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# The Phylogeny of Glyceraldehyde-3-Phosphate Dehydrogenase Indicates Lateral Gene Transfer from Cryptomonads to Dinoflagellates

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Sequence analysis of two nuclear-encoded Abstract. glyceraldehyde-3-phosphate dehydrogenase (GAPDH) genes isolated from the dinoflagellate Gonyaulax polyedra distinguishes them as cytosolic and chloroplastic forms of the enzyme. Distance analysis of the cytosolic sequence shows the Gonyaulax gene branching early within the cytosolic clade, consistent with other analyses. However, the plastid sequence forms a monophyletic group with the plastid isoforms of cryptomonads, within an otherwise cytosolic clade, distinct from all other plastid GAPDHs. This is attributed to lateral gene transfer from an ancestral cryptomonad to a dinoflagellate, providing the first example of genetic exchange accompanying symbiotic associations between the two, which are common in present day cells.

**Key words:** Glyceraldehyde-3-phosphate dehydrogenase — Gene transfer — Cryptomonads — Dinoflagellates

### Introduction

Dinoflagellates have features that make their phylogenetic affinities and evolutionary history enigmatic. Their nuclei contain up to 200 pg DNA per nucleus (Holm-Hansen 1969) and lack histones (Rizzo 1981), while the chromosomes remain permanently condensed through the S phase (Grasse and Dragesco 1957). Mitosis is distinct from that of other eukaryotes (Spector et al. 1981); there is no spindle and chromosomes are segregated by attachment to the nuclear envelope, which remains intact throughout.

Phylogenetic analysis based on large nuclear-encoded ribosomal RNA sequences has placed the dinoflagellates with ciliates and apicomplexans (Baroin et al. 1988; Gajadhar et al. 1991; Lenaers et al. 1991; Woese 1987). However, about 50% of dinoflagellate species are photosynthetic, with chloroplasts surrounded by a triple membrane; whether this is explained by capture of prokaryotic or eukaryotic endosymbionts is debated (Gibbs 1981a). In addition, most contain the carotenoid peridinin, which to date has been found only in dinoflagellates (Jeffrey et al. 1975; Loeblich 1976).

We have obtained the sequence of two glyceraldehyde-3-phosphate dehydrogenase (GAPDH) genes from *Gonyaulax polyedra*, a photosynthetic dinoflagellate. GAPDH has been extremely useful in phylogenetic analysis, notably in demonstrating a symbiotic origin of chloroplasts in vascular plants (Shih et al. 1986; Martin and Cerff 1986; Martin et al. 1993). It is highly conserved and its genes have been sequenced from a large number of different taxa. All known plastid-containing eukaryotes have two different forms of the enzyme (Cerff 1995; Martin and Schnarrenberger 1997). One, a glycolytic enzyme, specific for NAD<sup>+</sup>, is typically found in the cytosol. A second form, found in chloroplasts, can utilize both NAD<sup>+</sup> and NADP<sup>+</sup> and is involved in Calvin cycle reactions. We report here that the phylogeny of the

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cytosolic form of (GAPC) is consistent with previous nuclear ribosomal RNA analysis. However, as in the case of the recently reported cryptomonads (Liaud et al. 1997), the chloroplast form (GAPCp) is different from that found in all other plastids.

#### **Materials and Methods**

Clones for GAPDH were obtained by polymerase chain reaction and by screening of a G. polyedra cDNA library. Sequences were determined using the dideoxy chain termination method (Sanger et al. 1977), and their identities determined by BLAST searches of the NCB1 sequence data banks (Altschul et al. 1990). The forward degenerate primer GAPP 5a (TCSAACGCNTCSTGYACBAC), which codes for the conserved peptide sequence SNASCTT, surrounding the GAPDH catalytic cysteine residue, was used with the vector primer T7 to amplify a 765-bp fragment from a Gonyaulax cDNA library directionally cloned into the  $\lambda$  Zap vector. This fragment had significant homology with mammalian GAPDH genes and allowed design of the nondegenerate antisense primer GAPP 27 (CACAAAACAAGCGAGCTTCACTC), which, together with the vector primer T3, amplified a 1.3-kb product from the same library. This product contained a complete open reading frame which, based on sequence, was predicted to encode a GAPDH enzyme. GAPP 5a was also used together with the reverse degenerate primer GAPP 4a (RATSGGGTTVGTCTCSARSTC), the complement of which encodes the peptide DLETNPI, originally identified by peptide sequences of proteins isolated from 2D gels (Markovic et al. 1996), to amplify a 430-bp fragment. This fragment was then used to create the reverse primer GAPP 4b (TAGTCTCGAAGTCTGTGGACAC), which, together with the vector primer T3, amplified a 1.1-kb clone. This was used to isolate a 1.4-kb cDNA clone from the library, which, though different in sequence from the 1.3-kb clone, also contained a complete open reading frame and showed sequence similarities to GAPDH genes from other organisms.

Sequences from a wide range of species were utilized in order to obtain a comprehensive picture of GAPDH phylogeny. Sequences were aligned using ClustalW (Thompson et al. 1994) and adjusted manually; the N- and C-terminal ends of the sequences were trimmed to yield a common block of sequences 339 amino acids long, and equivocal residues were removed. Parsimony analysis was carried out using PAUP Version 3.1.1 written by David L. Swofford, and the 50% majority rule consensus tree was retained after a heuristic search of 100 bootstrap resamplngs. Distance analysis was carried out using software in the Phylogeny Inference Package (PHYLIP) Version 3.572, by Joseph Felsenstein, University of Washington. The Dayhoff PAM matrix was used to generate distance matrices (Protdist) from 100 bootstrap resamplings (Seqboot). The majority-rule consensus tree was computed (Consense) after unrooted trees were generated from the distance matrices by the neighbor joining method (Neighbor). Branch lengths were obtained from an unbootstrapped distance matrix using the unrooted consense tree as a user tree (Fitch). The consense tree is graphically displayed using TreeView 1.5 (Page 1996). The sequences used can be obtained from GENBANK using the following accession numbers: Anabaena 1, P34916; Anabaena 2, P34917; Arabidopsis A, P25857; Arabidopsis C, P25858; Chlamydomonas A, P50362; Chlamydomonas C, P49644; Chondrus A, P34919; Chondrus C, P34920; Drosophila, P07486; E. coli 1, P06977; E. coli 2, P11603; Euglena A, P21904; Euglena C, L21903; Giardia, M88062; Gonyaulax C, AF028562; Gonyaulax Cp, AF028560; Gracillaria C, P54270; Gracillaria A, P30724; Guillardia C, U39873; Guillardia Cp, U40032; Methanothermus, P19314; Neurospora, P54118; Pinus A, P12859; Pinus Cp, L07501; Pisum A, P12859; Pyrenomonas C, U39897; Pyrenomonas Cp, U40033; Pyrococcus, P20286; Rhodobacter, P29272; Saccharomyces, P00360; Sulfolobus, P39460; Synechocystis, P49433; Trypanosoma C, P10097; and Xenopus, P51469. The alignment is available upon request.

