated in $tazI\Delta$ are included in 119 late origins activated in $rifI\Delta$ (orange).



Figure 17.

(A) Summary of results. Taz1 binds to the internally located telomeric repeats near the late origins exerting a novel role in control of replication (repression of late origin firing in early S phase). Taz1 inhibits DDK-dependent Sld3 loading onto late origins. (B) A model for regulation of Taz1-dependent late origins. Taz1-Rif1 complex may tether Taz1-dependent late origins at the nuclear scaffold. The local environment of the nuclear scaffold may promote forming some specific chromatin structure and/or recruiting factors for limiting replication factors.








Figure 18.

(A) A model for regulation of sub-telomeric origins by counting the terminal telomere length by Taz1-Rif1 complex. In normal condition, Rif1 connected to telomere via Taz1 inhibits activation of sub-telomeric origins. Similarly, Taz1 (and Rif1) may repress internal late origins by binding to the nearby telomeric repeats. In $rap1\Delta$ and $poz1\Delta$, telomere length extensively elongates several times more than the length in WT. Excessive binding of Taz1-Rif1 complex to the elongated telomeres may cause depletion of these factors outside of telomeres, resulting de-repression of late origins specifically in arm regions. In $ccq1\Delta$, telomere length becomes shorter due to a defect of recruitment of telomerase. Then, a number of Taz1-Rif1 complex bound to telomere is insufficient for repression of subtelomeric origins. (B) Shelterin-like complex may bind to the telomeric repeats located in chromosome arms and mediates origin silencing through Rif1 accumulated in telomere clusters. Rap1 and Poz1 play a role in mediating repression of late origins, but Ccq1 is not requires for the function.

Supplementary Table S1. Comparison of origin activity in wild-type, *taz1*Δ and *rif1*Δ Chromosome I

Ori-number	AT-islands	Origin	Class	Fire	Fire	Fire	Position of	Telomeric	Localization	Localization	Localization	Orc1	Mcm6	5' Gene/ORF	3' Gene/ORF
(Hayashi)	(Segurado)	name		in WT	in taz1∆	in rif1 Δ	telomere seq	sequence	of Taz1	of Rif1	of LCS	binding	binding		
1001			L	-	+	+						15375.5	15375.5	SPAC212.07c	SPAC212.06c
1002			L	-	+	+						51625.5	*	SPAC977.09c	SPAC977.10
1003			L	-	+	+						54625.5	55375.5	SPAC977.10	SPAC977.11
1004	1011		L	-	+	+						63375.5	62875.5	SPAC977.14c	SPAC977.15
1005	1012			-	+	+						71125.5	35035.5	SPAC977.17	SPAPJ695.01c
1006	1010		L	-	+	+						/53/5.5	/53/5.5	0040 1005 04-	
1007	1013		L	-	+	+						80125.5	•	SPAPJ695.01C	gnt3/SPAC1F8.01
1000	1014		L .	-	+	+						00125.5	99625 F	SPAC1E8 02c	etra/SPAC1E8.02c
1009			L .	-	+	+						05125.5	06023.5	SPAC1E8.04c	ico3/SPAC1E8.05
1010	1015			-	-	-						112075 5	112075 5	SPAC11D3.03c	SPAC11D3 04c
1010	1015			+	+	+						1130/3.5	150075.5	SPACEH10.02c	SPACEH10.03
1012				-	+	+						151125.5	150875.5	amb1/6BACEH10.11	SPACSH10.03
1013				-	+	+						101105.5	100375.5	SBAC12CE 08	SPACSH10.120
1014	1019			+	+	+						200125.5	200625.5	SPAC1300.08	ape1/SPAC 24B11 02
1015	1010			Ŧ	- T	- T						200125.5	200023.5	01A024011.02	6DAC906.040
1010	1000		L .	-	+	+						239375.5	240675.5	EBAC906.040	SFAC800.040
1017	1020		L .	-	+	+						244675.5	245125.5	3FAC800.04C	OPACIODIA AA
1010	1021		L .	-	-	+					204402	295375.5	295375.5	5FAC1F5.02	SPAC18B11.00c
1019	1022		E	-	-	+				+	304403	265625 5	265625 5	SPAC630.00c	SPAC630.10
1020	1025			+	+	+	4105048	COTTACCACCTTACC				303023.5	303023.3	3FAC630.09C	SPAC030.10
1021	1020		E	-	+	+	410504	GGTTAGGAGGTTACC	+			411125.5	411375.5	rad32/SPAC13C5.07	fen1/SPAC23E2.01
1022	1027			Ŧ	Ŧ	-					457010	441023.5	441023.3	ete7/SPAC23E2.03c	SPAC24H6 13
1023			L C		-	-				Ŧ	437010	407070.0	407120.0	uba3/SPAC24H6 12c	SPAC24H6 11c
1024	1029			+	+	+						403123.5	403123.3	doad/SFA024H6.09	SPAC24H6.08
1025	1020			+	+	+						474373.3	474373.3	SPAC 24H6 02c	SPADB21E2.01
1020	1029		F	+	- T	+						563625 F	563625 F	SPAC2E7 140	rsm24/SPAC2E7 15
1027	1030			+	+	+						503025.5	503125.5	SPAC3H8 03	SPAC3HR 04
1028	1031		L	-	+ -							608625 F	600125.5	SPAC-3HR 00A	SD020/SPAC3H9 10
1029	1031		L	-		+						651105 5	650975 5	SPAC1D4 075	SPAC1D/ 00
1030	1032	OBI12	F	-	+	+			-			716125.5	715875 F	SX82/SPAC1296.036	SPAC1296.04
1020	1033	UNITZ	-	+	+	+						7/10/20.5	730075.5	SPAC220.000	ura1/SPAC220.04
1032			L	-	+ -	-						750875 5	750125 F	SPAC22G7.05	npk8/SPAC22G7.000
1033				-	-	-						760075.5	100125.5	01 A02207.070	ppnor0FA02207.08
1034	1034		L	-	+	+	7656444	GGTTAGTAGOTTATA	+			766105 5	765075 5	SPAC4G8.03c	SPAC4G8.15c
1035				-	+	+	765644-	GGTTAGTAGGTTATA	+		704007	705605.5	705875.5	ate10/6BAC4C9 11a	SBAC4C8 100
1030	1025		E	-	-	-				+	/6429/	703025.5	704025.5	2010/3FAC408.110	SFAC408.120
1037	1035		E	+	+	+						794875.5	/948/5.5	SPAC 1609.020	SPACIBUS/03
1030				+	+	+						040375.5	002075 5	SFAC321.02	SFAC321.03
1039	1020		E	+	+	+						894375.5	893875.5	SPAC23G3.120	SPAG22H12.010
1040	1039			+	+	+						902675.5	903375.5	3FA022H12.030	EBAC1697 100
1041	10.40		L	-	-	-						939375.5	939125.5	SSI3/SPAC 1087.180	SPAC 1687.190
1042	1040		E	+	+	+						1000606	1000106	for 2/SPAC222.100	PRAC120.05
1043	1041			-	+	+			-			1020020	1020120	nlb1/SPAC139.04c	SPAC 139.05
1044	1042		E	+	+	+						1080126	1080376	pib1/SPAC1A6.04c	SPACTA6.05C
1045	1042			+	+	+						1004120	1004370	Ineu31/SPAC1A6.00c	SPACIA0.07
1040	1043	ADC1		+	+	+						1091120	1091376	hue5/SPAC30D11 13	mi3802/SPAC20D11.12
1047	1044	Anor		Ŧ	Ŧ	-					1151600	11/0976	11/09/120	SPAC56E9 12	SPAC56E9 13
1040	1045		L E		-	-				Ŧ	1131022	1157276	1157626	01 A0301 0.12	DE02/SPAC22A12.01c
1049	1040			+	+	+						1162276	1162976	cep4/SPAC22A12.02c	rps2201/SPAC22A12.010
1050				+	+	+						1103370	1102070	SPAC 22A 12 17c	SPAC4C5.01
1051	1047			+	+	+						1107276	1107126	n/h1/SPAC4C5.02c	SPAC4C5.03
1052	1047			+	+	+						1006076	1006076	nym1/SFA0405.020	SPAC10E6 10
1053	1049			+	+	+						1220370	1220370	psilla/SPAC10F0.09C	SPACIOFO.10
1055	1040		-	+	-	+						1075976	1076106	cen2/SPAPB17E12.04c	rol3703/SPAPB17E12.05
1055	1049			+	Ŧ	+						1360626	1360626	fin1/SPAC19F9.02	nas1/SPAC19F9.03
1057	1050					+						1445126	1445126	SPAC3A12 13c	cam1/SPAC3A12.14
1057	1052			+	- -	+						1445120	1443120	SPAC9 07c	SPAC9 08c
1050	1050		1	T	Ŧ	Ŧ						1/100876	*	SPAC5D6.09c	mes1/SPAC5D6.08c
1060	1055		E	-	-	+						1510126	1509876	SPAC5D6.04	SPAC5D6.02c
1061	1000		F	+	+	+						1574126	1575126	SPAC23H4 19	rbx1/SPAC23H4 18c
1062			-	-	-	+				+	1601298	1600376	1600126	gln1/SPAC23H4.06	SPAC23H4.05c
1063			E	+	+	+						*	*		
1064	1056		F	+	+	+						1667376	1667626	msc1/SPAC343.11c	rds1/SPA343.12
1065	1057		E	+	+	+						1709126	1709126	SPAC664.02c	SPAC664.03
1066			E	+	+	+						1719626	1719626	SPAC664.08c	ggt1/SPAC664.09
1067	1059		L	-	-	-						1766126	1768126	ulp2/SPAC17A5.07c	SPAC17A5.08
1068			Е	+	+	+	1822620	GGTTATGGTGGTTAC	+			1823876	*	psu1/SPAC1002.13c	SPAC1002.20
1069	1061		E	+	+	+						1834876	1835126	SPAC1002.18	SPAC1002.21
1070			L	-	+	+			+			1892626	*	SPAPB1A10.14	SPAPB1A10.15
1071	1062		L	-	+	+	1894950	GGTTATTAGGTTAC	+			1894876	1895626	SPAPB1A10.15	sdh2/SPAC140.01
1072			L	-	-	+				+	1952635	1947376	1947126	SPAC3H1.08c	SPAC3H1.09c
1073	1000		L	-	-	+						1954876	1954876	004000000	004000000
1074	1063		L	-	-	+						*	1959376	SPAU3H1.10	SPAC3H1.11
1075	1064		E	+	+	+						1975876	1975876	rpl3001/SPAC9G1.03c	oxa101/SPAC9G1.04
1076			L	-	-	+						2026126	2026126	ddb1/SPAC17H9.10c	SPAC17H9.11
1077	1065		L	-	-	+						2042876	2042876	snu13/SPAC607.03c	SPAC607.04
1078	1067		L	-	-	+						2097126	2096876	obr1/SPAC3C7.14c	SPAC25A8.03c
1079	1068		L	-	-	+						2141376	2141126	pnk1/SPAC23C11.04c	SPAC23C11.05
1080	1069		E	+	+	+	2199362	GGTTACTGGTTAT				2195376	2195126	hst4/SPAC1783.04c	hrp1/SPAC1783.05
1081	1070		E	+	+	+						2228876	2228876	SPAC18G6.05c	SPAC18G6.06
1082			L	-	-	-						2233126	2233126	mra1/SPAC18G6.07c	SPAC18G6.09c
1083	1073		E	+	+	+						2250626	2250626	byr3/SPAC13D6.02c	SPAC13D6.03c
1084			L	-	-	-						2263876	2264126	SPAC4G9.06c	B8647-3/SPAC4G9.07
1085			E	+	+	+						2274626	2274376	arg11/SPAC4G9.09c	arg3/SPAC4G9.10
1086	1074		E	+	+	+						2280876	2280876	vps26/SPAC4G9.13c	SPAC4G9.14
1087			L	-	-	+						2305126	2305626	mac1/SPAC13G7.04c	SPAC13G7.05
1088	1077		L	-	-	+						2340376	2340626	SPAC6C3.08	SPAC6C3.09
1089			L	-	-	-						2363376	2363876	SPAC17G8.11c	SPAC17G8.12
1090	1079		L	-	-	+				+	2407146	2406876	2407126	sck1/SPAC1B9.02c	SPAC1B9.03c
1091			L	-	-	+						2417126	2416626	SPAC6B12.03c	SPAC6B12.04c
1092	1080		E	+	+	+						2439376	2439376	SPAC6B12.14c	cpc2/SPAC6B12.15
1093	1081		E	+	+	+						2442876	2442876	cpc2/SPAC6B12.15	meu26/SPAC6B12.16
1094	1082		E	+	+	+						2452876	2452626	SPAC32A11.02c	phx1/SPAC32A11.03c
			E		1							2457126	2458126	nhx1/SPAC32A11.03c	tro2/SPAC19A8 15