#### **Results and Discussion**

Two cDNAs encoding GAPDH were isolated from *Gonyaulax polyedra*, and though slightly different in size (~1.3 and ~1.4 kb), both show homology to cytosolic forms of GAPDH from other eukaryotes. The 1.3-kb form (GAPC) encodes a cytosolic enzyme (see below); it contains a 1029-bp open reading frame, predicting a protein of 36 kDa, similar to the 32 to 36 kDa reported for other cytosolic GAPDH enzymes.

Two lines of evidence indicate that the 1.4-kb form encodes a protein (GAPCp) localized to the chloroplast. First, it contains a presequence indicative of chloroplast targeting. Its 1275-bp open reading frame encodes a ~45kDa protein, considerably larger than the cytosolic form, but similar in mass to the 42 and 48 kDa for chloroplast GAPDH precursors from Arabidopsis and Pisum, respectively (Brinkmann et al. 1989; Shih et al. 1991, 1992) (Fig. 1a). Although the cleavage site has not been determined, the molecular mass of the mature protein (38-40 kDa; data not shown) is consistent with the removal of a presequence. In addition, the N-terminal region of the G. polyedra GAPCp is similar to those found in other chloroplast-localized proteins in dinoflagellates (Le et al. 1997) and Euglena (Chan et al. 1990; Henze et al. 1995; Sharif et al. 1989) (Fig. 1b), These N-terminal regions have in common a typical signal peptide structure (von Heijne 1986) with a charged N terminus, followed by a hydrophobic core and peptidase cleavage site, and a second region rich in hydroxylated and charged residues, containing another hydrophobic stretch (Fig. 1b). The similarity to the Euglena sequences, which are involved in directing proteins to the chloroplast via the endoplasmic reticulum (Kishore et al. 1993), suggests that proteins may be likewise targeted to plastids in dinoflagellates. Also, the chloroplasts in both groups are surrounded by a triple membrane, which in *Euglena* has been shown to be associated with the endoplasmic reticulum (Gibbs 1981b).

Second, a chloroplast location of the GAPCp is indicated by the identity of three key amino acid residues involved in nucleotide binding, which differ in the cytosolic and chloroplastic forms of the enzyme (Fig. 2) (Clermont et al. 1993). Eukaryotic cytosolic forms, which typically fulfill a catabolic role in glycolysis and are NAD<sup>+</sup> specific, have conserved aspartate, glycine, and proline residues at positions 32, 187, and 188, respectively, numbered as in *Bacillus* (Biesecker et al. 1977). Plastid GAPDHs, which typically have an anabolic role and are able to utilize both NAD<sup>+</sup> and NADP<sup>+</sup>, have substitutions at these positions. In *G. polyedra* the residues are indeed conserved in GAPC, confirming its identity as a cytosolic form, but not in GAPCp, where alanine occurs at positions 32 and 188, and serine at 187.

Based on the deduced amino acid sequence, *G. polyedra* GAPCp is less than 42% identical to the previously known chloroplast forms of vascular plants, chloro-



Fig. 1. A Hydrophobicity plot of *G. polyedra* GAPDH sequences, obtained using the Protean module of the DNASTAR (Madison, WI) package based on parameters of Kyte–Doolittle (1982). GAPC is the cystolic isoform, while GAPCp, with its additional N-terminal sequence, is the chloroplast form. **B** N-terminal amino acid sequences of nuclear-encoded chloroplast targeted proteins. G.p., *Gonyaulax polyedra:* E.g., *Euglena gracilis;* GAPCp, this paper; PCP, peridinin–

phytes, and rhodophytes, which among themselves are greater than 60% identical (Fig. 3). Indeed, excluding the N-terminal presequence, the G. polyedra GAPCp is more identical to the cytosolic than to the chloroplastic form of GAPDH found in other eukaryotes. However, G. polyedra GAPCp exhibits a high sequence similarity to the recently reported (Liaud et al. 1997) chloroplast GAPDH sequences from two cryptomonads, Guillardia theta and Pyrenomonas salina (67 and 68%, respectively). An analysis of the cryptomonad sequences suggested that they may have been derived from proteobacteria (Liaud et al. 1997), as proposed previously for the G. polyedra RuBisCO gene (Morse et al. 1995). Irrespective of their origin, it is clear from the amino acid sequence comparisons that dinoflagellate and cryptomonad plastid GAPCp proteins are similar to one another and different from GAPDHs found in other chloroplasts.

In order to obtain a more detailed picture of the evolution of *G. polyedra* GAPDH genes, phylogenetic analyses were performed using sequences from a broad array of taxa. Similar tree topologies were obtained with either maximum-parsimony or distance analysis (Fig. 2). In both analyses the taxa fall into three main clades: (i) chlorophyll a binding protein (Lee et al. 1997); GAPA, chloroplast glyceraldehyde-3-phosphate dehydrogenase (Henze et al. 1995). The symbols +, -, and  $\bigcirc$  refer to positively charged, negatively charged, and hydroxylated amino acids, respectively. Hydrophobic regions are *underlined. Superscripted numbers* identify amino acids positions. The N-terminal amino acids of the mature proteins are unknown.

the Archaea, which was used as an outgroup in the parsimony analysis; (ii) plastids of most higher plants and algae together with the eubacteria; and (iii) primarily eukaryotic cytosolic sequences.

In the parsimony analysis the cyanobacterial sequences (*Synechocystis* and *Anabaena*) appear as a polytomy with the red alga and vascular plant sequences, while the distance analysis shows modest support for earlier branching of the cyanobacterial lineages. The analyses are thus consistent with a cyanobacterial origin of chloroplasts in vascular plants and rhodophytes. Somewhat unexpectedly (as cyanobacteria are also thought to be the origin of *Euglena* chloroplasts), the *Euglena* lineage is more deeply rooted than the cyanobacterial branches. It may be noted that the *Euglena* sequence contains many insertions not present in GAPDH genes from other taxa.