1096		L	-	-	-						2510126	2511126	gly1/SPAC23H3.09c	ssr2/SPAC23H3.10
1097		L	-	+	+	2521205	GGTTATACGGTTACGCGGTTAT	+			2526376	2526376	SPAC25H1.01c	jmj1/SPAC25H1.02
1098		L	-	+	+			+			2528626	2528626	jmj1/SPAC25H1.02	mug66/SPAC25H1.03
1099		E	+	+	+						2579126	2579376	prs1/SPAC4A8.14	cdc3/SPAC4A8.15c
1100		L	-	-	-						2601126	2601376	SPAC823.11	SPAC823.12
1101	1095	 E	+	+	+						2615876	2615626	SPAC7D4.13c	SPAC7D4.12c
1102	1065	-	+	+	+						2010070	2010020	itr1/SPAC4E9 15	bes1/SPAC/E9 14c
1103	1000	L 	-	-	+					2666262	2044120	2044120	hyk2/SPAC4F8.07c	SPAC4F8.06
1105	1000	 F	+	+	+				+	2689933	2720626	2720626	SPAPB2B4.04c	vma5/SPAPB2B4.05
1106	1092	F	+	+	+					2000000	2762626	2762626	SPAC6F6.13c	vpt5/SPAC6F6.15
1107	1002	E	+	+	+						2804376	2804376	SPAC1805.16c	crm1/SPAC1B2.01
1108		L		-	+				+	2877795	2875626	2876126	SPACUNK4.17	SPACUNK4.19
1109	1094	L	-	-	+						2883876	2883626	SPACUNK4.15	SPACUNK4.14
1110		Е	+	+	+						2938876	2938626	SPAC2E1P3.05c	SPAPB2C8.01
1111	1095	Е	+	+	+						2960626	2961126	SPAPB24D3.07c	SPAPB24D3.08c
1112		Е	+	+	+						2978126	2978126	agl1/SPAPB24D3.10c	SPAPB1A11.01
1113		Е	+	+	+						*	2980626	SPAPB1A11.01	SPAPB1A11.02
1114		Е	+	+	+						2984126	2984126	SPAPB1A11.02	SPAPB1A11.03
1115	1096	Е	+	+	+						3010876	3010876	maf1/SPAC31G5.12c	SPAC31G5.21
1116	1097	Е	+	+	+						3023626	3022876	SPAC31G5.18c	SPAC31G5.19
1117		Е	+	+	+						3032126	3034126	SPAC1786.01c	SPAC1786.04
1118		Е	+	+	+						3053876	3053626	SPAC24C9.06c	bgs2/SPAC24C9.07c
1119	1098	 E	+	+	+						3060876	3061126	bgs2/SPAC24C9.07c	SPAC24C9.08
1120		 L	-	-	-						3071126	*	SPAC24C9.11	SPAC24C9.12c
1121	1099	E	+	+	+						3127876	3127876	srb8/SPAC688.08	SPAC688.09
1122	1100	E	+	+	+						3145376	3145376	SPAC688.14	bet5/SPAC3G9.16c
1123		L	-	-	+				+	3158966	3159376	3159376	peg1/SPAC3G9.12	SPAC3G9.11c
1124	1101	 E	+	+	+						3185376	3185376	SPAC3G9.01	SPAC1486.01
1125	1104	 E	+	+	+						3301626	3301626	emet/SPAPB1E7.06c	SPAPB1E7.07
1126	1105	Ē	+	+	+						3321876	3321876	rps602/SPAPB1E7.12	mns1/SPAC2E1P5.01c
1127	1106	 E	+	+	+						3405626	3405876	apco/SPAC959.090	5PAP32A8.02
1128	1107	 E	+	+	+						3411376	3411376	SPAP32A8.03c	rpi501/SPAC3H5.12c
1129	1109	E	+	+	+						3499126	3499126	rps502/SPAC328.10c	SPAU16E8.01
1130	1110		+	+	+						3542126	3542126	SPACIBLUZC	heud/SPAC1740.04
1131	1111		+	+	+						3549626	3549626	SPAC1740 15	USU1/SPAC1/A2.01
1132	1112		+	+	+						3577606	3577070	SPAC17A2.15	SPAC17A0 14
1133	1114		+	+	+						357/1026	35//8/6	SPAC17A2.100	SPAC1742.11
1134		E	+	+	+						2502976	2502276	SPAC17G6.02c	SPAC17GE 03
1100			+	+	-						3592676	3593376	SPAC17G6.020	3FAC1706.03
1130	1115	F	+	+	+						3635626	3635626	SPAC1142.04	ctr5/SPAC1142.05
1120	1115	 с С	+	+	Ŧ						2646126	2647126	01/SPAC9C9.03	SPACECO 04
1130	1116	F	+	+	-						3701376	3701626	mde6/SPAC15A10.10	ubr11/SPAC15A10.11
1140	1110	F	+	+	+						3746876	37/0876	ml1002/SPAP7G5.05	SPAP7G5.06
1140		F	+	+	+						3753626	3753626	SPAP7G5.06	centromere
1142		 F	+	+	+						3841126	3841376	SPAC4H3.07c	SPAC4H3.08
1143	1124	F	+	+	-						3853376	3853376	SPAC4H3.12c	SPAC4H3.13
1144		E	+	+	+						3878876	3879376		
1145	1125/1126	E	+	+	+						3882876	*	pma1/SPAC1071.10c	SPAC1071.11
1146	1127	Е	+	+	-						3898626	3898876	SPAC926.07c	SPAC926.08c
1147	1128	Е	+	+	+						3954126	3953876	SPAC2F3.14c	lsk1/SPAC2F3.15
1148		E	+	+	+						3992876	3992876	SPAPB15E9.01c	SPAPB15E9.02c
1149	1129	E	+	+	+						3995876	3995876	SPAPB15E9.02c	Tf2-5/SPAPB15E9.03c
1150		L	-	-	-						4010626	4010126	SPAC27E2.03c	SPAC27E2.11c
1151	1130	E	+	+	+						4020126	4020376	SPAC27E2.06c	pvg2/SPAC27E2.07
1152	1131	Е	+	+	+						4073126	4072376	SPAC19G12.13c	its3/SPAC19G12.14
1153	1132	E	+	+	+						4089126	4089126	mnl1/SPAC23A1.04c	SPAC23A1.05
1154	1133	E	+	+	+						4137376	4137376	bgl2/SPAC26H5.08c	SPAC26H5.09c
1155		 E	+	+	+						4141126	4141126	SPAC26H5.09c	tif51/SPAC26H5.10c
1156		E	+	+	+						4154626	4154626	SPAC26H5.13c	SPAC25B8.01
1157		L	-	-	+						4178126	*	SPAC25B8.11	SPAC25B8.12c
1158		 L	-	-	+						4180876	4180626	SPAC25B8.12c	isp7/SPAC25B8.13c
1159	1134	E	+	+	+						4185876	4185876	isp7/SPAC25B8.13c	mal2/SPAC25B8.14
1160		 E F	+	+	+						419/626	419/876	SPAC683.03	5PAU683.020
1161		 E r	+	+	+						4232626	4232626	SPAUTE /.06	IID 1/SPAG1F7.070
1102	1107		+	+	+						4240126	42398/6	norraPACIF7.08	orAUTE7.09C
1103	1100		+	+	+						4200120	4200120	SPAC2C4 074	SPAC2C4.09
1165	1130	F	+	+	+						4326626	4326876	SPAC27F1 05c	SPAC27F1 10
1166	1138	 -	-	-	+				+	4361585	4365876	4366626	SPAC23D3 12	SPAC23D3 13c
1167		 L	-	-	-						4387376	*	SPAC1527.03	sec72/SPAC30.01c
1168	1139	Е	+	+	+						4415626	4415876	SPAC29E6.06c	SPAC29E6.07
1169		 E	+	+	+						4439626	4439876	SPAC9E9.17c	leu2/SPAC9E9.03
1170	1140	L	-	-	+						4451376	4451376	ypt2/SPAC9E9.07c	rad26/SPAC9E9.08
1171		L	-	-	+				+	4458396	4459626	4457376	SPAC9E9.09c	cbh1/SPAC9E9.10c
1172		 L	-	-	-						4468876	4468376	SPAC9E9.12c	wos2/SPAC9E9.13
1173		Е	+	+	+						4484626	4484626	stm1/SPAC17C9.10	tim13/SPAC17C9.09c
1174	1141	E	+	+	+						4534126	4534126	SPAC27D7.11c	but1/SPAC27D7.12
1175	1142	L	-	+	+	4604051	GGTTATTCAGGTTAT	-			4605376	4605376	SPAC12B10.16c	SPAC1093.01
1176	1143	L	-	+	+			-			4653376	4653626	SPAC144.01	SPAC144.02
1177		 L	-	-	+						4674876	4675126	gwt1/SPAC144.10c	rps1102/SPAC144.11
1178	1145	 E	+	+	+						4740376	4740376	SPAC458.04c	pik3/SPAC458.05
1179	1146	 E	+	+	+				+	4789684	4779626	4779626	SPAC11H11.02c	SPAC11H11.03c
1180		 L	-	-	-						4803876	4803876	SPAC22F8.08	rrp16/SPAC22F8.09
1181		E	+	+	+						4845626	4845126	atg13/SPAC4F10.07c	SPAC4F10.08
		. – .		+	+						4853376	4853626	SPAC4F10.10c	spn1/SPAC4F10.11
1182	1147	E	+								4883126	4882876	SPAC19B12.02c	bgs3/SPAC19B12.03
1182	1147 1148	E	+	+	+							10.5	500 K - ·	
1182 1183 1184	1147 1148	E	+ + -	+	+						4912376	4913126	rpn502/SPAPB8E5.02c	mae1/SPAPB8E5.03
1182 1183 1184 1185	1147 1148	E	+ + + + + +	+ - +	+ - +						4912376	4913126 4917626	rpn502/SPAPB8E5.02c SPAPB8E5.04c	mae1/SPAPB8E5.03 mfm1/SPAPB8E5.05
1182 1183 1184 1185 1186	1147 1148 1149	E L E	+ + + + + + + +	+ - + +	+ + + +						4912376 4917376 4964126	4913126 4917626 4964126	rpn502/SPAPB8E5.02c SPAPB8E5.04c vht1/SPAC1B3.16c	mae1/SPAP88E5.03 mfm1/SPAP88E5.05 clr2/SPAC183.17
1182 1183 1184 1185 1186 1187	1147 1148 1149		+ + + + + + + - +	+ + + + -	+ + + + -						4912376 4917376 4964126 4985626	4913126 4917626 4964126 4984876	rpn502/SPAPB8E5.02c SPAPB8E5.04c vht1/SPAC1B3.16c SPAC1952.09c	mae1/SPAPB8E5.03 mfm1/SPAPB8E5.05 clr2/SPAC1B3.17 SPAC1952.10c
1182 1183 1184 1185 1186 1187 1188	1147 1148 1149 1152		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + +	+ + + + + + +						4912376 4917376 4964126 4985626 5025376	4913126 4917626 4964126 4984876 5025376	rpn502/SPAPB8E5.02c SPAPB8E5.04c vht1/SPAC1B3.16c SPAC1952.09c SPAC22E12.03c	mae1/SPAPB8E5.03 mfm1/SPAPB8E5.05 clr2/SPAC1B3.17 SPAC1952.10c ccs1/SPAC22E12.04
1182 1183 1184 1185 1186 1187 1188 1189 1189	1147 1148 1149 1152 1154		+ + + + + + + + - + - + + - + - + - + -	+ + + - + + +	+ + + + + + +						4912376 4917376 4964126 4985626 5025376 5098126	4913126 4917626 4964126 4984876 5025376 5097376	rpn502/SPAPB8E5.02c SPAPB8E5.04c vht1/SPAC183.16c SPAC1952.09c SPAC22E12.03c rpl3002/SPAC1250.05 SPAC02514.00	mae1/SPAPB8E5.03 mfm1/SPAPB8E5.05 clr2/SPAC1B3.17 SPAC1952.10c ccs1/SPAC22E12.04 att1/SPAC1250.04c SPAC22E1.11/status
1182 1183 1184 1185 1186 1187 1188 1189 1190	1147 1148 1149 1152 1154 1155		+ - + - + - + - + - + - + - + - + - + -	+ - + + + + + + +	+ + + + + + + +			-			4912376 4917376 4964126 4985626 5025376 5098126 5156626 5178626	4913126 4917626 4964126 4984876 5025376 5097376 5157376	rpn502/SPAPB8E5.02c SPAPB8E5.04c vht1/SPAC1B3.16c SPAC1952.09c SPAC22E12.03c rpl3002/SPAC1250.05 SPAC26E1.12c SPAC26E1.12c	mae1/SPAPB8E5.03 mfm1/SPAPB8E5.05 clr2/SPAC1B3.17 SPAC1952.10c ccs1/SPAC22E12.04 at1/SPAC1250.04c SPAC26F1.11/dubious art1/SPAC1251.04c
1182 1183 1184 1185 1186 1187 1188 1189 1190 1191	1147 1148 1149 1152 1154 1155		+ + + + + + + + + + + + + + + + + + + +	+ - + + + + + + +	+ + + + + + + + + + + + + + + + + + + +						4912376 4917376 4964126 4985626 5025376 5098126 5156626 5178626 5100370	4913126 4917626 4964126 4984876 5025376 5097376 5157376 5178626 51903270	rpn502/SPAPB8E5.02c SPAPB8E5.04c vht1/SPAC183.16c SPAC1952.09c SPAC22E12.03c rpl3002/SPAC1250.05 SPAC26F1.12c SPAC26F1.105 SPAD_E01.05	mae1/SPAP88E5.03 mfm1/SPAP88E5.05 clr2/SPAC183.17 SPAC1952.10c ccs1/SPAC22E12.04 atl1/SPAC22E12.04 atl1/SPAC22510.04c SPAC26F1.11/dublous etr1/SPAC22F1.04c SPADE01.05
1182 1183 1184 1185 1186 1187 1188 1189 1190 1191 1192	1147 1148 1149 1152 1154 1155		+ + + + + + + + + + + + + + + + + + + +	+ - + + + + + + + -	+ - + + + + + + + + + +						4912376 4917376 4964126 4985626 5025376 5098126 5156626 5178626 5190376 5224402	4913126 4917626 4964126 4984876 5025376 5097376 5157376 5178626 5190376	rpn502/SPAPB8E5.02c SPAPB8E5.04c vh11/SPAC183.16c SPAC1952.09c SPAC22E12.03c rpl3002/SPAC1250.05 SPAC26F1.12c SPAC26F1.05 SPAPJ091.02 mak1/SBAC14C14C	mae1/SPAP88E5.03 mfm1/SPAP88E5.05 cf2/SPAC183.17 SPAC1952.10c ccs1/SPAC22E12.04 al11/SPAC2250.04c SPAC26F1.11/dublous etr1/SPAC26F1.04c SPAP.0691.03 SPAP.0691.03 SPAP.0691.03
1182 1183 1184 1185 1186 1187 1188 1189 1190 1191 1192 1193	1147 1148 1149 1152 1154 1155 1156 1156 1158		+ + + + + + + + + + + + + + + + + + + +	+ - + + + + + + + + -	+ - + + + + + + + + + + +			-			4912376 4917376 4964126 4985626 5025376 5098126 5156626 5178626 5190376 5234126 5272376	4913126 4917626 4964126 4984876 5025376 5097376 5157376 5178626 5190376 5234626 5272376	Tpn502/SPAP88E5.02c SPAP88E5.04c vh11/SPAC183.16c SPAC1952.09c SPAC22E12.03c pl3002/SPAC1250.05 SPAC26F1.05 SPAC26F1.05 SPAP.1691.02 mek1/SPAC14C4.03 add1(SPAP1/PR0.02c	mae1/SPAPB8E5.03 mm1/SPAPB8E5.05 clr/2/SPAC183.17 SPAC182.10c cos1/SPAC2212.04 at1/SPAC2250.04c SPAC28F1.11/d/ubious etr1/SPAC226F1.04c SPAPJ691.03 B22316-2/SPAC14C.04 SPAC24F1.01 nt