The topology of the cytosolic clade is less well defined, and not all nodes are well supported. The high degree of similarity between the cytosolic sequences compromises reliable tree resolution and produces the polytomy and poorly supported branches observed in the parsimony and distance analyses, respectively. NevertheParsimony

## Distance



**Fig. 2.** Phylogenetic analysis of 33 GAPDH sequences generated by maximum parsimony (length = 2493 steps, CI = 0.606, RI = 0.629, RC = 0.381) and by distance analysis. Dinoflagellate and cryptomonad branches are shown in *boldface*, with the chloroplast sequences *underlined*. Both trees separate archaeal (i), plastisd (ii), and cytosolic (iii) sequences with similar topology. Bootstrap support is given as the number of times a given node appeared in 100 reiterations; those with values below 50 are shown as polytomies. Where two values are shown, the second was obtained from an analysis of the eukaryotic

less, apart from the E. coli/T. brucei clade, which has previously been observed as an outgroup to the vertebrate and plant clades, the branching order is consistent with a previously reported phylogenetic analysis (Martin et al. 1993). In particular, the relatively late branching of the cryptomonad cytosolic sequences has been previously documented (Liaud et al. 1997). Three chloroplast targeted sequences, which unexpectedly fall into the cytosolic clade, have been described previously. Two are the cryptomonad chloroplast GAPDH sequences, described above. The other, from the gymnosperm Pinus sylvestris, is thought to be derived from the introduction of a chloroplast-targeting sequence to the N terminal of the plant cytosolic isoform (Meyer-Gauen et al. 1994). The function of this isoform is unclear, as it lacks the necessary modifications for binding NADP<sup>+</sup> used in the Calvin cycle; it has been suggested that it may play a role in "chlororespiration" (Liaud et al. 1997).

subset using *Anabaena* 1 as an outgroup. In the distance analysis the scale bar represents the number of substitutions per site. The branch length between the outgroup (i) and the rest of the tree is greater than can be represented by the diagram, indicated as a *break* in the line. *Filled circles* indicate the presence of aspartate<sup>32</sup>, glycine<sup>187</sup>, or proline<sup>188</sup> in a given sequence, indicative of a specificity for NAD<sup>+</sup>, while substitutions in these positions (*open circles*) are indicative of a dual specificity and chloroplast localization.

Both parsimony and distance analyses place the NAD<sup>+</sup> specific *G. polyedra* GAPC sequence within the cytosolic clade (Fig. 2). Distance analysis shows branching close to and before *Giardia* and *Chlamydomonas* but the bootstrap support is weak. Reanalysis of the cytosolic clade, with the *Anabaena* 1 sequence as the outgroup, reveals the same overall topology but with better support values.

The phylogeny of the chloroplast form of the enzyme (GAPCp) places it outside the plastid clade, where most of the other plastid forms are found. In both analyses there is a well-supported grouping of the *G. polyedra* and cryptomonad GAPCp sequences within the cytosolic clade, well separated from the chloroplast forms of other eukaryotes (Fig. 2). The distance analysis shows this group branching deeply within this clade. Reanalysis of the cytosolic subset reveals the same branching order, with even higher support values (Fig. 2).

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0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.055         0.0</th><th>0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</th><th>886 0.8<br/>885 0.8<br/>553 0.5<br/>555 0.</th><th><ul> <li>5</li> <li>0.86</li> <li>5</li> <li>0.86</li> <li>0.58</li> <li>0.58</li> <li>0.53</li> <li>0.57</li> <li< th=""><th>0.87<br/>0.57<br/>0.57<br/>0.55<br/>0.55<br/>0.55<br/>0.55<br/>0.58<br/>0.58<br/>0.58<br/>0.58</th><th>0.87 (0.87 (0.87 (0.87 (0.87 (0.86 (0.86 (0.86 (0.055 (0.055 (0.057 (0.055 (0.057 (0.055 (0.0</th><th>0.0.87 0.0.87 0.0.88 0.0.0.86 0.0.0.86 0.0.0.86 0.0.0.86 0.0.0.55 0.0.0.0.</th><th>84 0.85 0.85 0.85 0.85 0.85 0.85 0.85 0.85</th><th>3 0.84<br/>9 0.86<br/>9 0.51<br/>9 0.51<br/>9 0.51<br/>9 0.51<br/>9 0.51<br/>9 0.52<br/>9 0.52<br/>9 0.51<br/>9 0.52<br/>9 0.52</th><th>0.286         0.286         0.285         0.285         0.285         0.285         0.285         0.256         0.255         <td< th=""><th>0.0.2540.<br/>0.0.2540.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.0.5510.0.5510.0.5510.0.55100.0.</th></td<></th></li<></ul></th></th></th0<></th0.85<> | 5         0         86         4         0         86           0         5         1         1         0         57         1         0         53         1         0         53         3         3         3         1 <th>0.86 0<br/>0.85 0<br/>0.55 0<br/>0.55 0<br/>0.55 0<br/>0.55 0<br/>0.49 0<br/>0.49 0<br/>0.49 0<br/>0.49 0<br/>0.49 0<br/>0.49 0<br/>0.49 0<br/>0.41 0<br/>0.42 0<br/>0.43 0<br/>0.53 0<br/>0<br/>0.53 0<br/>0<br/>0.53 0<br/>0<br/>0.55 0<br/>0<br/>0.55 0<br/>0<br/>0.55 0<br/>0<br/>0.55 0<br/>0<br/>0.55 0<br/>0.55 0<br/>0000000000</th> <th>2.86 0.8<br/>2.87 0.8<br/>2.55 0.5<br/>2.55 0.55 0.55 0.55 0.55 0.55 0.55 0.55</th> <th>886 0.87<br/>886 0.87<br/>855 0 0.56<br/>855 0 0.55<br/>855 0 0.55<br/>855 0 0.55<br/>85 0 0.55</th> <th>0.86<br/>0.53<br/>0.53<br/>0.53<br/>0.53<br/>0.53<br/>0.53<br/>0.53<br/>0.53</th> <th>0.85         0.85         0.85         0.85         0.055        
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   | 886 0.8<br>885 0.8<br>553 0.5<br>555 0.  | <ul> <li>5</li> <li>0.86</li> <li>5</li> <li>0.86</li> <li>0.58</li> <li>0.58</li> <li>0.53</li> <li>0.57</li> <li< th=""><th>0.87<br/>0.57<br/>0.57<br/>0.55<br/>0.55<br/>0.55<br/>0.55<br/>0.58<br/>0.58<br/>0.58<br/>0.58</th><th>0.87 (0.87 (0.87 (0.87 (0.87 (0.86 (0.86 (0.86 (0.055 (0.055 (0.057 (0.055 (0.057 (0.055
(0.055 (0.0</th><th>0.0.87 0.0.87 0.0.88 0.0.0.86 0.0.0.86 0.0.0.86 0.0.0.86 0.0.0.55 0.0.0.0.</th><th>84 0.85 0.85 0.85 0.85 0.85 0.85 0.85 0.85</th><th>3 0.84<br/>9 0.86<br/>9 0.51<br/>9 0.51<br/>9 0.51<br/>9 0.51<br/>9 0.51<br/>9 0.52<br/>9 0.52<br/>9 0.51<br/>9 0.52<br/>9 0.52</th><th>0.286         0.286         0.285         0.285         0.285         0.285         0.285         0.256         0.255         <td< th=""><th>0.0.2540.<br/>0.0.2540.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.0.5510.0.5510.0.5510.0.55100.0.</th></td<></th></li<></ul> | 0.87<br>0.57<br>0.57<br>0.55<br>0.55<br>0.55<br>0.55<br>0.58<br>0.58<br>0.58<br>0.58  | 0.87 (0.87 (0.87 (0.87 (0.87 (0.86 (0.86 (0.86 (0.055 (0.055 (0.057 (0.055 (0.057 (0.055 (0.0  | 0.0.87 0.0.87 0.0.88 0.0.0.86 0.0.0.86 0.0.0.86 0.0.0.86 0.0.0.55 0.0.0.0.   
  | 84 0.85 0.85 0.85 0.85 0.85 0.85 0.85 0.85  | 3 0.84<br>9 0.86<br>9 0.51<br>9 0.51<br>9 0.51<br>9 0.51<br>9 0.51<br>9 0.52<br>9 0.52<br>9 0.51<br>9 0.52<br>9 0.52  | 0.286         0.286         0.285         0.285         0.285         0.285         0.285         0.256         0.255 <td<
th=""><th>0.0.2540.<br/>0.0.2540.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.<br/>0.0.5510.0.5510.0.5510.0.5510.0.55100.0.</th></td<> | 0.0.2540.<br>0.0.2540.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.<br>0.0.5510.0.5510.0.5510.0.5510.0.55100.0.  |
| C.86         0.85         0.85         0.85         0.86         0.85         0.86         0.86         0.88         0.44         0.44         0.44         0.20         0.21         272         124         127         127         127         127<  
   
   
   | 0.87         0.87         0.87           0.450         0.48         0.48           0.255         0.23         0.23           0.21         0.21         0.21           0.21         0.21         0.21           0.13         0.11         0.13           1         0.13         0.01           31         -         0.03           331         -         0.03           94         86         91           94         88         91           94         111         107           111         107         178           183         184         183           185         183         184           180         180         180           170         178         178  | 0.86 0.85<br>0.51 0.51<br>0.26 0.25<br>0.26 0.23<br>0.26 0.22<br>0.27 0.28<br>0.27 0.28<br>0.27 0.28<br>0.27 0.28<br>0.27 0.28<br>100 108<br>173 170<br>190 199<br>190 199<br>190 191<br>190 191<br>190 191   | 0.85         0.85         0.0           0.47         0.47         0.4           0.023         0.3         0.3           0.027         0.23         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.030         0.3         0.3           0.30         0.3         0.3           0.30         0.3         0.3           1         1         1           1         1         1           1         1         1           1         1         1   
   
   
  | 4         0.83           8         0.52           0.52         0.54           0.53         0.52           0.53         0.52           0.53         0.53           0.53         0.55           0.53         0.53           0.53         0.53           0.53         0.53           0.53         0.53           0.53         0.53           0.53         0.53           1.54         1.24           1.54         1.54  
   
   | 0.85     0       0.51     0       0.51     0       0.51     0       0.51     0       0.49     0       0.49     0       0.49     0       0.49     0       0.49     0       0.49     0       0.49     0       0.49     0       0.49     0       0.44     0       0.44     0       0.44     0       0.44     0       0.44     0       0.44     0       0.44     0       1.42     1   
   
  | 0.87 0.87 0.8<br>0.58 0.6<br>0.55 0.6<br>0.55 0.6<br>0.55 0.6<br>0.55 0.6<br>0.55 0.5<br>0.55 0.5<br>0.55 0.5<br>0.55 0.5<br>0.55 0.5<br>0.55 0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5   
  | 86 0.87<br>57 0.56<br>55 0.55<br>55 | 0.85<br>0.53<br>0.51<br>0.51<br>0.52<br>0.52<br>0.53<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52  | 0.85 C 0.85 C 0.85 C 0.52 C 0.52 C 0.55 C 0.   
  | 0.86         0.         0   
   | 85 0.85 0.85 0.85 0.85 0.85 0.85 0.85 0.  
  | 55         0.866           33         0.586           33         0.587           33         0.573           33         0.573           33         0.573           33         0.573           33         0.573           34         0.573           35         0.573           36         0.574           37         0.574           38         0.574           39         0.574           30         0.574           31         0.574           32         0.574           32         0.574           32         0.574           32         0.574           32         0.574           33         0.574           34         0.574           35         0.435           36         0.574           37         0.574           38         0.574           39         0.574           30         0.574           31         0.574           32         0.574           33         0.574           34         0.574 <th>0.87<br/>0.57<br/>0.57<br/>0.55<br/>0.55<br/>0.55<br/>0.55<br/>0.55<br/>0.5</th> <th>0.86 (0.55 (</th> <th>0.86         0.           0.053         0           0.055         0           0.055         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0</th> <th>85 0.8'<br/>54 0.5'<br/>55 0.5'<br/>55 0.5'<br/>55 0.5'<br/>55 0.5'<br/>57 0.5'<br/>57 0.5'<br/>57 0.5'<br/>41 0.5'<br/>41 0.5'<br/>41 0.5'<br/>41 0.3'<br/>41 0.5'<br/>51 0.5'<br/>55 0.5</th> <th>3     0.86       2     0.51       1     0.51       2     0.52       2     0.52       3     0.52       3     0.52       3     0.52       4     0.52       0     0.49       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54</th> <th>0.85         0           0.56         0           0.56         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0</th> <th>0.0.3600.000000000000000000000000000000</th>  
   | 0.87<br>0.57<br>0.57<br>0.55<br>0.55<br>0.55<br>0.55<br>0.55<br>0.5   | 0.86 (0.55 (  | 0.86         0.           0.053         0           0.055         0           0.055         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0           0.056         0   
   | 85 0.8'<br>54 0.5'<br>55 0.5'<br>55 0.5'<br>55 0.5'<br>55 0.5'<br>57 0.5'<br>57 0.5'<br>57 0.5'<br>41 0.5'<br>41 0.5'<br>41 0.5'<br>41 0.3'<br>41 0.5'<br>51 0.5'<br>55 0.5 | 3     0.86       2     0.51       1     0.51       2     0.52       2     0.52       3     0.52       3     0.52       3     0.52       4     0.52       0     0.49       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54       0     0.54   | 0.85         0           0.56         0           0.56         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.58         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0           0.55         0  | 0.0.3600.000000000000000000000000000000  
   |
| 275-     0.50     0.48     0.48       275     162     0.35     0.33       280     156     116     7     0.2       281     156     114     70     44       283     157     112     70     44       281     160     114     70     44       281     156     112     70     44       281     156     112     70     37       281     160     114     70     37       281     156     112     70     37       281     154     124     96     87       274     154     124     96     87       272     168     174     178     170       275     160     165     165     165     167       275     161     165     164     182       275     161     165     182     182       275     195     195     182     182       275     161     165     182     182       275     161     165     182     182       279     195     185     182     182       279     171     167     182  
   