	1100		-									5034120	5050070	0010100000	61V1/01 A0000.00
1197	1162		E	+	+	+						5449126	5449626	SPAC1039.01	SPAC1039.02
1198			E	+	+	+						5470376	5470376	isp5/SPAC1039.09	mmf2/SPAC922.01
1199	1163		E	+	+	+						5477126	5476876	SPAC1039.11c	SPAC922.03
1200	1164		E	+	+	+						5483376	5482626	SPAC922.04	SPAC922.05c
1201			F	+	+	+						5487626	5487376	SPAC922.06	SPAC922.07c
1201	1166		-	Ŧ	Ŧ	T						5500606	5500076	mol1/CBAC960.07o	CRACERO ORO
1202	1100			_	Ŧ	т						3302020	5502070	00100000000	0010000.000
1203	1167		L	-	+	+						-	5506626	SPAC869.000	SPAC809.000
1204			L	-	+	+						5510876	*	SPAC869.05c	SPAC869.04
1205			L	-	+	+						5517876	5516126	SPAC869.03c	SPAC869.02c
1206	1168		L	-	+	+						5521876	*	SPAC869.02c	SPAC869.01
1207	1169		L	-	+	+						5529876	*	SPAC186.01	SPAC186.02c
Chromosom															
Chromoson					1	1									
Ori-number	AT-islands		Class	Fire	Fire	Fire	Position of	Telomeric	Localization	Localization	Localization	Position	Position	5' Gene/ORF	3' Gene/ORF
(Hayashi)	(Segurado)			in WT	in taz1∆	in rif1∆	telomeric seq	sequence	of Taz1	of Rif1	of LCS	of Orc1	of Mcm6		
2001			L	-	+	+						*	31375.5	SPBC1348.10c	SPBC1348.11
2002			L	-	+	+						38125.5	38125.5	SPBC1348.13	SPBC1348.14c
2003			L	-	+	+						53125.5	53125.5	grt1/SPBPB8B6.04c	SPBPB8B6.05c
2004			1		+	+						63375.5	61875.5	SPBPB21E7 02c	SPBPB21E7 04c
2005			1			<u> </u>	65104	GGTTACGTTGGTTAT				66975.5		SPRPR21E7.05	SDBDB21E7.06
2003					Ŧ	Ŧ	03134	darradarradarra	-			00875.5	*	000002127.00	010102127.00
2006			L	-	+	+						69875.5	*	SPBPB21E7.06	aes1/SPBPB21E7.07
2007			L	-	+	+						74375.5	74375.5	SPBPB21E7.08	SPBPB21E7.09
2008			L	-	+	+						78125.5	*	SPBPB21E7.09	SPBPB21E7.10
2009			L.	-	+	+						81875.5	81375.5	SPBPB21E7.10	SPBPB10D8.01
2010	2001		L	-	+	+						86875.5	*	SPBPB10D8.02c	SPBPB10D8.03
2011	2002		L	-	+	+						90875.5	91375.5	SPBPB10D8.03	SPBPB10D8.04c
2012	2006		L	-	+	+						104625.5	*	SPBPB10D8.07c	SPBC359.01
2013	2007				+	+						112125.5	111875.5	alr2/SPBC359.02	SPBC359.03c
2014	2007		-	-	+	- T						112120.0	117625.5	SPBC359.03c	SPBC359.04c
2014	2008		L .	-	+	+						*	11/025.5	3FBC339.030	3FBC339.040
2015	2010		L	-	+	+						132375.5	132625.5	SPBC359.06	SPBC1683.01
2016	2011		L	-	+	+	147229	GGTTACGCGGTTAT	-			142375.5	142125.5	SPBC1683.03c	SPBC1683.04
2017	2012		Е	+	+	+						152125.5	152125.5	SPBC1683.05	SPBC1683.06c
2018	2013		L	-	-	+				+		201875.5	202125.5	fbp1/SPBC660.04c	SPBC660.05
2019	2014		L	-	-	+						204375.5	*	SPBC660.05	SPBC660.06
2020										4	228966	228875 5	228875 5	SPBC660 15	SPBC660 16
2020	2015		C								220300	250125 5	250105 5	dr3/SDBC900.02	mi4301/mi37o 1
2021	2015		-	+	+	+				+		200125.5	203125.5	000000000000000000000000000000000000000	opposes ::
2022	2016		E	+	+	+				+		278625.5	278625.5	SPBC800.11	SPBC800.12c
2023			E	+	+	+						282375.5	282375.5	SPBC800.13	SPBC1773.01
2024			E	+	+	+						324125.5	*	SPBC1773.17c	car1/SPBP26C9.02c
2025	2018		Е	+	+	+				+		326625.5	326625.5	car1/SPBP26C9.02c	SPBP26C9.03c
2026	2019		E	+	+	+						333375.5	333375.5	SPBP26C9.03c	SPBC1271.15c
2027			F	+	+	-				+		354875.5	357375.5	SPBC1271.09	SPBC1271.08c
2028	2023		-	-	+	+	459208	GGTTATGGGTTAT	-			454625.5	454625.5	SPBC428.06c	meu6/SPBC428.07
2020	2020		-				100200					495275.5	494975 5	aln6/SPBC902.01c	ctf18/SPBC902.02c
2029			L	-	-	-						405375.5	404075.5	alp0/3FBC902.010	cti16/3FBC902.020
2030			E	+	+	+						*	518625.5	rps27/SPBC 1085.10	np1/SPBC1085.11
2031	2024		E	+	+	+						521125.5	*	rlp1/SPBC1685.11	SPBC1685.12c
2032	_		E	+	+	+						523625.5	523125.5		
2033			Е	+	+	+						529375.5	529625.5	SPBC1685.13	SPBC1685.14c
2034	2025		E	+	+	+						571125.5	570625.5	SPBC354.09c	SPBC354.10
2035			E	+	+	+						502275 F	502975 F	tea4/wsh3	wtf2/SPBC1706.02c
					- T							0900/0.0	392073.3	100-1110110	1112/01/2011/00.020
2036	2026		E	+	+	+						604125.5	604125.5	rpl803/rpkD4	rps1701/SPBC839.05c
2036	2026		E	+	+ +	+++						604125.5 670125.5	604125.5 670375.5	rpl803/rpkD4 SPBC947.05c	rps1701/SPBC839.05c SPBC947.04
2036 2037	2026		E	+ +	+++	+++						604125.5 670125.5	604125.5 670375.5	rpl803/rpkD4 SPBC947.05c	rps1701/SPBC839.05c SPBC947.04
2036 2037 2038	2026 2028		E	++++++	+++++	+++++						604125.5 670125.5 674875.5	604125.5 670375.5 675125.5	rpl803/rpkD4 SPBC947.05c SPBC947.04	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c
2036 2037 2038 2039	2026 2028		E	+ + + +	+++++++++++++++++++++++++++++++++++++++	+++++++++++++++++++++++++++++++++++++++						604125.5 670125.5 674875.5 717875.5	604125.5 670375.5 675125.5 717625.5	rpl803/rpkD4 SPBC947.05c SPBC947.04 ubc4/SPBC119.02	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c SPBC119.03
2036 2037 2038 2039 2040	2026		шшш	+ + + + + +	+++++++++++++++++++++++++++++++++++++++	+ + + + +						604125.5 670125.5 674875.5 717875.5 721875.5	604125.5 670375.5 675125.5 717625.5 *	rpl803/rpkD4 SPBC947.05c SPBC947.04 ubc4/SPBC119.02 mel3/SPBC119.04	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c SPBC119.03 csh3/SPBC119.05c
2036 2037 2038 2039 2040 2041	2026		E E E E	+ + + + +	+ + + + + + + + + + + +	+ + + + + +						604125.5 670125.5 674875.5 717875.5 721875.5 724125.5	604125.5 670375.5 675125.5 717625.5 * 723875.5	rpl803/rpkD4 SPBC947.05c SPBC947.04 ubc4/SPBC119.02 mel3/SPBC119.04 csh3/SPBC119.05c	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c SPBC119.03 csh3/SPBC119.05c sco1/SPBC119.06
2036 2037 2038 2039 2040 2041 2041	2026 2028 2029		E E E E E	+ + + + + +	+ + + + + + + +	+ + + + + + + + +						604125.5 670125.5 674875.5 717875.5 721875.5 724125.5 746375.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5	rpl803/rpkD4 SPBC947.05c SPBC947.04 ubc4/SPBC119.02 mei3/SPBC119.04 csh3/SPBC119.05c SPBC119.18	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c SPBC119.03 csh3/SPBC119.05c sco1/SPBC119.06 rti1/SPBC119.14
2036 2037 2038 2039 2040 2041 2041 2042 2043	2026 2028 2029		E E E E E E	+ + + + + + +	+ + + + + + + + + +	+ + + + + + + + + +						604125.5 670125.5 674875.5 717875.5 721875.5 724125.5 746375.5 833875.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5	rp803/rpkD4 SPBC947.05c SPBC947.04 ubc4/SPBC119.02 mei3/SPBC119.04 csh3/SPBC119.05c SPBC119.18 SPBC530.15c	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c SPBC119.03 csh3/SPBC119.05c sco1/SPBC119.06 rtl1/SPBC119.14 SPBC36.01c
2036 2037 2038 2039 2040 2041 2042 2043 2044	2026 2028 2029		E E E E E E E E	+ + + + + + + + + +	+ + + + + + + + + + + + +	· + + + + + + + + + + + +						604125.5 670125.5 674875.5 717875.5 721875.5 724125.5 746375.5 833875.5 838875.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 *	rp803/rpkD4 SPBC947.05c SPBC947.04 ubc4/SPBC119.02 mei3/SPBC119.04 csh3/SPBC119.05c SPBC119.18 SPBC530.15c SPBC38.01c	rps1701/SPBC839.05C SPBC947.04 SPBC947.03c SPBC19.03 csh3/SPBC119.05 csc01/SPBC119.05 rt11/SPBC119.14 SPBC36.02c
2036 2037 2038 2039 2040 2041 2042 2043 2044 2045	2026 2028 2029		E E E E E E E E F	+ + + + + + + + + + +	+ + + + + + + + + + + + + +	+ + + + + + + + + + + + +						604125.5 670125.5 674875.5 717875.5 721875.5 724125.5 746375.5 833875.5 8388625.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 * 841375.5	UB47517 PI803/PKD4 SPBC947.05 SPBC947.04 ub4/SPBC119.02 mei3/SPBC119.04 SPBC119.05 SPBC119.18 SPBC530.15c SPBC36.01c	rps1701/SPBC839.05c SPBC947.04 SPBC947.03c SPBC119.03 csh3/SPBC119.05 sco1/SPBC119.06 rtl1/SPBC119.14 SPBC36.01c SPBC36.02c
2036 2037 2038 2039 2040 2041 2042 2043 2044 2045 2046	2026 2028 2029 2029 2031		E E E E E E E E E E	+ + + + + + + + + + +	+ + + + + + + + + + + + + + +	+ + + + + + + + + + + + +						604125.5 670125.5 674875.5 721875.5 724125.5 746375.5 833875.5 838625.5 *	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 * 841375.5 841875.5	rpl803/pkD4 SPBC947.05c SPBC947.05 Ubc4/SPBC119.02 mel3/SPBC119.04 esh3/SPBC119.05 SPBC119.18 SPBC530.15c SPBC36.01c	PB1701/SPBC939.05c SPBC947.04 SPBC947.04 SPBC119.03 csh3/SPBC119.05c sco.1/SPBC119.05c rti1/SPBC119.14 SPBC36.01c SPBC36.02c SPBC36.03c
2036 2037 2038 2039 2040 2041 2042 2043 2044 2045 2046 2046	2026 2028 2029 2029 2031			+ + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + +	· + + + + + + + + + + + + + + +						604125.5 670125.5 674875.5 721875.5 724125.5 746375.5 833875.5 838625.5 * 844625.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 * 841375.5 843875.5	ubitation pill03/ipkD4 SPBC947.05 SPBC947.04 ubc4/SPBC119.02 mei/3/SPBC119.04 csh3/SPBC119.05 SPBC119.18 SPBC530.15c SPBC38.01c SPBC38.02c	mEdo 5010380,050 SPBC947.04 SPBC947.04 SPBC947.03 SPBC119.03 sco1/SPBC119.05 sco1/SPBC119.06 rtl/SPBC19.14 SPBC36.01c SPBC36.02c SPBC36.03c
2036 2037 2038 2039 2040 2041 2042 2043 2044 2045 2046 2047	2026 2028 2029 2029 2031 2032			+ + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + +	· + + + + + + + + + + + + + + +						604125.5 670125.5 674875.5 721875.5 721875.5 724125.5 746375.5 833875.5 833875.5 838625.5 * 844625.5 844625.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 841375.5 8441375.5 8448175.5	Pil803/PikD4 SPBC947.05c SPBC947.05 Ubc/4/SPBC119.02 mei3/SPBC119.04 esh3/SPBC119.05 SPBC119.16 SPBC38.01c SPBC38.01c SPBC38.02c SPBC38.02c	MEDIC SOFTOGENER SPECIAT 04 SPECIAT 04 SPECIAT 03 SPECI19 03 csh3/SPEC19 03 csh3/SPEC19 03 csh3/SPEC19 04 mi/SPEC19 14 SPEC36.01c SPEC36.02c SPEC36.03c SPEC36.04 wid SPEC36.04
2036 2037 2038 2039 2040 2041 2042 2043 2044 2045 2044 2045 2046 2047 2048	2026 2028 2029 2029 2031 2032 2033 2033			+ + + + + + + + + + + + + + + -	+ + + + + + + + + + + + + + + + + +	· + + + + + + + + + + + + + + + +	0.0077	00111110000000		+	892038	604125.5 670125.5 674875.5 717875.5 721875.5 724125.5 746375.5 833875.5 8338625.5 * 844625.5 848125.5 848125.5	604125.5 670375.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 841375.5 8441375.5 8441375.5 844125.5 848125.5	npl803/pkD4 SPBC947.05c SPBC947.05 ubc4/SPBC119.02 mel3/SPBC119.04 esh3/SPBC119.05 SPBC36.01c SPBC36.01c SPBC36.02c SPBC36.02c SPBC36.03c prpp1/SPBC713.11c	HEDO 50170324 P91701/SPBC939.05c SPBC947.04 SPBC119.03 csh3/SPBC119.05c scot/SPBC119.05c ft1/SPBC119.04 rt1/SPBC119.04 SPBC36.01c SPBC36.02c SPBC36.03c cys11/SPBC38.04 erg1/SPBC713.12
2036 2037 2038 2039 2040 2041 2042 2043 2044 2044 2045 2046 2047 2048 2049	2026 2028 2029 2029 2031 2032 2033 2035			+ + + + + + + + + + + + - -	+ + + + + + + + + + + + + + + + +	· + + + + + + + + + + + + + + + +	949359	GGTTATTGGGTTAC	+	+	892038	604125.5 670125.5 674875.5 717875.5 721875.5 724125.5 724125.5 724125.5 8338675.5 8338675.5 838625.5 * 844625.5 8490875.5 949625.5	604125.5 67037.5.5 675125.5 717625.5 71625.5 728875.5 746125.5 833875.5 8413875.5 8413875.5 8443875.5 8443875.5 848125.5	npl833rpkD4 SPBC347.05c SPBC347.05c SPBC347.05 ubc4x5PBC119.02 mel3SPBC119.05c SPBC119.18 SPBC38.015c SPBC38.01c SPBC38.01c SPBC38.02c SPBC36.02c SPBC36.03c pmp1/SPBC713.11c gap1/SPBC46.12c	mED6 5010581 part701/SPBC989.05c SPBC947.04 SPBC947.04 SPBC947.03c SPBC119.03 sco1/SPBC119.05 sco1/SPBC119.04 SPBC36.01c SPBC36.02c SPBC36.03c cys11/SPBC36.04 erg1/SPBC73.12 sds23/SPBC46.13
2036 2037 2038 2039 2040 2041 2042 2043 2044 2045 2046 2046 2046 2049 2050	2026 2028 2029 2029 2031 2032 2033 2035 2036			+ + + + + + + + + + + + - -	+ + + + + + + + + + + + + + + + +	· + + + + + + + + + + + + + +	949359	GGTTATTGGGTTAC	+	+	892038	36337.5 604125.5 674875.5 71875.5 721875.5 724125.5 746375.5 838625.5 838625.5 848125.5 949087.5 9490825.5 949625.5	604125.5 67037.5.5 675125.5 717625.5 * 723875.5 746125.5 833875.5 * 841375.5 843875.5 843875.5 843875.5 892875.5 949625.5 958125.5	npl833rpkD4 SPBC947.05c SPBC947.05c SPBC947.04 ubc4/SPBC119.02 mel3/SPBC119.04 esh3/SPBC119.05 SPBC119.18 SPBC38.01c SPBC38.02c SPBC38.02c SPBC38.02c SPBC38.03c gap1/SPBC48.12c	HELOS DOFIGUES 2015 SPEC347.04 SPEC347.04 SPEC119.03 csh3/SPEC119.05 csh3/SPEC119.05 r11/SPEC319.04 SPEC36.02 SPEC36.02 SPEC36.03 cys11/SPEC36.04 sch2/SPEC13.12 sch2/SPEC13.12 sch2/SPEC46.15
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2005			E	+	+	-						1965626	1965876	SPBC1E8.03c	nseudo/SPBC1E8.04
2086	2063		Е	+	+	+						2025626	2024876	SPBP23A10.11c	SPBP23A10.12
2087	2065		F	+	+	+						2053626	2053876	SPBC29A3.07c	pof4/SPBC29A3.08
2089	2066		-									2071976	2071626	SPBC 2043 16	gef3/SPBC20A3 17
2000	2000		E		Ŧ	-						2071870	20/1020	01 D028A0.10	geloror DO23A3.17
2089	2067		L	-	-	+						2106376	2106626	nift/SPBC23G7.04c	sui1/SPBC23G7.05
2090			L	-	-	-				+	2114000	2112626	2112376	SPBC23G7.07c	rga7/SPBC23G7.08c
2091	2068	ARS756	E	+	+	+						2119626	2119376	matmc_2/SPBC23G7.09	SPBC23G7.10c
2092			F	+	+	+						*	2131126		
2002	2069/2070		-				1						0101020	rpp202/SPBC23G7.15c	matmi_1/SPBC1711.01c
2093			E	+	+	+						2134126	2134376		
2094	2071		E	+	+	+						2139626	2139126	matmc_1/SPBC1711.02	SPBC1711.03
2095			E	+	+	+						2178876	2178876	nup85/SPBC17G9.04c	cyp6/SPBC17G9.05
2096	2072		F	+	+	+						2188626	2187626	csx2/SPBC17G9.08c	tif213/SPBC17G9.09
0007	2072		-									0047076	0047076	SDBC15C4.04a	CDDC1EC4.0E
2097	2073			+	+	+						224/6/6	224/8/6	3FBC1304.040	3FBC13C4.03
2098			L	-	+	+			+			2267126	2267626	SPBC21H7.06C	his5/SPBC21H7.07c
2099	2074		E	+	+	+						2320626	2320876	trx2/SPBC12D12.07c	ned8/SPBC24C6.01c
2100			L	-	+	+	2339313	GGTTATGGGGTTAC	+			2340126	2341126	SPBC24C6.09c	SPBC24C6.10c
2101	2075		1	-	+	+			-			2412876	2412376	mex67/SPBC1921.03c	SPBC1921.04c
0100	2070		-									0145070	0145400		faut/00000400040a
2102	2076		E	+	+	+						2445376	2445126	ucp3/SPBC21D10.05c	IIIX1/SPBC1202.130
2103			E	+	+	+						2525376	2525376	SPBC365.14c	alp4/SPBC365.15
2104			L.	-	-	-						2532876	2532876	alp4/SPBC365.15	SPBC365.16
2105	2078		E	+	+	+						2554876	2554876	SPBC29A10.07	SPBC29A10.08
2106	2080	AT2080	1	-		+				+	2580042	2582876	2583126	SPBC2G5.02c	SPBC2G5.03
2100	2000	A12000	-		-					T	2303042	2302070	2300120		0000000000
2107	2081		E	+	+	+						2595626	2595626	rpc25/SPBC2G5.0/c	SPBC25B2.01
2108			L	-	-	-						2614626	*	SPBC25B2.08	SPBC25B2.09c
2109			L	-	-	+				+	2647595	2649876	2650126	SPBC6B1.08c	SPBC6B1.12c
2110	2084		F	+	+	+						2704876	2703626	mrpl39/SPBC4F6.08c	str1/SPBC4F6.09
2111	2095		F									2740626	2740270	SPBC336.02	efc25/SPBC336.02
0110	2000	-		+	+	+			-			2140020	21403/0	aput/CDBC000540.02	tual/PDB000540.03
2112	2086		E	+	+	+						2793126	2/923/6	урх и эмвс 32112.030	ug1/5PBC32F12.04
2113	2087		E	+	+	+						2801376	2801376	duo1/SPBC32F12.08c	rum1/SPBC32F12.09
2114	2088	ARS745	L	-	+	+	2828987	GGTTACGAGGTTAT	+			2829876	2830126	SPBC19C7.04c	SPBC19C7.05
2115	2080	ABS772	F	-	+	+						2903126	2902376	SPBP4H10 14c	SPBP4H10.15
2113	2005	110/12	-	-	-	-						2000120	2302310	SDBD4110.140	SDBD4H10.10
2116			L	-	-	-						2911876	*	3FDF4/110.18C	arbr4/110.190
2117	2091		E	+	+	+						2941126	2940876	ubp9/SPBC1703.12	SPBC1703.13c
2118	2092		E	+	+	+						2988876	2988626	SPBC2D10.11c	rhp23/SPBC2D10.12
2119	2094		L	-	-	+						3054126	3053876	SPBC13E7.06	SPBC13E7.07
2120	2005											2000976	2000276	7001/SPBC20D10.01	ran1/SPBC1778.02
2120	2095		L .	-	-	-						3033870	3099370	2001/01 0000010.01	1401001001110.02
2121			L	-	-	+						3163376	3163876	SPBC609.01	ptn1/SPBC609.02
2122	2097		E	+	+	+						3177876	3177876	dis2/SPBC776.02c	SPBC776.03
2123	2100		E	+	+	+						3288876	3289126	SPBC20F10.02c	SPBC20F10.03
2124			F	+	+	+						3339126	3339626	SPBC17D1.05	dbp3/SPBC17D1.06