   
   | 0.48         0.48           0.35         0.34           0.25         0.34           0.21         0.21           0.13         0.11           1         0.13           1         0.13           1         0.13           1         0.13           1         0.09           8         8           8         8           94         88           111         107           174         170           183         184           183         184           185         158           185         173           185         173           186         173           180         180           180         180           177         178   | 0.51 0.53<br>0.40 0.39<br>0.26 0.27<br>0.26 0.27<br>0.26 0.27<br>0.28 0.28<br>- 0.08<br>- 100<br>- 1000<br>- 100<br>- 100<br>- 100<br>- 1000<br>- 1000<br>- 1000<br>- 1000                | 0.47         0.47         0.4           0.038         0.4         0.3           0.029         0.3         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.027         0.3         0.3           0.030         0.3         0.3           0.1030         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300         0.3         0.3           0.300<  
   
   
  | 8 0.52<br>1 0.53<br>2 0.54<br>2 0.52<br>2 0.53<br>3 0.53<br>3 0.53<br>0 0.53<br>1 12<br>0 53<br>1 12<br>1 24<br>1 25<br>1 2<br>1 25<br>1 2<br>1 2<br>1 2<br>1 2<br>1 2<br>1 2<br>1 2<br>1 2  
   
   | 0.50         0           0.51         0           0.51         0           0.51         0           0.51         0           0.51         0           0.49         0           0.49         0           0.49         0           0.49         0           0.49         0           0.49         0           0.49         0           0.49         0           0.49         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44         0           0.44 <t< th=""><th>1,58 0.5<br/>1,54 0.5<br/>1,57 0.5<br/>1,56 0.1<br/>1,56 0.5<br/>1,59 0.5<br/>1,59 0.5<br/>1,59 0.5<br/>1,59 0.5<br/>1,59 0.5<br/>1,59 0.5<br/>1,57 0.5<br/>1,5</th><th>57         0.56           57         0.56           55         0.55           56         0.55           56         0.55           55</th><th>0.53<br/>0.51<br/>0.51<br/>0.52<br/>0.52<br/>0.52<br/>0.52<br/>0.52<br/>0.52<br/>0.52<br/>0.52</th><th>0.52 0.52 0<br/>0.56 0<br/>0.55 0<br/>0.55 0<br/>0.55 0<br/>0.55 0<br/>0.55 0<br/>0.51 0<br/>0.51 0<br/>0.40 0<br/>0.43 0<br/>0.43 0<br/>0.43 0<br/>0.43 0<br/>0.43 0<br/>0.43 0<br/>0.51 0<br/>0.51 0<br/>0.55 0<br/>0000000000</th><th>0         0</th><th>53         0.5         5         0.5           555         0.5         55         0.5         5           563         0.5         5         0.5         5         5           555         0.5         5         0.5         5
        5         5         5         5         5         5         5         5         5         5</th></t<> <th>3         0.58           4         0.58           3         0.57           3         0.57           3         0.57           3         0.58           3         0.58           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           4         0.57           4         0.43           4         0.43</th> <th>0.57<br/>0.57<br/>0.55<br/>0.57<br/>0.57<br/>0.57<br/>0.57<br/>0.58<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.058<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.057<br/>0.0000000000</th> <th>0.55 (</th> <th>0.53         0.55         0.           0.55         0.055         0.         55         0.           0.055         0.055         0.056         0.         56         0.           0.055         0.055         0.055         0.055         0.         50         0.           0.055         0.055         0.055         0.055         0.055         0.         0.055</th> <th>5.4         0.5.5           5.3         0.51           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           6.4         0.5           6.4         0.5           6.4         0.5           6.4         0.4           0.4         0.4           0.4         0.4           0.4         0.4</th> <th>2     0     5     1     5     0     5       5     0     5     2     2     5     5     5       7     0     5     3     0     5     1     0     5     1       7     0     5     3     0     5     1     0     5     1     1     0     5     1<th>0.56 (0.58 (</th><th>0.0540.00000000000000000000000000000000</th></th> | 1,58 0.5<br>1,54 0.5<br>1,57 0.5<br>1,56 0.1<br>1,56 0.5<br>1,59 0.5<br>1,59 0.5<br>1,59 0.5<br>1,59 0.5<br>1,59 0.5<br>1,59 0.5<br>1,57 0.5<br>1,5 | 57         0.56           57         0.56           55         0.55           56         0.55           56         0.55           55         0.55          
55         0.55           55         0.55           55         0.55           55  | 0.53<br>0.51<br>0.51<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52  | 0.52 0.52 0<br>0.56 0<br>0.55 0<br>0.55 0<br>0.55 0<br>0.55 0<br>0.55 0<br>0.51 0<br>0.51 0<br>0.40 0<br>0.43 0<br>0.43 0<br>0.43 0<br>0.43 0<br>0.43 0<br>0.43 0<br>0.51 0<br>0.51 0<br>0.55 0<br>0000000000  
  | 0          
   