0105	0100		-									0060076	0060106	EBBC11C11 10	m11907/CDDC11C11.07
2125	2102			+	+	+						3363376	3303120	3FBG11G11.12	трпоологвопоп.ол
2126	2103	ARS727	L	-	-	+				+	3381484	3381126	3381126	SPBC3B8.08	dsd1/SPBC3B8.07c
2127	2104		L	-	-	-						3410126	3410126	ptr2/SPBC13A2.04c	SPBC4B4.01c
	04.05														
2128	2105		E	+	+	+						3423876	3424126	smg1/SPBC4B4.05	vps25/SPBC4B4.06
2128	2105		E	+	+	+						3423876	3424126	SPBC2G2 16	vps25/SPBC4B4.06 SPBC2G2 17c
2128 2129	2105		E	++	++	++						3423876 3468376	3424126 3468376	smg1/SPBC4B4.05 SPBC2G2.16	vps25/SPBC4B4.06 SPBC2G2.17c
2128 2129 2130	2105		E	+++++++	++++++	++++++						3423876 3468376 3489876	3424126 3468376 3489626	smg1/SPBC4B4.05 SPBC2G2.16 zfs1/SPBC1718.07c	vps25/SPBC4B4.06 SPBC2G2.17c SPBPB7E8.01
2128 2129 2130 2131	2105		E E E	+ + + + + +	+ + + + +	+ + + + +						3423876 3468376 3489876 3493126	3424126 3468376 3489626 3493126	smg1/SPBC4B4.05 SPBC2G2.16 zfs1/SPBC1718.07c	vps25/SPBC4B4.06 SPBC2G2.17c SPBPB7E8.01
2128 2129 2130 2131 2132	2105		E E E E	+ + + + -	+ + + +	+ + + +			-			3423876 3468376 3489876 3493126 3503876	3424126 3468376 3489626 3493126 3504126	smg1/SPBC4B4.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02	vps25/SPBC4B4.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01
2128 2129 2130 2131 2132 2133	2105			+ + + + - + - +	+ + + + +	+ + + + +			-			3423876 3468376 3489876 3493126 3503876 3512876	3424126 3468376 3489626 3493126 3504126 3511876	smg1/SPBC4B4.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c	vps25/SPBC4B4.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01 cbp1/SPBC1105.04c
2128 2129 2130 2131 2132 2133 2134	- 2105			+ + + + + + +	+ + + + + + + +	+ + + + +			-			3423876 3468376 3489876 3493126 3503876 3512876 2515126	3424126 3468376 3489626 3493126 3504126 3511876 2515126	smg1/SPBC484.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c chp1/SPBC1105.04c	vps25/SPBC484.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01 cbp1/SPBC1105.04c exp1/SPBC1105.04c
2128 2129 2130 2131 2132 2133 2134	2105			+ + + + + + + + + + + +	+ + + + + +	+ + + + + + +			-			3423876 3468376 3489876 3493126 3503876 3512876 3515126	3424126 3468376 3489626 3493126 3504126 3511876 3515126	smg1/SPBC4B4.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c cbp1/SPBC1105.04c	vps25/SPBC4B4.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01 cbp1/SPBC1105.04c exg1/SPBC1105.04c
2128 2129 2130 2131 2132 2133 2134 2135	2105			+ + + + + + + + +	+ + + + + + + + +	+ + + + + + + + +			-			3423876 3468376 3489876 3493126 3503876 3512876 3515126 3558376	3424126 3468376 3489626 3493126 3504126 3511876 3515126 3558376	smg1/SPBC4B4.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC887.09c	vps25/SPBC4B4.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01 cbp1/SPBC1105.04c exg1/SPBC1105.05 mcs4/SPBC887.10
2128 2129 2130 2131 2132 2133 2134 2135 2136	2105		E E E E E E E E E E E	+ + + + + + + + + + +	+ + + + + + + + + + +	+ + + + + + + + + + +			-			3423876 3468376 3493126 3503876 3512876 3515126 3558376 3599126	3424126 3468376 3489626 3493126 3504126 3511876 3515126 3558376 3599126	smg1/SPBC484.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC887.09c dna2/SPBC16D10.04c	vps25/SPBC484.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01 cbp1/SPBC1105.04c exg1/SPBC1105.05 mcs4/SPBC887.10 mok13/SPBC46D10.05
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137	2105 2107 2108 2110			+ + + + + + + + + + +	+ + + + + + + + + + + +	+ + + + + + + + + + + + +			-			3423876 3468376 3493126 3503876 3512876 3515126 3558376 3599126 3607126	3424126 3468376 3489626 3493126 3504126 3511876 3515126 3558376 3599126 3607376	smg1/SPBC484.05 SPBC2G2.16 zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC887.09c dna2/SPBC16D10.05 mok13/SPBC16D10.04c	vps25/SPBC484.06 SPBC2G2.17c SPBPB7E8.01 SPBC1105.01 cbp1/SPBC1105.04c exg1/SPBC1105.05 mcs4/SPBC887.10 mok13/SPBC18D10.05 SPBC16D10.06
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138	2105 2107 2108 2110 2111			+ + + + + + + + + + +	+ + + + + + + + + + + +	+ + + + + + + + + + + + +			-			3423876 3468376 3499876 3503876 3512876 3515126 3558376 3599126 3607126 3636876	3424126 3468376 3489626 3504126 3504126 3511876 3515126 3558376 3599126 3607376 3636876	smg1/SPBC484.05 SPBC202.16 Zfs1/SPBC1718.07c SPBPB7E8.02 mrp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC887.09c dma2/SPBC16D10.04c mok13/SPBC16D10.05 SPBPBR7.01c	vps25/SPBC484.06 SPBC262.17c SPBP87E8.01 SPBC1105.01 cbp1/SPBC1105.04c exg1/SPBC1105.05 mcs4/SPBC87.10 mok13/SPBC16D10.05 SPBC16D10.06 SPBP887.02
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138 2129	2105 - 2107 - 2108 - 2110 2111			+ + + + + + + + + + + + +	+ + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +			-		2702040	3423876 3468376 3499876 3503876 3512876 3515126 3558376 3599126 3607126 3636876 3702120	3424126 3468376 3489626 3493126 3504126 3511876 3515126 3558376 3559126 3607376 3636876 3705100	smg1/SPBC484.05 SPBC202.16 zts1/SPBC1718.07c SPBPB7E8.02 mrp1/6/SPBC1105.03c cbp1/SPBC1105.04c SPBC887.03c mok13/SPBC16D10.04c mok13/SPBC16D10.05 SPBPB87.01c mok13/SPBC16D10.05	vps25/SPBC484.06 SPBC262.17c SPBP8788.01 SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.05 mcs4/SPBC887.10 mok13/SPBC1601.05 SPBC16D10.06 SPBP887.02 SPBP887.02
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138 2139 2139	2105 2107 2107 2108 2110 2111			+ + + + + + + + + + + + + + +	+ + + + + + + + + + + + + -	+ + + + + + + + + + + + + + +			-	+	3703810	3423876 3468376 349876 3503876 3512876 3512876 3515126 3558376 3599126 3607126 3636876 3703126	3424126 3468376 3489626 3504126 3504126 3511876 3515126 3558376 3599126 3607376 360876 3705126	smg1/SPBC484.05 SPBC202.16 Zfs1/SPBC1718.07c SPBPB7E8.02 mrp1/6/SPBC1105.04c SPBC887.08c dna2/SPBC16D10.04c SPBC887.08c mok13/SPBC16D10.04c SPBP887.01c puc1/SPBC19F5.01c	vps25/SPBC4B4.06 SPBC2G2.17c SPBC2G2.17c SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.05 mox4/SPBC4B7.00 SPBC16D1.06 SPBC4B7.02 SPBC19F5.02c
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138 2139 2140	2105 2107 2107 2108 2110 2111 2111			+ + + + + + + + + + + + +	+ + + + + + + + + + + + +	+ + + + + + + + + + + +			-	+	3703810	3423876 3468376 349976 3493126 3503876 3512876 3515126 3558376 3559126 3607126 3636876 3703126 3722876	3424126 3468376 3489626 3493126 3504126 3511876 3515126 3558376 3599126 3607376 3636876 3705126 3722376	sing1/SPBC484.05 SPBC202.16 zfs1/SPBC1718.07c SPBP8758.02 mp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC87.09c dna2/SPBC16D10.04c mok13/SPBC16D10.05 SPBP887.01c puc1/SPBC219F5.01c mcm7/SPBC25D12.03c	vps25/SPBC484.06 SPBC262.17c SPBP878.01 SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.04c exg1/SPBC185.105 mcs4/SPBC887.10 mcs1/SPBC887.10 SPBC16D10.06 SPB2165.02 SPBC16F5.02 suc22/SPBC25D12.04
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138 2139 2140 2141	2105 2107 2107 2108 2110 2111 2111 2114 2115			+ + + + + + + + + + + + + +	+ + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + +				+	3703810	3423876 3468376 3499126 3503876 3512876 3512876 3558376 3559126 3607126 3636876 3703126 3722876	3424126 3468376 3489626 3493126 3504126 3515126 3558376 3607376 3636876 3705126 3722376 3764376	smg1/SPBC484.05 SPBC202.16 zfs/SPBC1718.07c SPBP87E8.02 mp116/SPBC1105.04c SPBC87.08c dna2/SPBC18D10.04c mok13/SPBC16D10.05 SPBP887.01c puc1/SPBC19F5.01c mm7/SPBC28712.02c art/SPBC31F10.06c	vps25/SPBC484.06 SPBC262.17c SPBP67E8.01 SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.05 mok13/SPBC1801.05 SPBC16010.06 SPBP887.02 SPBC19F0.02 suc22/SPBC25012.04 SPBC31F10.07
2128 2129 2130 2131 2133 2134 2135 2136 2137 2138 2139 2140 2141 2142	2105 2107 2107 2108 2110 2111 2111 2114 2115			+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	3775231	GGTTATACTGGTTAC	-	+	3703810	3423876 3468376 3498276 3503876 3512876 3512876 3551276 3559126 3607126 3636876 3703126 3703126 3765126 3765126 3765126	3424126 3468376 3498626 3504126 3504126 3511876 3515126 3558376 3699126 3607376 3636876 3705126 3722376 3764376 3779376	sing1/SPBC484.05 SPBC202.16 zts1/SPBC1718.07c SPBP67E8.02 mp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC887.09c dna2SPBC16D10.04c mok13/SPBC16D10.04c sPBP887.01c puc1/SPBC19F5.01c mcm7/SPBC25D12.03c sar1/SPBC31F10.08c hp1/SPBC31F10.13c	vps25/SPBC484.06 SPBC202.17c SPBD7E8.01 SPBC105.01 cbp1/SPBC1105.04c exg1/SPBC1105.04c exg1/SPBC1105.05 mcs4/SPBC887.10 mcs4/SPBC887.10 SPBC16D10.06 SPBC16D10.06 SPBC16D10.06 SPBC16F5.02 su22/SPBC225D12.04 SPBC31F10.07 hjp3/SPBC31F10.17c
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2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138 2139 2140 2141 2142 2141 2142	2105 2107 2107 2108 2110 2111 2111 2114 2115			+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + - -	+ + + + + + + + + + + + + + + + + + +	3775231	GGTTATACTGGTTAC		+	3703810	3423876 3468376 349876 3503876 3551276 3551276 3551276 3559376 3607126 3607126 3703126 3703126 3703126 3703276 3705126 3705326 38168276	3424126 3468376 3489626 3493126 3504126 35511876 35515126 3558376 359126 3607376 3658876 3705126 3705126 3772376 3764376 3774376 3804126 3801719	sing1/SPBC484.05 SPBC202.16 zfs1/SPBC1718.07c SPBPB7E8.02 mp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC287.03e dna2/SPBC16D10.04c mek1/SPBC704 puc1/SPBC19F5.01c mem7/SPBC25D12.03c ast1/SPBC31F10.08c hjp1/SPBC31F10.13c SPBPC31C3.04c SPBC21C3.04c	vps25/SPBC484.06 SPBC262.17c SPBP676.01 SPBC105.01 cbp1/SPBC1105.04c exg1/SPBC1105.04c mok13/SPBC16D10.05 SPBP887.02 SPBC16D10.06 SPBP887.02 SPBC1670.02 SPBC19F5.02c SPBC19F5.02c SPBC19F1.007 hip3/SPBC31F10.14c SPBC21C3.03 SPBC21C3.03
2128 2129 2130 2131 2132 2133 2134 2135 2136 2137 2138 2139 2140 2141 2141 2142 2143 2143	2105 2107 2107 2108 2110 2111 2114 2115 2115		E E E E E E E E E E E E E E E E E E E	+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	3775231	GGTTATACTGGTTAC		+	3703810	3423876 3468376 3489876 3503876 3512876 3515126 3559126 3659126 3607126 3703126 3703126 3779376 3804126 3816876 3816876	3424126 3468376 3489626 3504126 3504126 3511876 3558376 3559126 3607376 3636876 3705126 3705126 3772376 3764376 3764376 3764376 3764376 3764376	sing1/SPBC484.05 SPBC202.16 zfs1/SPBC1718.07c SPBP8758.02 mrp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC87.09 ina2/SPBC16D10.04c mok13/SPBC16D10.05 SPBP887.01c mcm7/SPBC25D12.03c sar1/SPBC31F10.13c SPBC21C3.02c SPBC21C3.10c SBBC07C7 cc	vps25/SPBC484.06 SPBC262.17c SPBP87E8.01 SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.04c exg1/SPBC105.04c mc44/SPBC887.10 mc41/3/SPBC16D10.05 SPBC16D10.06 SPBC16D10.06 SPBC16D10.06 SPBC16D10.06 SPBC25PBC25D12.04 SPBC31F10.07 hip3/SPBC31F10.14c SPBC21C3.03 SPBC21C3.11 SPBC21C3.11
2128 2129 2130 2131 2131 2132 2133 2134 2135 2136 2137 2138 2139 2140 2141 2141 2142 2143 2144	2105 2107 2107 2108 2110 2111 2114 2115 2114 2115 2116		E E E E E E E E E E E E E E E E E E E	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	3775231	GGTTATACTGGTTAC		+	3703810	3423876 3468376 3493126 3503876 3512876 3515126 3559126 3607126 3607126 3607276 3703126 3703126 3703126 3703126 3703126 3703126 3703276 3804126 3804126	3424126 3468376 3489626 3504126 3504126 3511876 35515126 3559126 3607376 3603876 3705126 3705126 3764376 3779376 3804126 3804126 3817126	smg1/SPBC484.05 SPBC202.16 zts1/SPBC1718.07c SPBPB7E8.02 mp116/SPBC1105.03c dna2/SPBC165.03c dna2/SPBC16D10.04c mk1/3/SPBC16D10.04c mk1/SPBC19F5.01c mk1/SPBC31F1.03c hip1/SPBC31F1.03c SPBD287.01c SPBC21C3.04c SPBC21C3.04c SPBC221C3.04c SPBC221C3.04c	vps25/SPBC484.06 SPBC202.17c SPBP678.01 SPBC105.01 cbp1/SPBC1105.04c exg1/SPBC1105.04c mok13/SPBC16D10.05 SPB26887.10 mok13/SPBC16D10.05 SPBP2687.02 SPBC16P10.07 hip3/SPBC31F10.14c SPBC21C3.03 SPBC21C3.03
2128 2129 2130 2131 2132 2133 2134 2135 2134 2135 2136 2137 2138 2139 2140 2141 2142 2143 2144 2145 2146	2105 2107 2107 2108 2110 2111 2114 2115 2116 2116 2119		E E E E E E E E E E E E E E E E E E E	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	3775231	GGTTATACTGGTTAC		+	3703810	3423876 3468376 3489876 3503876 3512876 3512876 3558376 3607126 3636876 3703126 372876 3703126 372876 3702876 3703126 372876 3703126 372876 3804876 3840876 3840876 3917876	3424126 3468376 3489626 3504126 3504126 3511876 3558376 3558376 3558376 3638876 3705126 3705126 372376 3764376 3779376 3804126 3840876 3918126	smg1/SPBC484.05 SPBC202.16 Zfs1/SPBC1718.07c SPBPB7E8.02 mrp16/SPBC1105.03c cbp1/SPBC1105.04c SPBC87.09c dna2/SPBC16D10.04c mok13/SPBC16D10.04c sPBP887.01c put1/SPBC216F5.01t mcm7/SPBC25D12.03c sar1/SPBC31F10.36c SPBC21C3.10c SPBC21C3.10c SPBC21C3.10c SPBC21E8.611t SPBC21E8.611t	vps25/SPBC484.06 SPBC262.17c SPBP678.01 SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.04c exg1/SPBC105.05 SPBC16D10.06 SPBP67.02 SPBC16F5.02c Suc22/SPBC25D12.04 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC31F1.07.16 SPBC3216.02 imp1/SPBC1604.08c
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2128 2129 2130 2131 2131 2133 2134 2135 2136 2137 2138 2139 2140 2141 2141 2142 2143 2144 2144 2145 2144 2147	2105 2107 2107 2108 2110 2111 2111 2114 2115 2116 2119 2120		E E E E E E E E E E E E E E E E E E E	+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	3775231	GGTTATACTGGTTAC	-	+	3703810	3428876 3468876 3493126 3503876 35152876 3551526 3559126 3607126 36087126 3703126 3703126 3703126 3703126 3703126 3703126 3779376 3804126 38140876 3917876 3940126 3946126	3424126 3468376 3489626 3504126 3511276 3515126 3558376 359126 3607376 3638876 3705126 3764376 3779376 3804126 3817126 3840876 3918126 3928626 3940876	sing1/SPBC484.05 SPBC202.16 Zfs1/SPBC1105.03c mp116/SPBC1105.03c cbp1/SPBC1105.04c SPBC87.09c ma2/SPBC16D10.04c mok13/SPBC16D10.04c mok13/SPBC16D10.05 SPBPB87.01c mcm7/SPBC25D12.03c sar1/SPBC31F10.05c SPBC20167.03c SPBC21C3.02c SPBC21C3.02c SPBC21C40.09c SPBC1604.04 SPBC1677.03c	vps25/SPBC484.06 SPBC262.17c SPBP8788.01 SPBC105.01 cbp1/SPBC105.04c exg1/SPBC105.04c exg1/SPBC105.04c exg1/SPBC105.04c SPBC16D10.06 SPBC16D10.06 SPBC16D10.06 SPBC16F5.02c suc22/SPBC25D12.04 SPBC31F10.07 hip3/SPBC31F10.14c SPBC2163.03 SPBC2163.03 SPBC2163.03 SPBC2164.03 SPBC2164.03 SPBC2164.03 SPBC2164.03 SPBC2164.03
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Ori-number	AT-islands		Class	Fire	Fire	Fire	Position of	Telomeric	Localization	Localization	Localization	Position (bp	osition (bp	5' Gene/ORF	3' Gene/ORF
(Hayashi)	(Segurado)			in WT	in taz1∆	in rif1∆	telomeric seq	sequence	of Taz1	of Rif1	of LCS	of Orc1	of Mcm6		
3001	3002		E	+	+	+						35375.5	35375.5	SPCP20C8.03	SPCC1884.01
3002	3003		E	+	+	+						76375.5	76625.5	SPCC757.12	SPCC757.13
3003	3005	ars3002/4	Е	+	+	+						123875.5	122875.5	SPCC330.07c	alg11/SPCC330.08
3004			E	+	+	+						188125.5	189125.5	fft2/SPCC1235.05c	sif1/SPCC1235.06
3005	3006		Е	+	+	+						206875.5	207875,5	ght6/SPCC1235.13	ght5/SPCC1235.14
3006	3007		E	+	+	+						232125.5	231875.5	SPCC548.06c	ght1/SPCC548.07c
3007	3009		E	+	+	+						254125.5	253875.5	SPCC794.04c	SPCC794.6
3008			E	+	+	+						279375.5	278125.5	mae2/SPCC794.12c	SPCC794.15
3009	3010		E	+	+	+						286375.5	286625.5	SPCC553.10	spb70/pol12
3010			E	+	+	+						305875.5	305875.5	SPCC553.03	SPCC553.02
3011			L	-	-	-						347625.5	347625.5	dis1/SPCC736.14	SPCC736.15

3012	3012		E	+	+	+						370125.5	370375.5	SPCC594.07c	qcr9/SPCC1682.01
3013	3013		E	+	+	+						398125.5	398125.5	ubp16/SPCC1682.12c	SPCC1682.13
3014	3015		F	+	+	+						505625.5	505625.5	SPCC970.06	rpl3601/SPCC970.05
2015	2016		-									51000E F	510075 F	rod16/PBCC070.01	pro11/PRCC10H11.01
3015	3016			+	+	+						516625.5	516675.5	1au10/3FCC9/0.01	pip11/3FCC10H11.01
3016	3017		E	+	+	+						565625.5	565625.5	sap1/SPCC16/2.020	SPCC1672.030
3017	3018		E	+	+	+						575125.5	575125.5	asp1/SPCC1672.06c	SPCC1672.07
3018			E	+	+	+						605625.5	605375.5	ung1/SPCC1183.06	SPCC1183.07
3019	3019		Е	+	+	+						643125.5	643125.5	taf72/SPCC5E4.03c	cut1/SPCC5E4.04
3020	3020		Е	+	+	+						666125.5	666125.5	pin1/SPCC16C4.03	SPCC16C4.04
3021	3021		F	+	+	+						720125.5	720125.5	SPCC18B5 02c	wee1/SPCC18B5.03
2000	2021		-									764105 5	764105.5	0000//EBCC1000.10	EBCC1020.00
3022	3022			+	+	+						764125.5	764125.5	002/3F001020.10	3FCC1020.09
3023	3023		E	+	+	+						826875.5	82/8/5.5	SPCC1393.13	SPCC2H8.02
3024			E	+	+	+						847875.5	847875.5	SPCC63.06	SPCC63.07
3025	3024		E	+	+	+						853625.5	853625.5	ppk36/SPCC63.08c	SPCC63.10c
3026	3025		E	+	+	+						936375.5	936875.5	SPCC24B10.19c	SPCC24B10.20
3027			L	-	-	-						966375.5	967875.5		
3028	3026		F	+	+	+						971125.5	971375.5	SPCC1795.13	SPCC1795.12c
0020			-	- T	T	T						000405.5	005075.5	00004705.07	
3029			E .	+	+	+		0.077170.000.07717				960125.5	965675.5	3FCC1793.07	map2/3FCC1795.00
3030	3027		L	-	+	+	1039066	GGTTATGGCGGTTAT	+			1039626	1039626	SPCC1259.020	rpa12/SPCC1259.03
3031			E	+	+	+						1066126	1065876	meu27/SPCC1259.14c	centromere
3032			E	+	+	+						1141876	1142126	centromere	SPCC4B3.18
3033	3039		E	+	+	+						1254126	1254126	snd1/SPCC645.08c	mrpl37/SPCC645.09
3034	3040		F	+	+	+						1324126	1323876	ml3402/SPCC1322 15	SPCC1322 16
3025	0040		F									13/2276	13/2270	SPCC339 19	rad21/SPCC339 170
3035				+	+	+						1343376	1343376	ar-00338.18	18021/0F00338.1/C
3036	3042		Ē	+	+	+						1371876	1371126	SPCC338.02	ags1/SPCC1281.01
3037			E	+	+	+						*	1373876		
3038			Е	+	+	+						1393626	*	rsc7/SPCC1281.05	SPCC1281.06c
3039			E	+	+	+						1396876	1396876	SPCC1281.06c	SPCC1281.07c
3040	3043		F	+	+	+						1411126	1411376	SPCC622.07	hta1/SPCC622.08c
2041	2044		-									1417976	1417976	SPCC622.10c	SPCC622.11
3041	3044		-	Ŧ	Ŧ	Ŧ						1417070	1417070	0100022.100	000022.11
3042	3045		E	+	+	+						1449126	1449126	SPCC61.04c	SPCC61.05
3043	3046		E	+	+	+						1511876	1511876	dcr1/SPCC584.10c	SPCC584.11c
3044			L.	-	-	-						1524876	1524876	SPCC584.15c	SPCC584.16c
3045	3047		E	+	+	+						1532626	1532126	SPCC584.01c	cuf2/SPCC584.02
3046			F	+	+	+						1556376	1556376	SPCC162 12	SPCC162 11c
2047			-									1576076	1576606	opti /PRCC162.07	SBCC162.06a
3047			C	+	+	+						15/06/0	15/0020	0000102.07	3F00102.000
3048	3048		E	+	+	+						1595376	1595126	SPGC13B11.020	SPCC13B11.03C
3049	3049		E	+	+	+						1609876	1609876	SPCC777.06c	SPCC777.07
3050			E	+	+	+						1672876	1672876	dad5/SPCC417.02	SPCC417.03
3051			E	+	+	+						1675876	1675626	SPCC417.04	chr2/SPCC417.05c
3052			F	+	+	+						1680626	1680626	ppk35/SPCC417.06c	mto1/SPCC417.07c
3053	3051		F	+	· ·	· ·						1687126	1685126	mto1/SPCC417.07c	tef3/SPCC417.08
0050	0051		-	T	T	T						1007120	1000120	4-40/00000447.00	0000447.00-
3054	3052		E	+	+	+			-	-		1690126	1690626	tel3/SPCC417.08	SPCC417.09C
3055	3053		E	+	+	+						1720126	*	SPCC191.08	gst1/SPCC191.09c
3056			E	+	+	+						*	1723376	SPCC191.10	inv1/SPCC191.11
3057	3054		Е	+	+	+						1728626	1728876	SPCC1450.01c	SPCC1450.02
3058			F	+	+	+						1754626	1754876	cek1/SPCC1450.11c	SPCC1450.12
2050			-									1015276	101/606	coc2/SPCC285.09c	SPCC295 10c
3039	0055		-	Ŧ	-	T						1013370	1014020	0000005 40-	0000005.44
3060	3055		E	+	+	+						1823126	1823126	SPC6285.13C	SPU0285.14
3061	3056		E	+	+	+						1838376	1838626	SPCC1223.01	nmt1/SPCC1223.02
3062	3057		E	+	+	+						1845376	1845376	gut2/SPCC1223.03c	SPCC1223.04c
3063			Е	+	+	+						1861376	1860626	SPCC1223.09	SPCC1223.10c
3064	3058		E	+	+	+						1868126	1868376	ptc2/SPCC1223.11	meu10/SPCC1223.12c
3065			F	+	+	-						1878626	1879126	SPCC297 01	ssp1/SPCC297 03
2066			-		t :	l						1000606	1002606	SPCC74.09	slv1/SPCC74.01
3000	0050			+	+	+ -						1922020	1923020	000074.00	3191/01 0074.01
3067	3059		E	+	+	+						1930126	1929876	SPUU74.02c	ssp2/SPCC74.03c
3068			E	+	+	+					I	1937376	1936126	ssp2/SPCC74.03c	SPCC74.04
3069															
			Е	+	+	+						1969376	1969626	SPCC18.06c	rpc53/SPCC18.07
3070	3060		E	++	+ +	++						1969376 2036376	1969626 2036376	SPCC18.06c SPCC1739.04c	rpc53/SPCC18.07 set5/SPCC1739.05
3070 3071	3060		E	++++++	+ + +	+ + +						1969376 2036376	1969626 2036376	SPCC18.06c SPCC1739.04c set5/SPCC1739.05	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c
3070 3071	3060		E	+ + +	+ + +	++++++						1969376 2036376 * 2042626	1969626 2036376 *	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.09c
3070 3071 3072	3060		Е Е Е Е	+ + + + +	+ + + +	+ + + +						1969376 2036376 * 2042626	1969626 2036376 * *	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c
3070 3071 3072 3073	3060		E E E E	+ + + + +	+ + + + +	+ + + + +						1969376 2036376 * 2042626 2046376	1969626 2036376 * 2046626	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c cox13/SPCC1739.09c
3070 3071 3072 3073 3074	3060		шшш	+ + + + + +	+ + + + + +	+ + + + +						1969376 2036376 * 2042626 2046376 2064376	1969626 2036376 * 2046626 2064626	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c npp106/SPCC1739.14	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c cox13/SPCC1739.09c wtf21/SPCC1739.15
3070 3071 3072 3073 3074 3075	3060			+ + + + + + + + + + + + + + + + + + + +	+ + + + + + +	+ + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2068626	1969626 2036376 * 2046626 2064626 2068626	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c npp106/SPCC1739.14 wtf21/SPCC1739.15	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c cox13/SPCC1739.09c wtf21/SPCC1739.15 amt1/SPCPB1C11.01
3070 3071 3072 3073 3074 3075 3076	3060		E E E E	+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + +	+ + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2068626 2072376	1969626 2036376 * 2046626 2064626 2068626 2072876	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c np106/SPCC1739.14 wtf21/SPCC1739.15 antt1/SPCPB1C11.01	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c cox13/SPCC1739.09c wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02
3070 3071 3072 3073 3074 3075 3076 3077	3060			+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2068626 2072376 2076376	1969626 2036376 * 2046626 2064626 2068626 2072876 2076626	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c npp106/SPCC1739.14 wtf21/SPCC1739.15 amt1/SPCPB1C11.02 SPCPB1C11.02	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c cox13/SPCC1739.09c wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.03
3070 3071 3072 3073 3074 3075 3076 3077 3078	3060	AP\$744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + -	+ + + + + + + + + + -						1969376 2036376 * 2042626 2046376 2064376 2068626 2072376 2076376 2108376	1969626 2036376 * 2046626 2064626 2068626 2072876 2076626 2108376	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c npp106/SPCC1739.14 wtf21/SPCC1739.15 amtt/SPCPB1C11.01 SPCPB1C11.02 ksp1/SPCC578.15c	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c cox13/SPCC1739.08c cox13/SPCC1739.09c wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.03 wtf2/SPCP576.16-0
3070 3071 3072 3073 3074 3075 3076 3077 3078	3060	ARS744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2068626 2072376 2076376 2108376	1969626 2036376 * 2046626 2064626 2068626 2072876 2076626 2108376	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.07 SPCC1739.08c mp106/SPCC1739.14 wtt21/SPCC1739.15 amt1/SPCCP81C11.01 SPCPB1C11.02 ksg1/SPCC576.15c	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06c SPCC1739.08c cox13/SPCC1739.09c wtt21/SPCC1739.09c ant1/SPCP81C11.01 SPCP81C11.02 SPCP81C11.02 SPCP81C11.02
3070 3071 3072 3073 3074 3075 3076 3077 3078 3079	3060 3062 3064	ARS744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + +	+ + + + + + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2068626 2072376 2076376 2108376 2201876	1969626 2036376 * 2046626 2064626 2068626 2072876 2076626 2108376 2201876	SPCC18.06c SPCC1739.04c set5:SPCC1739.05 SPCC1739.07 SPCC1739.08c mp166/SPCC1739.16 amt1/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 ksg1/SPCC576.15c SPCC830.09c	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06 SPCC1739.06 SPCC1739.08 wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.03 wtf22/SPCC576.16 SPCC380.10
3070 3071 3072 3073 3074 3075 3076 3077 3078 3079 3080	3060 3062 3064	ARS744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + +	+ + + + + + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2068626 2072376 2076376 2108376 2201876 2201876	1969626 2036376 * 2046626 2064626 2068626 2072876 2076626 2108376 2201876 2201876	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c mp106/SPCC1739.14 amt1/SPCP81C11.01 SPCP81C11.02 ksg1/SPCC578.15c SPCC830.09c bgs4/SPCC1840.02c	rpc53/SPCC18.07 set5/SPCC1739.06 SPCC1739.08c SPCC1739.08c cox13/SPCC1739.08c wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.02 SPCPB1C11.03 wtf22/SPCC576.16c SPCC630.10 sat3/SPCC1840.03
3070 3071 3072 3073 3074 3075 3076 3077 3078 3079 3080 3081	3060 3062 3064 3065	ARS744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + +	+ + + + + + + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2064376 2072376 2072376 2076376 2108376 2201876 2201876 2258376	1969626 2036376 * 2046626 2064626 2064626 2072876 2076826 2108376 2201876 2221876 2258626 2277126	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.07 SPCC1739.08c mp106/SPCC1739.14 wtt21/SPCC1739.14 wtt21/SPCC1739.15 amt1/SPCCP810.10 ksg1/SPCC576.15c SPCC830.09c bg4/SPCC1840.02c SPCC1840.09	rpc53/SPCC18.07 sel5/SPCC1739.05 SPCC1739.06 SPCC1739.06 cox13/SPCC1739.08 wtt21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.03 wtt22/SPCC576.16 SPCCB30.10 sal3/SPCC1840.03 ismb/SPCC1840.10
3070 3071 3072 3073 3074 3075 3076 3077 3078 3079 3080 3080 3081 3082	3060 3062 3062 3064 3065	ARS744		+ + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + +						1969376 2036376 * 2042626 2046376 2064376 2064376 2064376 2078376 2078376 2201876 2201876 2258376 2277126 2300876	1969626 2036376 * 2046626 2064626 2064626 2072876 2076626 2108376 2201876 2221826 2277126 2277126	SPCC18.06c SPCC1739.04c set5/SPCC1739.05 SPCC1739.07 SPCC1739.08c np106/SPCC1739.14 wtt21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 ksg1/SPCC781.5c SPCC830.09c bgs4/SPCC1840.02c SPCC1840.09 altr/SPCC856.06c	rpc53/SPCC18.07 set5/SPCC1739.06 SPCC1739.06 SPCC1739.08 cox13/SPCC1739.09 wt21/SPCC1739.09 wt21/SPCC1739.15 amt1/SPCCB1C11.01 SPCPB1C11.02 SPCPB1C11.03 wt22/SPCC576.16 SPCC830.10 sal3/SPCC1840.03 Ism8/SPCC1840.10 SPCC965.09
3070 3071 3072 3073 3074 3075 3076 3077 3078 3079 3080 3081 3081 3082 3083	3060 3062 3064 3065 3066	ARS744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + + + +				+	2310626	1969376 2036376 * 2042626 2046376 2064376 2064376 2076376 2072776 20000000000	1969626 2036376 * 2046626 2064626 2068626 2072876 2072876 2072876 2072876 2072876 2072876 2072876 2072876 2072876 207287720 2072876 207287720 2072876 2072876 207287720 2072876 2072876 207287720 2072876 2072876 207287720 2072876 2072876 2072876 2072876 2072876 2072877 2072876 2072976 2072976 2072976 2072976 2072976 2072976 2072976 2072976 2072976 2072976 207297777777777777777777777777777777777	SPCC18.06c SPCC1739.04c set5:SPCC1739.05 SPCC1739.07 SPCC1739.07 SPCC1739.08c mp106/SPCC1739.14 wtt21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 ksg1/SPCC576.15c SPCC830.09c bg4/SPCC1840.02c SPCC1840.09 alt1/SPCC865.06c SPCC985.12	rpc53/SPCC18.07 sel5/SPCC1739.05 SPCC1739.08c SPCC1739.08c wtf21/SPCC1739.08c wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.03 wtf22/SPCC576.18c SPCC80.10 sal3/SPCC1840.03 lsm8/SPCC1840.10 SPCC986.13
3070 3071 3072 3073 3074 3075 3076 3077 3078 3079 3080 3081 3082 3083	3060 3062 3064 3065 3066	ARS744		+ + + + + + + + + + + + + + + + + + + +	+ + + + + + + + + + + + + + + + -	+ + + + + + + + + + + + + + + + + +				+	2310626	1969376 2036376 * 2042626 2046376 2064376 2064376 2078376 2078376 2201876 2201876 2258376 2277126 2300876 2300826	1969626 2036376 * 2046626 2068626 2078276 2076276 2076266 2076276 2076826 2078276 2078276 201876 2258626 2277126 2301376 2309027	SPCC18.06c SPCC1739.04c set5:SPCC1739.05 SPCC1739.07 SPCC1739.07 SPCC1739.08c mt1/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 ksg1/SPCC576.15c SPCC830.09c gs4/SPCC1840.022 SPCC1840.09 alr1/SPCC965.08c SPCC965.12 SPCC965.12	rpc53/SPCC18.07 set5/SPCC1739.05 SPCC1739.06 SPCC1739.06 SPCC1739.06 wtf21/SPCC1739.15 amt1/SPCPB1C11.01 SPCPB1C11.02 SPCPB1C11.03 wtf22/SPCC576.16 SPCC390.10 sa3/SPCC1840.03 Ism%/SPCC1840.10 SPCC965.09 SPCC965.13 SPCC965.13