   | 53         0.5         5         0.5           555         0.5         55         0.5         5           563         0.5         5         0.5         5         5           555         0.5         5         0.5            | 3         0.58           4         0.58           3         0.57           3         0.57           3         0.57           3         0.58           3         0.58           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           3         0.57           4         0.57           4         0.43           4         0.43  
   | 0.57<br>0.57<br>0.55<br>0.57<br>0.57<br>0.57<br>0.57<br>0.58<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.058<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.057<br>0.0000000000 | 0.55 (  | 0.53         0.55         0.           0.55         0.055         0.         55         0.           0.055         0.055         0.056         0.         56         0.           0.055         0.055         0.055         0.055         0.         50         0.           0.055         0.055         0.055         0.055         0.055         0.         0.055         0.055         0.055        
0.055           | 5.4         0.5.5           5.3         0.51           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.5         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           5.7         0.5           6.4         0.5           6.4         0.5           6.4         0.5           6.4         0.4           0.4         0.4           0.4         0.4           0.4         0.4  | 2     0     5     1     5     0     5       5     0     5     2     2     5     5     5       7     0     5     3     0     5     1     0     5     1       7     0     5     3     0     5     1     0     5     1     1     0     5     1 <th>0.56 (0.58
(0.58 (</th> <th>0.0540.00000000000000000000000000000000</th>                  | 0.56 (0.58 (   | 0.0540.00000000000000000000000000000000  |
| $\begin{array}{c c c c c c c c c c c c c c c c c c c $   
   
   
   | 0.35         0.34           0.21         0.21           0.13         0.11           0.13         0.11           10.13         0.11           31         0.09           8         91           86         91           111         107           111         107           113         111           174         170           174         170           183         184           183         184           182         183           182         183           182         183           182         183           182         183           182         183           182         170           180         180           177         178  | 0.40 0.39<br>0.26 0.25<br>0.26 0.27<br>0.26 0.27<br>0.27 0.28<br>- 100<br>- 1 | 0         0.38         0.4           0         0         0.29         0.3           0         0         0.29         0.3           0         0         0.29         0.3           0         0         0.27         0.3           0         0         0.27         0.3           0         0         0.37         0.3           0         0         0.37         0.3           0         0         0         0           1         0         0         0           1         79         -         0           1         1         1         1           1         1         1         1           1         1         1         1         1   
   
   
  | 1         0.53           2         0.54           2         0.52           2         0.52           3         0.53           3         0.53           3         0.53           3         0.53           3         0.53           3         0.53           4         0.51           7         1.24           153         1.54   
   
   | 0.51 0<br>0.51 0<br>0.48 0<br>0.48 0<br>0.49 0<br>0.49 0<br>0.49 0<br>0.49 0<br>0.49 0<br>0.48 0<br>0.48 0<br>0.48 0<br>0.38 0<br>0.38 0<br>1.132 - 1   
   
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   | 0.21         0.21         0.21           0.13         0.13         0.13           31         0.09         31           31         94         88           94         88         94           111         107         174           174         170         176           183         184         183           183         184         183           183         184         170           183         184         170           183         184         170           183         184         170           183         184         170           183         184         170           183         184         170           183         184         170           183         184         170           183         170         170           177         178         178   | 0.26 0.25<br>0.26 0.27<br>0.26 0.27<br>0.26 0.26<br>0.26 0.26<br>0.27 0.28<br>25 -<br>25 -<br>25 -<br>25 -<br>173 170<br>193 195<br>193 195<br>195<br>195<br>195<br>195<br>195<br>195<br>195<br>195<br>195  | 0         0.29         0.3           0         0.27         0.3           0         0.27         0.3           0         0.29         0.3           0         0.20         0.3           0         0.20         0.3           0         0.20         0.3           0         0.20         0.3           0         0.30         0.3           0         0.30         0.3           0         0.30         0.3           0         0.30         0.3           0         0.30         0.3           0         16         0.3           0         16         16           1         177         18           1         16         178  
   
   
  | 2 0.54<br>2 0.52<br>2 0.53<br>3 0.53<br>3 0.53<br>3 0.53<br>3 0.53<br>3 0.53<br>3 0.53<br>1 154<br>1 154<br>1 151<br>1 154   
   
   | 0.51 0<br>0.48 0<br>0.49 0<br>0.49 0<br>0.49 0<br>0.49 0<br>0.48 0<br>0.48 0<br>0.48 0<br>0.38 0<br>0.38 0<br>0.38 0<br>1.132 1<br>1.132 1  
   
  | 0.57 0.5<br>1.56 0.1<br>1.55 0.5<br>1.55 0.55 0.5<br>1.55 0.55 0.55 0.55 0.55 0.55 0.55 0.55  | 55 0.55<br>56 0.55<br>56 0.55<br>56 0.55<br>55 0.5<br>55 0.5<br>55 0.5<br>55 0.5<br>57 0.5<br>29 0.3<br>29 0.3<br>20 0.1<br>10<br>20 0.1<br>20<br>20 0.3<br>20 0.3<br>20 0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>0.5<br>55<br>55<br>55<br>0.5<br>55<br>55<br>55<br>55<br>55<br>55<br>55<br>55<br>55<br>55<br>55<br>55<br>5  | 0.49           0.50           0.51           0.52           0.52           0.52           0.52           0.52           0.52           0.52          
0.52           0.52           0.52           0.52           0.52           0.52           0.52           0.52           0.43           0.40           0.40           0.40           0.40  | 0.53 C<br>0.55 C<br>0.55 C<br>0.55 C<br>0.55 C<br>0.51 C<br>0.51 C<br>0.51 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.43 C<br>0.55 C<br>0.   
  | D         D <thd< th=""> <thd< th=""> <thd< th=""> <thd< th=""></thd<></thd<></thd<></thd<>  
   | <b>552</b> 0.5<br><b>533</b> 0.5<br><b>54</b> 0.5<br><b>54</b> 0.5<br><b>554</b> 0.5<br><b>554</b> 0.5<br><b>54</b> 0.5<br><b>54</b> 0.5<br><b>54</b> 0.5<br><b>54</b> 0.5<br><b>55</b> 0.5<br><b>55</b> 0.5<br><b>56</b> 0.5<br><b>57</b> 0.5<br><b>5</b> | 22 0.57<br>3 0.57<br>3 0.58<br>6 0.57<br>6 0.57<br>6 0.57<br>6 0.57<br>7 0.58<br>14 0.56<br>17 0.38<br>17 0.38   
   