Ori number (Hayashi): Number of origins identified in Hayashi etal (2007); first digit indicates chromosome number (1-3). Late origins that are activated in HU-treated *laz1*∆ and *rif1*∆, in *rif1*∆ only and those not activated are highlited in purple, brown and gray, respectively.

AT-islands (Segurado): Origins predicted by Bioinformatics (Segurado et al., 2003).

Class: Activity of origins defined by BrdU incorporation in HU-treated wild-type cells (Hayashi et al, 2007). E; Early origin, L; Late or dormant origin (highlighted in light blue).
 E (in red); Early origins that had been previously classified as late origins, L (in red); Late/dormant origins that had been previously classified as late origins.
 Firing in *taz1*Δ or *rif1*Δ. "*" denotes a late origin that incorporates BrdU in HU-treated *taz1*Δ and *rif1*Δ (highlighted in purple) or *rif1*Δ (highlighted in brown), respectively, in Supplementary Figure S4.

Positions of telomere seq: Positions (bp) of GGTTAY-N(1-3)-GGTTAY sequence found within 10 kb from the Orc1 binding site using "fuzznuc" program. Telomeric sequences near ori1021, ori1034 and ori2069 (with a

Telomeric sequence: The telomeric sequence found in the internal arm regions.

Localization of Taz1; ** and ** denotes Taz1-dependent late international meterination (general Localization of Taz1; ** and ** denotes Taz1-dependent late origins where Taz1 was localized and not localized, respectively, in 10 kb distance in ChIP-seq analysis (Supplementary Figure S4). Localization of RI1; *** denotes origins where Rif1 was localized in 5 kb distance (Hayao et al, 2012). Localization of LCS: Positions (bp) where LCS-like sequence was identified (Hayao et al, 2012, Supplemental Table S3)

Positions of Orc1: The peak position (bp) of Orc1 (Havashi et al. 2007).

Positions (b) of Mcm6. The peak position (b) of Ort (regarding et al. 2007). Positions (b) of Mcm6. The peak position of Mcm6 (Hayashi et al. 2007). 5' Gene/ORF, 3' Gene/ORF: The name of the 5' gene/ORF or 3' gene/ORF flanking the region containing theOrc1-Mcm6 binding sites.

Supplementary Table S2. Characteristics of replication origins and genes near the internal telomeric repeats.

Chr	Proximal origin	Class	Early firing in	Localization	Start	End	St	Sequence	Left ORF	Response to	Response to	Response to	Remarks (gene)	Right ORF	Response to	Response to	Response to	Remarks (gene)
Chr1	1068	E	NA	+	1822620	1822634	-	GGTTATGGTGGTTAC	SPAC1002.13c	30,033	+	pricromone		itt1	+	+	pricromone	ubiguitin-protein ligase E3
	1071/AT1062	L	+	+	1894950	1894963	+	GGTTATTAGGTTAC	SPAPB1A10.15		+		Arv1-like family protein	SPAC140.01				ubiquinone iron-sulfur protei n
	1080/AT1069	E	NA	-	2199362	2199374	-	GGTTACTGGTTAT	SPAC1783.05									
	1097	L	+	+	2521205	2521226	-	GGTTATACGGTTACG CGGTTAT	SPAC23H3.13c				G protein alpha-2, Gpa2	SPAC23H3.14				LAIv9 family protein
		NA	NA	-	2859912	2859926	+	GGTTACTCGGGTTAT	SPAC8F11.04					SPAC8F.06		+		nuclear envelope protein Brr6/Brl1
		NA	NA	-	3982509	3982521	-	GGTTATCGGTTAT						SPAPB18E9.04c				
		NA	NA	-	4547725	4547739	-	GGTTATCCTGGTTAT						SPAC637.05c				
	1175/AT1142	L	+	-	4604051	4604065	-	GGTTATTCAGGTTAT	SPAC12B10.16c		+		conserved protein Mug157	SPAC1093.01				PPR repeat protein Ppr5
		NA	NA	-	5250680	5250692	+	GGTTATCGGTTAT	SPAC14C4.11				polyphosphate synthetase	SPAC14C4.12c				Clr6 L associated factor 1 Laf1
Chr2	2005	L	+	-	65194	65208	-	GGTTACGTTGGTTAT	SPBPB21E7.05					SPBPB21E7.05				
	2016/AT2011	L	+	-	147229	147242	+	GGTTACGCGGTTAT	SPBC1683.04	+			glycosyl hydrolase family	SPBC1683.05		+	+	
	2028/AT2023	L	+	-	459208	459220	-	GGTTATGGGTTAT	SPBC428.08c		+		histone H3 methylase Clr4	SPBC428.10			+	
	2049/AT2035	L	+	+	949359	949372	-	GGTTATTGGGTTAC	SPBC646.12c				GTPase activating Gap1	SPBC646.13	+			PP2A inhibitor Sds23/Moc1
		NA	NA	-	1626423	1626436	-	GGTTACAGGGTTAC	cnt									
	2081/AT2062	L	+	+	1868344	1868357	-	GGTTATTGGGTTAT	SPBC3H7.09		+		palmitoyltransferase Erf2	SPBC3H7.08c	+		+	conserved fungal protein
	2100	L	+	+	2339313	2339326	+	GGTTATGGGGTTAC	SPBC24C6.09c	+	+	+	phosphoketolase family	SPBC24C6.10c				cytoskeletal protein
	2114/AT2088	L	+	+	2828987	2829000	-	GGTTACGAGGTTAT	SPBC19C7.04c	+	+		conserved fungal protein	SPBC19C7.05				cell wall organization
		NA	NA	-	3011366	3011378	+	GGTTACTGGTTAT	SPBC15D4.01c	+	+		kinesin-like protein Klp9	SPBC15D4.02		+		transcription factor
	2142	L	-	-	3775231	3775245	-	GGTTATACTGGTTAC	SPBC31F10.13c				histone chaperone Hip1	SPBC31F10.14c		+		HIRA interacting protein Hip3
		NA	NA	+	3861682	3861694	-	GGTTATCGGTTAC	SPBC23E6.08					SPBC23E6.09				transcriptional corepressor Ssn6
	2148/AT2120	E	NA	-	3946958	3946972	+	GGTTATGCTGGTTAT	SPBC26H8.03					SPBC26H8.04c		+		DEP domain protein
	sub-telomeric	L	+	+	4535529	4535542	+	GGTTACATGGTTAT	tlh2									
Chr3		NA	NA	+	4815	4828	-	GGTTACATGGTTAC						SPRRNA.47				
		ΝΔ	NΔ		15685	15608		GGTTACATGGTTAC	SPRRNA 43					SPRRNA 48				

3		NA NA	NA NA	+	4815	4828	-	GGTTACATGGTTAC	SPRRNA 43			SPRRNA.47		
	3030/AT3027	L	+	+	1039066	1039080	+	GGTTATGGCGGTTAT	SPCC1259.02c		ER metallopeptidase 1	SPCC1259.03		RNA polymerase I subunit Rpa12
		NA	NA	+	2448448	2448461	+	GGTTACATGGTTAC	SPRRNA.49			SPNCRNA.1299		

Proximal origin : the name of ealry and late origins idnetified by Hayashi et al. (2007)/AT-island identified by Segurado et al. (2003), located within 10-kb from the telomeric sequence.

Class : "E" and "L" indicate early and late/dormant origins, respectively. NA show no origin is located.

Early firing in *taz1*∆ : "+" denotes BrdU-incorporation at late origin in Supplementary Fig. S5.

Localization of Taz1 : "+" shows enrichment of Taz1 localization in Supplementary Fig. S5.