   | 0.55<br>0.57<br>0.57<br>0.56<br>0.58<br>0.58<br>0.58<br>0.58<br>0.58<br>0.58<br>0.58<br>0.53<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57  | 0.57 (0.57 (0.56 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.55 (  | 0.55         0.55         0.55         0.54         0.55 <th< td=""><td>55 0.5<br/>555 0.5<br/>555 0.5<br/>54 0.5<br/>57 0.5<br/>551 0.5<br/>551 0.5<br/>551 0.5<br/>450 0.3<br/>43 0.4<br/>43 0.5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5<br/>5</td><td>1         0.51           2         0.52           3         0.521           3         0.551           4         0.544           0         0.49           0         0.49           0         0.51</td><td>0.54 (<br/>0.55 (<br/>0.</td><td>0.000000000000000000000000000000000000</td></th<> | 55 0.5<br>555 0.5<br>555 0.5<br>54 0.5<br>57 0.5<br>551 0.5<br>551 0.5<br>551 0.5<br>450 0.3<br>43 0.4<br>43 0.5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5  | 1         0.51           2         0.52           3         0.521           3         0.551           4         0.544           0         0.49           0         0.49           0         0.51  
   | 0.54 (<br>0.55 (<br>0.   | 0.000000000000000000000000000000000000   |
| 280         156         110         67           281         160         114         70         44           283         157         112         70         43           283         157         112         70         47           283         157         112         70         47           276         168         112         87         87           276         168         124         96         87           274         154         124         96         87           272         157         135         107         106           272         168         174         178         170           272         163         165         165         167           275         160         165         167         196           275         161         165         167         184           285         194         187         182         184           279         161         167         182         184           279         171         167         182         184           279         171         167         184   
   
   
   | 0.13         0.11           31         0.09           31         9           86         91           86         91           94         89           94         89           95         94           96         91           97         174           174         170           183         184           183         184           183         184           183         184           183         184           183         184           183         184           183         184           183         184           183         170           183         170           183         170           183         170           180         180           177         178  | 0.26 0.27<br>0.26 0.28<br>0.27 0.28<br>25 - 0.08<br>25 - 0.08<br>25 - 0.08<br>25 - 0.08<br>109 108<br>173 170<br>190 191<br>190 191<br>190 191  | 0.27         0.3           0.29         0.3           0.29         0.3           0.20         0.3           0.20         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.31         0.3           0.31         0.3           0.31         0.3           0.31         0.3           0.31         0.3  
   
   
  | 2 0.52<br>0.53<br>0.53<br>0.55<br>0.55<br>0.55<br>0.55<br>0.55<br>0.53<br>0.53   
   
   | 0 48 0<br>0 49 0<br>0 49 0<br>0 49 0<br>0 49 0<br>0 49 0<br>0 49 0<br>0 47 0<br>0 47 0<br>0 38 0<br>0 0 38 0<br>1 122<br>1 122  
   
  | 0.5500.5500.5500.5500.5500.5500.5500.5   
  | 556 0.55<br>566 0.55<br>566 0.55<br>55 0.58<br>55 0.58<br>57 0.57<br>57 0.57<br>29 0.30<br>29 0.30<br>29 0.30<br>29 0.30<br>29 0.30<br>20 0.10<br>20 0.10<br>20 0.10<br>20 0.10<br>20 0.58<br>20 0.57<br>20 0.57<br>2000000000000000000000000000000000000   | 0.52<br>0.53<br>0.53<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52  | 0.55 0.55 0.55 0.55 0.55 0.55 0.55 0.55  
  | 0.53 0.055 0   
   
   | 553 0.5<br>554 0.5<br>554 0.5<br>555 0.5<br>556 0.5<br>554 0.5<br>554 0.5<br>554 0.5<br>554 0.5<br>399 0.3<br>399 0.3<br>30 0.3<br>30 0.3<br>30 0.3<br>30 0.3<br>30 0.5<br>5<br>5<br>4<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5   | 3 0.57<br>3 0.58<br>3 0.57<br>6 0.57<br>6 0.57<br>2 0.57<br>4 0.57<br>14 0.57<br>17 0.38<br>14 0.43  
   | 0.57<br>0.56<br>0.56<br>0.56<br>0.58<br>0.58<br>0.58<br>0.58<br>0.58<br>0.53<br>0.57<br>0.57<br>0.53<br>0.54<br>0.58  | 0.56 0.57 0.57 0.57 0.57 0.57 0.57 0.57 0.57  
   | 0.54 0.<br>0.54 0.<br>0.56 0.<br>0.56 0.<br>0.55 0.<br>0.53 0.<br>0.43 0.<br>0.43 0.<br>0.43 0.<br>0.43 0.<br>0.43 0.<br>0.45 0.<br>0.45 0.<br>0.45 0.<br>0.45 0.<br>0.45 0.<br>0.<br>0.45 0.<br>0.<br>0.45 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.56 0.<br>0.<br>0.55 0.<br>0.05 0.000 0.<br>0.05 0.0000000000   | 555 0.55<br>556 0.55<br>557 0.55<br>551 0.55<br>551 0.55<br>550 0.55<br>445 0.4<br>445 0.4<br>43 0.4<br>43 0.4<br>43 0.4  | 2 0.52<br>3 0.52<br>3 0.51<br>3 0.54<br>3 0.54<br>0 0.49<br>8 0.46<br>8 0.46<br>4 0.46<br>4 0.48<br>0 0.42<br>2 0.42<br>2 0.42<br>2 0.42<br>2 0.42<br>2 0.52   
  | 0.556 (<br>0.556 (<br>0.555 (<br>0.555 (<br>0.555 (<br>0.556   | 0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.000<br>0.0000<br>0.0000<br>0.0000<br>0.0000<br>0.00000<br>0.00000<br>0.00000<br>0.000000  |
| 281         160         114         70         44           283         157         112         70         37           286         168         139         87         88         3           276         168         139         87         88         3           274         154         124         96         87         37           272         157         135         107         106         37           272         157         135         107         106         37           272         160         174         178         170         37           272         160         165         165         167         36           275         160         165         164         182         36           275         191         185         182         36         37         36         37           281         191         165         184         182         36         37         37           279         171         165         183         173         178         37         37         37         37           278         171         1   
   
   
   | 0.03           31         0.03           31         0.03           86         91           86         91           94         89           94         89           111         107           174         170           158         158           163         184           183         184           183         184           183         184           183         184           183         170           173         171           177         178   | 0.26 0.28<br>0.27 0.28<br>- 0.08<br>- 0.08<br>- 0.08<br>- 0.08<br>- 0.08<br>- 0.08<br>- 100<br>103 100<br>103 100<br>113 170<br>113 170<br>113 195<br>195<br>195<br>195<br>195<br>195<br>195<br>195<br>195<br>195   | 0.29         0.3           0.27         0.3           0.27         0.3           0.20         0.3           0.31         0.3           1.30         18           1.30         18  
   
   
  | 4         0.53           2         0.52           3         0.52           3         0.52           4         0.51           5         0.53           7         124           15         124   
   
   | 0.49 0<br>0.49 0<br>0.50 0<br>0.50 0<br>0.47 0<br>0.47 0<br>0.38 0<br>0.38 0<br>132 1<br>132 1<br>132 1   
   