Start/end : positions of start and end of telomeric sequence.

St : strandness is shown either "+" or "-".

Response to stress, meiosis and pheromone: a plas sign indicates increase in mRNA level (>2) of mRNA in the stress (high temperature, ionic and oxidative stresses), during meiosis and sporulation, and to the phoromone, according to Gene Data Base at Sanger Center.

Figure S1

Figure S1.

BrdU-labeled DNA prepared at 120 min after G2/M release from HU-treated wild-type, $taz1\Delta$ and $rif1\Delta$ strains and separated by CsCl density gradient centrifugation, and those obtained by FLAG-Taz1-IP were used for SOLiD deep sequencing analysis, which was performed according to the manufacturer's standard protocol (Applied Biosystems).



Taz1/notag

laz1/notag

4.0

2.0 0.0

0.130M 0.110M 0.140M 0.160M 0.180M 0.190M 0.100M 0.120M 0.150M 0.170M SPAC1F5.08c SPAC1F5.05c SPAC1F5.03c SPAC1F5.09PAC1F5.07c SPAC1F5.04c SPAC806.05 SPAC806.07 SPAC24B11.14 SPAC24B11.13 SPAC1F5.11c SPAC24B11.05 SPAC13G6.14 SPAC24B11.09 genes

0.200 0.210M 0.200 0.220M 0.250M 0.25



chrl 2





genes

SPAC227.05 SPACSP27C0247.06

SPAC227.035PAC227.12 SPAC227.10 SPAC227.14 SPAC227.14 _ _ _ 0.530M 0.540M 0.550M SPAC227.17c SPAC2F7.03c SPAC2F7.06c SPAC2F7.08c SPAC227.16&PAC2F7.02c SPAC2F7.05&SPAC2F7.07&PAC2F7.09c 0.500M - 0.520M SPAC227.0FRAC227.03c SPAC227.02c SPAC227.07c SPAC227.13c

SPAC227.18

SPAC2F7.04

SPAC2F7.11

SPAC2F7.10

SPAC2F7.17

SPAC2F7.15

SPAC13A11.05 SPAC3H8.**SP**AC3H8.04 SPAC13A11.03 SPAC13A11.06 SPAC3H8.03 SPAC3H8.06 ____ 0.590M SPAC3H8.05c 0.580M - 0.5











genes

 SPAC30D11.06c
 SPAC30D11.04c
 SPAC30D11.04c
 SPAC56F8.02
 SPAC56F8.03
 SPAC56F8.03
 SPAC56F8.13
 SPAC56F8.13
 SPAC56F8.13
 SPAC2412.10
 SPAC22412.11
 SPAC22412.13
 SPAC22412.13
 SPAC22412.11
 SPAC2412.11
 SPAC22412.11
 SPAC22412.11
 SPAC22412.11
 SPAC22412.11
 SPAC2412.11
 SPAC440.00
 SPAC440.00
 SPAC40.00
 SPAC2412.11<





SPAC3A12.08 SPAC3A12.12LTR.SPAC3A12.15 SPAC3A12.08PAC3A12.10 SPAC3A12.14 SPAC9.09 SPAC9.11 SPAC9.10 SPAC3A12.02 tRNA_Cysteine SPAC9.04TR.29 LTR.28 SPAC9.05 SPAC5D6.09c SPAC5D6.106PAC5D6.08 SPAC20G8.06 SPAC3A12.18 genes - --- ---_ -1.460M SPAC9.03c 1.410M - 1.420M - 1.430M - 1.440M - 1.450M - 1.4
 SPAC9.07c
 1.480M
 1.490M

 SPAC9.066PAC9.08c
 tRNA_Methionine
 SPAC9.13cSPAC5D6.13
 1.400M SPAC20G8.05c 1.470M





genes

SPAC17A5.01 SPAC17A5.03 SPAC664.09 SPAC664.11 SPAC664.14 SPAC664.10 SPAC664.13 SPAC664.15 SPAC17A5.06 **SRAVA1646006RA**C17A5.12 SPAC17A5.14 SPAC17A5.08 SPAC17A**5RA**C17A5.13 SPAC664.05 SPAC664.05 SPAC1610.01 SPAC17A5.16 SPAC1002.01 SPAC16PA004002.02 tRNA_Lysine tRNA_Tyrosine _ _ ____ 1.700M SPAC824.09c SPAC664.02c SPAC664.01c SPAC664.04c SPAC664.07c 1.720M 1.730M 1.740M 1.750M 1.760M 1.770M SPAC664.12c tRNA_Lysine SPAC105.01c SPAC105.03c SPAC17A5.02cSPAC17A5.05c SPAC17A5.09c SPACUNK12.02c SPAC105.02c SPAC17A5.186PAC17A5.04c SPAC17A5.07c 1.790M _____ SPAC1610.02c SPAC1610.03c 1.780M SPAC17A5.15c







genes	SPAC17H9.02	SPAC17H9.07 SPLATCR1374H9.05 SPAC17H9.08	SPAC17H9.11 SPAC17H9.16	SPAC17H9.20 SPAC607.05 SPAC607.04	SPAC732.01 SPAC607.10	SPAC3C7.04	SPAC3C7.09 SPAC3C7.12 SPAC3C7.10	
genes	2.000 M SPAC17H9.	010M 2.020M 03c SPAC17H9.06c SPAC1 17H9.04c SPAC17H9.09c	7H9.10cSPAC17H9.132PAC137H9C11774 SPAC17H5PA2d7H9.5#AAC17H9.1	2.040M- 19.19c SPAC607.03c SPAC6079E 8c SPAC607.02c SPAC6079E	2.050M 2.060M 7AC607.09c SPAC3C7. 07.08c SPAC732.02c SF	2.070M .016PAC3C7.03c SPAC3C7.06c PAC3C7.02c SPAC3C7.05c SPAC	2.080M 2.090M SPAC3C7.08c SPAC3C7.136PAC2 3C7.07c SPAC3C7.11c	:5A8.03c GPAC25A8.01







genes

 SPAC13G7.06
 SPAC13G7.07
 SPAC13G7.07







genes	SPAC823.12 SP	03.14 SPAC7D4.148PAC7D4.12 PAC823.15 SPAC7D4.13c SPA	c SPAC7D4.0%PAC7D C7D4.11c SPAC7D4.07	4.06c S c SPAC7D4.	PAC7D4.02c .03c SPAC4F	SPAC4F8.13c 8.14c SPAC4F8	SPAC4F8.1	0c SPAC4F8.05c SPAC4F8.07c SPAC	SPAC644.04 4F8.02c	SPAC644 SPA C644.10 SPAC644 SPA C644.09 SPAC644.12	
2	.600M SPAC823.13c	2.610M SPAC823.16c	2.620M SPAC7D4.1SPAC7D4.08 SPAC7D4.15c	2.630M SPAC7D4.04 SPAC7D4.05	2.640M SPAC4F8.15	2.650M	2.660M SPAC4F8.11 SP	2.670M SPAC4F8.065PAC4F8 AC4F8.08 SPAC4F8.04 S	2.680M .03 SPAC644.05c tRNA_L PAC4F8.01 SPAC644.06c	ysine 2.690M	2644.14 13c







- -2.990M SPAC31G5.05c SPAC31G5.09c 2.900 M 2.910 A 2.920 2.980M SPAPB1A11.04c

_ _ _ _







SPAC6G10.0&PAC6G10.08 SPAC6G10.07 SPAC6G10.09 SPAC1486.06 SPAC1486.09 SPAC1486.08 SPAC1486.10 SPAC6G9.04 SPAC6G9.05 SPAC6G9.12 SPAC6G9.11 SPAC6G9.14 SPAPB1E7.05 SPAC6G9.08 SPAC652.01 LTR.52 SPAC1486.0 SPAPB1E7.03 genes SPAC1486.07c 3.210M 3.220M SPAC6G10.03&PAC6G10.05c SPAC6G10.02cSPAC6G10.04c - 3.240M - 3.250M SPAC6G10.5FAC6G9.01c SPAC6G9.03c SPAC6G105FAC6G9.02c **3.260M –** SPAC6G9.07c SPAC6G9.10c SPAC6G9.06c SPAC6G9.09c **3.270M** - **3.280M** - **3.290M** SPAC6G9.13c SPAC6G9.15c SPAPB1E7.01c SPAC6G9.13c SPAC6G9.16c SPAPB1E7.02c 3.200<mark>M</mark> 3.230M SPAPB1E7.06c





Taz1/notag

genes

0.0

3.400M

3.410M

3.420M

SPAC16E8.13SPAC16E8.16 SPAC16E8.15 SPAC17A2.12 LTR.58 SPAC17G6.03 SPAC17G6.06 SPAC17A2.11 SPAC16E8.02 SPAC16E8.03 SPAC16E8.08 SPAC16E8.09 SPAC1B1.01 SPAC17A2.05 _ **3.510M** SPAC16**58**A9426E8.06c SPAC16E8**395**AC16E8.07c 3.520M 3.530M SPAC16E8.\$9AC16E8.14c SPAC15E8.\$0C116E8.12c SPAC16E8.17c 3.540M SPAC1B1.02c SPAC1B1.04c SPAC1B1.03c SPAC17A2.03c SPAC17A2.03c SPAC17A2.03c SPAC17A2.03c SPAC17A2.03c SPAC17A2.09c 30M - 3.590M SPAC17A2.13c SPAC17G6.02c 3.500<mark>M</mark> 3.580M SPAC17G6.05c SPAC17G6.04c

3.450M

SPAC17A2.01

3.460M

3.470M

SPAC17A2.15

3.480M

3.490M



3.440M

3.430M





 SPAC1556.09E
 SPAC1556.09E
 SPAC1556.09E
 SPAC1F12F0AC1F12.09
 SPAC4H3.05
 SPAC4H3.06
 SPAC4H3.13
 SPAC1071.05PAC1071.06
 SPAC1071.11
 SPAC926.02

 SPAC1556.09E
 SPAC1556.09E
 3.800M
 3.820M
 3.820





0.0 4.030M 4.050M 4.070M 4.080M 4.090M 4.000M 4.010M 4.020M 4.040M 4.060M 4.0 rif1 2.0 0.0 4.080M 4.040M 4.090M 4.000M 4.010M 4.020M 4.030M 4.050M 4.060M 4.070M 4.0 Taz1/notag 2.0

0.0 4.000M 4.010M 4.020M 4.030M 4.040M 4.040M 4.050M 4.060M 4.070M 4.080M 4.080M 4.090M

genes	SPAC23A1.17	SPAC26H5.03 SPAC26H SPAC26H5.04	15.05 SPAC26H5.06	SPAC26H5.11 SPAC26H5.12	SPAC2588.0PAC2588.03 SPAC2588.02 SPAC2588.05	SPAC25B8:D8C25B8.10 SPAC25B8:09AC25B8.11	SPAC25B8.14SPAC25B8.17 SI SPAC25B8PMC25B8.18	PAC683.03
80	4.110M 4.110M SPAC23A1.12GPAC23A1.15c SPAC2 SPAC23A5PAG23A1.16c	4.120M 23A1.18&PAC26H5.02c SPAC23A1.19c	4.130M 4.1 SPAC26H5.08c SPA SPAC26H5.07c SPAC26H5.09	40M - 4.150M 40786965.10c c SPAC26H	4.160M SPAC25B8.04c SPA 5.13c SPAC25B8	4.170M 4. AC25B8.07c SPA 3.06c SPAC25B8.12c	180M 4.190M C25588.13c SPAC25B8.15c	19c SPAC683.02c







SPAC16.04 SPAC9E9.01 SPAC17C9.05c SPAC17C9.01 SPAC17C9.02c SPAC9E9.550AC17C9.15c SPAC17C9.11c SPAC9E57AC17C9.1680PAC17C9.13c SPAC17C9.09c
 SPAC29E6.02
 SPAC29E6.09

 SPAC29E6.01
 SPAC29E6.04
 SPAC29E6.08
 SPAC9E9.05 SPAC9E9.04 SPAC9E9.11 SPAC16.01 SPAC9E9.08 genes - ---4.410M SPAC29E6.05c SPAC29E6.03cSPAC29E6.06c 4.420M SPAC29E6.10c SPAC16.03c SPAC9E9.02 SPAC16.02c SPAC16.05cSPAC9E9.17c 4.450M SPAC9E9.06c SPAC9E9.07c 4.460M SPAC9E9.10c SPAC9E9.13 4.480M 4.490M SPAC17C9.14 SPAC17C9.10SPAC17C9.07 SPAC17C9.03 SPAC17C9.12 SPAC17C9.058PAC17C9.06 — 4.47о́М 4.400M SPAC30.04c



genes





 SPAC1834.05
 SPAC17894_08reconine
 SPAC17D4.01
 SPAC17D4.04
 SPAC458.05
 SPAC458.06
 SPAC458.06
 SPAC1782.01
 SPAC1782.11
 SPAC11H11.04
 SPAC22F8.04
 SPAC22F8.06

 SPAC1834.04
 SPAC1834.07
 SPAC17834.09
 SPAC17D4.02
 SPAC458.03
 SPAC458.06
 SPAC1782.01
 SPAC1782.07
 SPAC11H11.01
 SPAC11H11.06
 SPAC22F8.04
 SPAC22F8.06
 SPAC458.05
 SPAC458.06
 SPAC1782.01
 SPAC1782.07
 SPAC11H11.01
 SPAC11H11.06
 SPAC22F8.04
 SPAC22F8.06
 SPAC458.05
 SPAC458.05
 SPAC1782.01
 SPAC1782.07
 SPAC11H11.01
 SPAC11H11.06
 SPAC22F8.04
 SPAC22F8.04
 SPAC22F8.06
 SPAC458.05
 SPAC458.05
 SPAC458.05
 SPAC458.05
 SPAC458.05
 SPAC1782.01
 SPAC1782.07
 SPAC11H11.01
 SPAC11H11.06
 SPAC22F8.04
 SPAC22F8.06
 SPAC458.05
 SPAC458.05

4.700 4.710 4.720 4.720 4.720 4.720 4.730 4.720 4.730 4.740 4.750 4.740 4.750 4.750 4.760 4.770 4.750 4.780 4.750 4.790 4.790 4.790 5PAC1834.11c 5PAC1834.11c 5PAC1834.11c 5PAC1834.10c 5PAC17D4.03c 5PAC458.04c 5





0.0 4.930M 4.910M 4.920M 4.940M 4.950M 4.960M 4.970M 4.980M 4.990M 4.900M

SPAC22E12.12 SPAC22E12.15

SPAC22E12.07 SPAC22E12.08

SPAC22E12.18SPAC2E12.02 SPAC1006.01 SPAC22E12.19 SPAC2E12.05 SPAC1006.02

 SPAC890.05
 SPAC890.08
 SPAC890.08
 SPAC890.08
 SPAC22E12.02
 genes - - --____ 5.020M - 5.030M 5.040M 5.050M SPAC22E12.03c SPAC22E12.06c SPAC22E12.10c SPAC22E12.13c SPAC22E12.16c 90.07c SPAC22E12.05c SPAC22E12.09cSPAC22E122RNA_SPA022E12.14c SPAC22E12.17c 5.000 SPAC1952.17c SPAC890.04c SPAC890.02c SPAC890.07c

SPAC1006.06 SPAC1006.08 SPAC1250.04c SPAC1006.07 SPAC1006.09 5.060M - 5.080M SPAC2E12.03c LTR.82 5.070M SPAC1006.04c SPAC1006.03c SPAC1006.05c SPAC12500.03 SPAC5250.03 5.090M







genes

 SPAC11E3.12
 SPAC11E3.15
 SPAP8A3.05
 SPAP8A3.06
 SPAP8A3.07
 SPAP8A3.07<











genes

SPBC660.06 SPBC660**S9B**C660.10 PBC660.05 SPBC660.**3P**BC660.0**3**PBC660.11 SPBC660.14 SPBC660.15 SPBC660.16

0.200M 0.210M 0.220M 0.220M 0.220M 0.220M 0.240M 0.240M 0.250M 0.250M 0.260M 0.260M 0.260M 0.270M 0.280M 0.290M 0.

SPBC31E1.05 SPBC800.02 SPBC31E1.04\$PBC31E1.06 **SRRBA_2GW0.10**@mine SPBC800.06 SPBC800.09 SPBC800.08 SPBC800.13 tRNA_Alanine SPBC1773.04 SPBC800.11 SPBC1773.01







genes

SPBC1685.16 SPBC1685.05 SPBC1685.09 SPBC168539938C1685.04 SPBC1685.06 SPBC1**685409**685.11 SPBC354.12 SPBC354.15 SPBC354.13 SPBC1706.01 SPBC1685.13 SPBC649.03 SPBC649.05 SPBC649.0**2**PBC649.04SPBC354.01 SPBC354.03 SPBC354.04 SPBC354.06 tRNA_Glycine SPBC354.10 SPBC1706.03 SPBC839.02 - -0.580M SPBC354.14c OM - 0.530M SPBC1685.12c SPBC1685.15c 550M 0.570M 0.570M 0.570M 0.570M SPBC354.09c 0.570M 0.500<mark>M</mark> 0.540M 0.520M 0.550M -0.590M - -SPBC839.03c SPBC354.02c SPBC354.11c SPBC1700780205







genes

SPBC36.07 SPBC36.10 SPBC36.09 SPBC36.11 SPBC713.03 SPBC713.06 SPBC713.09 SPBC713.05 SPBC713.08SPBC713.10 SPBC216.02 SPBC530.08 SPBC36.04 0.890M 0.800N 0.820M - 0.830M - 0.820M - 0.830M - 0.840 0.06c SPBC530.09c SPBC530.11c SPBC530.12c SPBC530.14c SPBC36.01c SPBC36.02c **0.840M** SPBC36.03dTR.108 SPBC36.05c SPBC36.05c SPBC36.05c SPBC36.05c 0.870M SPBC36.12c SPBC713.02c SPBC713.02c **-0**.86о́М 0.880M SPBC713.07c SPBC216.01c

SPBC713.12



tRNA_Glutamic_acid SPBC530.13



0.0 1.030M 1.090M 1.000M 1.010M 1.020M 1.040M 1.050M 1.060M 1.070M 1.080M

genes

 SPBC1709.05/98021709.05/98021709.08
 LTR:SPIBC1709.12
 SPBC1709.17
 SPBC409.03
 SPBC409.03

 SPBC1709.03
 SPBC1709.19
 SPBC1709.14
 SPBC1709.18
 SPBC409.05
 SPBC4.05 SPBC4.06 _ **1.120M 1.130M 1.140M** SPBC1709.10cSPBC1709.13c SPBC1709.16c SPBC409.04c SPBC1709.11c SPBC1709.15c SPBC1709.19c SPBC409.07c 1.150M - 1.160M - 1.170M - 1.180M SPBC409.09c tRNA_Arginine SPBC409PBtc409.17c SPBC409.20c SPBC409.12c SPBC409.16cPBC409.19c SPBC1306.01c 1.190M SPBC4.02c SPBC4.04c SPBC4.03c _ 1.110M 1.180M SPBC1709 PBC1709.04c SPBC4.07c

SPBC409.08

SPBC409.10 SPBC409.11

 SPBC409.13
 SPBC409.18
 SPBC1306.02

 SPBC409.15
 SPBC409.21
 SPBC4.01





0.0 1.330M 1.360M 1.390M 1.300M 1.310M 1.320M 1.340M 1.350M 1.370M 1.380M

genes

SPBC17A**S/706**C17A3.08SPBC691.01 SPBC17A3.057PBC17A3.10

SPBC17A3.02

SPBC11B10.01 SPBC11B10.06 SPBC11B10.03 SPBC11B10.08 _ _
 1.400 M
 1.410 M
 1.410 M
 1.420 M
 1.430 M
 1.430 M

 SPBC17A3.01c
 SPBC17A3.04c
 SPBC17A3.09c
 SPBC691.03c
 SPBC22H7.02c
 SPBP22H7.02c
 1.450M SPBP22H3705C32H8.02c SPBC32H8.01c 1.480M SPBC32H8.13c SPBC32H8.12c 1.490M SPBC11B10.0#BC11B10.07c SPBC11B10.02EBC11B10.05c SPBC32H8.08c 1.460[′]M SPBC32H8.04c

SPBP22H57.08 SPBP22H7.07

SPBC32H8.095BC32H8.07 SPBC32H8.10 SPBC32H8.035PBC32H8.06 SPBC32H8.035PBC32H8.11



SPBP22H7.03 SPBP22H7.04

SPBC691.04





genes

SPBC11G11.05PBC11G11.05PBC11G11.07 SPR0A18Hyb0cp&an SPBC1D7.02c SPBC116PB00BIG11.05 SPBC18H10.02 SPBC18H10.07 SPBC18H**5**(78)4810.15 SPBC18H10.05 SPBC18H10.09 SPBC18H10.5 SPBC18H10.05 SPBC18H10.16
 SPB
 C19C2.14 SPBC2F12.14c
 SPBC2F12.11c
 SPBC2F12.03c
 SPBC2F12.05c
 SPBC2F12.02c

 SPBC190
 C.52*BC2F12.15c
 SPBC2F12.12c
 SPBC2F12.30c
 SPBC2F12.07c
 SPBC2F12.03c
 _ _ -_ _ _ 1.730M SPBC2F12.04 1.700M SPBC19C2.13c SPBC19C2.15c 1.740M – 1.750M SPBC1D7.04 SPBC1D7.05 SPBC1D7.03 - 1.760M -SPBC1D7.01 SPBC11G11.06c SPBC11G11.02c 1.710M SPBC2F12.13 1.720M 1.770M SPBC2F12.10 SPBC18H10.04c


























2.900M 2.910M 2.920M 2.920M 2.920M 2.920M 2.930M 2.940M 2.950M 2.960M 2.950M 2.950M 2.980M 2.980M 2.980M 2.980M 5PBC2ASP652A9.07c SPBC2A9.11c SPBC1703.13c SPBC1703.13c SPBC1703.13c SPBC1703.13c SPBC1703.13c SPBC2A9.06PBC2A9.06PBC2A9.08c SPBC2A9.03c SPBC2D10.09PBC2D10.09c SPBC2D10.10c SPBC2D10.10c SPBC2D10.10c SPBC2D10.09c SPBC2D10.09c SPBC2D10.09c SPBC2D10.09c SPBC2D10.09c SPBC2D10.15c SPBC2D10.09c SPBC2D





genes

3.200M 3.210M 3.220M 3.230M 3.250M 3.250M 3.250M 3.250M 3.250M 3.260M 3.270M 3.







genes

SPBC1105.01 02

SPBPB7E8

 3.500 M
 3.510 M
 3.520 M
 3.530 M
 3.540 M
 3.550 M
 3.560 M
 3.570 M
 3.580 M
 3.590 M

 SPBC1105.026 PBC1105.03c
 SPBC1105.03c
 SPBC1105.13c
 SPBC105.13c
 SPBC105.13c

SPBC887.08 SPBC887.07

- -

SPBC887.11 SPBC887.10 SPBC887.12 SPBC887.16 SPBC887.19 SPBC16D10.02 SPBC887.17 SPBC418.02 SPBC16D10.03

SPBC16010.05



 SPBC1105.06
 SPBC1105.09
 SPBC1105.12
 SPBC1105.\$\$

 SPBC1105.05
 SPBC1105.08
 SPBC1105.10
 SPBC1105.14
 SPBC887.01





 SPBC21C3.05
 tRNA_T\$P66024 C3.11
 SPBC21C3.18
 SPBC21C3.19
 SPBC23E6.02
 SPBC23E6.05
 SPBC23E6.09
 SPBC21.01
 SPBC211.06
 SPBC21604.20
 SPBC1604.20
 SPBC1604.20
 SPBC1604.20
 SPBC211.05
 SPBC211.05
 SPBC211.06
 SPBC211.07
 SPBC211.06
 SPBC211.07







 SPBC56F2.05
 SPBC56F2.05
 SPBC1861.02 SPBC56F2.06
 SPBC1861.02 SPBC56F2.06
 SPBC1861.02 SPBC1861.00
 SPBC1861.05 SPBC1861.04
 SPBC1861.09BC14F5.02 SPBC1861.06
 SPBC14F5.07 SPBC14F5.01
 SPBC14F5.07 SPBC14F5.06
 SPBC14F5.07 SPBC14F5.07
 SPBC14F5.07 SPBC14F5.07
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 SPBC14F5.07
 SPBC14F5.07
 SPBC14F5.07
 SPBC14F5.07
 SPBC1







SPBC8E4.05c

genes

SPBC1289.12 LTSPE059289.17 SPBC1289.11 LTRSPE0C1289.14 LTR.150SPBC1289.15 LTR.152 SPBC8E4.01c SPBP4G3.03 LTR.153 SPBC8E4.02c SPBP4G3.02 SPBPB2B2.02 SPBPB2B2.05 SPBPB2B2.01 SPBPB2B2.04 LTR.154 SPBPB2B2.08 SPBPB2B2.11 LTR.157 SPBPB2B2.13 4.400M SPBC1289.10c 4430M 4 SPBC1289.16c SPBC8E4.03 SPBC8E4.04 LTR.151 4.470M - 4.480M - 4.490M SPBPB2B2.06c SPBPB2B2L09c155 SPBPB2B2.12c SPBPB SPBPB2B2.07c SRBRB22B2.10c SPBPB SPBPB2B2.14c SPBPB2B2.16c 4.420M - 4.440M 4.450M 4.410M 4.460M _____ SPBC1289.13c SPBPB2B2.03c

SPBPB2B2.15









genes

SPCC1235.11 SPCC1235.13 SPCC1235.15 SPCC1235.14 SPCC794.03 SPCC794.02 SPCC553.09c SPCC553.07c SPCC553.08c SPCC1529.01 SPCC794.07 SPCC794.06 SPCC794.08 SPCC553.12c SPCC799705553.11c SPCC794.10 SPCC548.04 LTR.175 -----07220M 0.230M LTR.1502C548.03c SPCC548.06c SPCC548.02c ISPCC548.05c SPC LTR.171 LTR.172 0.280M SPCC794.09c SPCC794.11c SPCC794.11c OM - 0.290M SPCC553.10 SPCC553.06 SPCC5**53.0**574 0.200 M SPCC1235.12c 0.240M SPCC794.01c 0.210M 0.250M **-** 0.260M SPCC794.04c SPCC548.07c







genes

SPCC970.04c

SRC0970.07c

SPCP31B10.03c 0.500 M LTR 185PCC970.06 SPCC970.08CC970.12 SPCC970.05 SPCC970.082CC970.01 0.550M 0.560M 0.570M SPCC962.02c SPCC962.06c SPCC1672.05c SPCC962.0Bc182 SPCC1672.02c SPCC1672.02c 0.580M SPCC1672.08c 0.590M SPCC1672.12c SPCC1183.04c SPCC1672.11c SPCC1183.05c 0.520M 0.540M SPCP31B10.08c

SPCC962.05 SPCC962.04 SPCC1672.01

SPCC1183.02 SPCC1183.01

SPCIENNA7281977hine SPCC1672.10 SPCC1672.09



SPCC10H5P.0231B10.04 SPCP31B10.06 SPCC962.01 SPCC10H11.0PCP31B10.02CP31B10.05 SPCP31B10.07





 SPEC1393.05
 SPCC1393.10SPCC1393.12
 SPCC2HRC02H8.04
 SPCC63.04
 SPCC63.04
 SPCC63.14
 SPCC16A11.02
 SPCC16A11.07
 SPCC16A11.11
 SPCC16A11.14

 0.800M
 0.800M
 0.820M
 0.820M
 0.830M
 0.840M
 0.840M
 0.850M
 0.860M
 0.870C
 SPCC16A11.05c
 SPCC16A11.05c
 SPCC16A11.05c
 SPCC16A11.05c
 SPCC16A11.05c
 SPCC16A11.10c
 SPCC16A11.10c<







70000	tRNA_Leជាដាង_នារូវភើលាe tRNA_Threonine	SPCC4B3.10c SPCC4B3.06c SPCC4B3.04c SPCC4B3.02c SPCC550.05 SPCC4B3.01% SPCC4B3.05c SPCC4B3.03c SPCC2B3.03c SPCC550.07
genes	1.100M '' 1.110M 1.120M 1.130M tRNA_Valine tRNA_Asparagine	1.140M 1.150M 1.160M 1.170M tRNA_Lysine SPCC4B3.16SPCC4B3.15PCC4B3.12 1.160M 1.170M 1.180M 1.190M tRNA_Phenylalanin®PCC4B3SIPCC4B3.15SPCC4B3.13 SPCC4B3.08 SPCC4B3.01 SPCC550.04c SPCC550.04c





genes

SPCC11E10.03PCC11E10.04 SPCC61.05 SPCC11E10.03 SPCC188.02 SPCC188.05 LTRSP303C11E10.08 tRNA_Lysine SPCC188.03 **SFRC1622.21** SPCC62**2F0**2C622.07 SPCC1281.08 SPCC6225**P2**C622.05SPCC622.09 SPCC62**2**.19 SPCC61.03 SPCC622.18 SPCC61.02 SPCC622.14 SPCC188.07 _ SPCC61.01c 1.450M DM 1.460M 1.470M 1.470M 5PCC11E10.07c SPCC11E10.02c SPCC11E10.056R.195 SPCC11E10.09c 1.480M SPCC188.04c SPCC188.06c 1.490M SPCC188.08c SPCC188.09c SPCC188.10c

LTR.197



SPCC622.11



genes

____ 1.700M SPCC417.15 1-710M---- 1.720M SPCSP0C032.05c LTR.205 SPCC19P022591.04c SPCC191.09c OM 1.780M 1.780M 5PCC1442.056PCC1442.08c SPCC1442.1162PCC1564642.16c SPCCRN42324468PCC1442.07c SPCC1442.1065PCC156442.17c 1.770M



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genes

 SPCC4F11.02
 SPCC1906.01
 SPCC1906.04
 SPCC1739.03
 tRNA_Glycin& C1739.07
 SPCC1739.07
 SPCC1739.12
 SPCC1739.13
 SPCC1739.15
 SPCPB1C11.01
 SPCC576.04
 SPCC576.07
 SPCC576.09
 SPCC576.09</th

00	M <u>2.0</u> 10M		2 .0 30M	2.040M -	2.050M	2.060M	2.070M	2.080M -	2.090M — — —
	SPCC4F11.03c	SPCC1906.02c LTR.213	SPCC1739.04c	SPCC1739.08c	SPCC1739.11c			SPCC576.19c	SPCC576.06c SPCC576.10c
	SPCC4F11.04c	LTR.212	SPCC1739.02c SF	PCC1739.06c SPCC1	739.09c		tRNA_Glut	amine SPCC576.01c SPCC576.03c	SPCC576.08c





SPCC965.09 SPCC965.12 SPCC965SP3CC1494.01 SPCC965.14c SPCC1494.07 SPCC1827.04 LTR.232 SPCP1E11.03 SPCP1E11.02 SPCC70.06 SPCC1494.03 SPCC1494.10 SPCC70.10 genes 2.300M SPCC965.11c 2:320M - 2:330M LSRC250494.11c SPCC1494.05c SPCC1494.02c LTRSPECC1494.04c SPCC1494.06c 2.340M - -SPCC1494.08c SPCC1494.09c 2.350M SPCC70.02c SPCC70.04c SPCC70.03c 2.390M 2.380M 2.390M SPCC70007670.09c SPCC1827.05FCC1827.03c SPCC1827.06c SPCC70.08ECC1827.08cSPCC1827.02c SPCC1827.05cPCC1827.07c 2.360M 2.310M SPCP1E11.04c SPCP1E11.05c SPCC70.05c



chrIII_9



chrM