  | 0.56 0.5<br>0.57 0.5<br>0.55 0.5<br>0.55 0.5<br>0.55 0.5<br>0.57 0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5<br>0.5  
  | 556         0.55           556         0.54           559         0.58           554         0.58           554         0.58           446         0.46           229         0.30           229         0.30           29         0.30   | 0.53<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52<br>0.52  | 0.55 (   
  | D         D <thd< th=""> <thd< th=""> <thd< th=""> <thd< th=""></thd<></thd<></thd<></thd<>  
   
   | 540.5500.5540.55500.55500.55500.55500.55500.55500.55500.55500.55500.55500.55500.55500.55500.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.55000.5000000   | 0.58<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57   
   | 0.57<br>0.56<br>0.58<br>0.58<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57<br>0.57  
   | 0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.57 (0.55 (  | 0.54 0.<br>0.56 0.<br>0.56 0.<br>0.56 0.<br>0.54 0.<br>0.43 0.<br>0.54 0.<br>0.56 0.<br>0.57 0.<br>0.56 0.<br>0.57 0.<br>0.50 0.0000000000  | 55 0.5<br>57 0.5<br>57 0.5<br>56 0.5<br>56 0.5<br>6<br>45 0.4<br>40 0.3<br>43 0.4<br>43 0.4<br>43 0.4   | 3 0.52<br>3 0.51<br>4 0.54<br>0 0.49<br>0 0.49<br>8 0.46<br>4 0.46<br>4 0.42<br>4 0.42  
   | 0.55 (<br>0.55 (<br>0.58 (<br>0.59 (<br>0.59 (<br>0.55 (<br>0.55 (<br>0.55 (<br>0.42 (<br>0.42 (<br>0.43 (<br>0.43 (<br>0.43 (<br>0.43 (<br>0.43 (<br>0.43 (<br>0.56 (<br>0.56 (<br>0.55 (<br>0.   | 0.052 0.052 0.052 0.055 0.055 0.055 0.055 0.055 0.05550 0.0555 0.0555 0.0555 0.0555 0.05550 0.05555 0.05555 0.05550 0.05555 0.05555 0.0555 0.0555 0.05550 0.05555 0.05550 0.05550 0.0555   |
| 283         157         112         70         37           280         168         131         87         87           276         168         131         87         87           274         154         154         92         88           274         154         124         96         87           274         154         124         96         87           272         157         135         107         106           272         166         155         157         105         106           272         160         155         167         106         157           275         161         165         167         104         182           275         191         187         182         158         157           279         191         187         182         182         152           279         171         167         159         171           279         170         183         173         178  
   
   
   | 31 -         31 -           87         89           87         89           94         81           94         87           111         107           174         170           158         158           163         184           183         184           183         184           183         184           183         184           183         184           183         184           185         183           186         173           173         173           177         178  | 0.27 0.28<br>- 0.08<br>- 25 - 25<br>- 25 - 100<br>99 100<br>109 108<br>170 190 199<br>190 191<br>190 191<br>191 193 195<br>192 195<br>191 193 195<br>192 193 195<br>193 195<br>195<br>195<br>195<br>195<br>195<br>195<br>195<br>195<br>195  | 0.27         0.3           0.0.20         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.2           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.30         0.3           0.40         1.3           1.100         1.18  
   
   
  | 20.52<br>30.53<br>0.51<br>0.51<br>70.51<br>7154<br>7154<br>7154<br>754<br>754<br>7554<br>7554<br>7554  
   
   | 0.49 0<br>0.49 0<br>0.50 0<br>0.48 0<br>0.48 0<br>0.48 0<br>0.48 0<br>0.38 0<br>1 132 - 0   
   
  | 0.57 0.5<br>0.58 0.5<br>0.55 0.5<br>0.55 0.5<br>0.47 0.4<br>0.41 0.4<br>0.5<br>95 - 0   | 556 0.54<br>59 0.58<br>57 0.55<br>57 0.55<br>46 0.46<br>29 0.30<br>29 0.30   
  | 0.52<br>0.52<br>0.52<br>0.49<br>0.47<br>0.43<br>0.42<br>0.42<br>0.42  | 0.55 0.55 0.55 0.55 0.55 0.55 0.55 0.55  
  | 0.54 0.<br>0.55 0.<br>0.53 0.<br>0.42 0.<br>0.42 0.<br>0.42 0.<br>0.43 0.<br>0.43 0.<br>0.43 0.<br>0.43 0.<br>0.43 0.<br>0.<br>0.43 0.<br>0.<br>0.<br>0.<br>0.<br>0.<br>0.<br>53 0.<br>0.<br>53 0.<br>53 0.<br>53 0.<br>53 0.<br>53 0.<br>55 0.<br>50 0.<br>55 0.<br>50 0.<br>55 0.<br>50 0.<br>55 0.<br>50 0.<br>55 0.<br>50 0.   
   
  | 554 0.55<br>555 0.55<br>545 0.5<br>545 0.5<br>545 0.5<br>545 0.5<br>545 0.5<br>5<br>5<br>5<br>6<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5<br>5   | 0.57<br>0.57<br>0.58<br>0.57<br>0.57<br>17<br>0.43<br>17<br>0.43<br>17<br>0.44  
  | 0.56<br>0.58<br>0.57<br>0.57<br>0.57<br>0.43<br>0.43<br>0.38  | 0.57 0.57 0.57 0.57 0.57 0.55 0.55 0.55   | 0.54 0.<br>0.56 0.<br>0.55 0.<br>0.54 0.<br>0.43 0.<br>0.43 0.<br>0.45 0.<br>0.43 0.   
  | 57 0.5<br>57 0.5<br>56 0.5<br>56 0.5<br>50 0.5<br>10.4<br>40 0.3<br>43 0.4<br>43 0.4<br>43 0.4  | 3     0.51       4     0.54       0     0.49       0     0.51       0     0.51       4     0.46       0     0.51       4     0.46       4     0.46       0     0.51  
  | 0.55 0.59 0.58 0.58 0.59 0.59 0.59 0.59 0.59 0.55 0.55 0.55  | 0.52 0.<br>0.56 0.<br>0.51 0.<br>0.45 0.<br>0.45 0.<br>0.43 0.<br>0.43 0.  |
| 280         168         131         87         87           276         168         129         82         88           274         154         129         82         88           274         154         124         96         87           272         157         135         107         106           272         168         174         178         176           275         160         155         157         168         170           275         160         174         178         184         182           275         191         187         182         184         182         182           275         191         187         182  
   
   
   | 87         89           86         91           94         88           111         107           111         107           114         170           114         170           115         183           183         184           183         184           183         181           183         171           173         171           180         180           177         178  |   | 1     0.30     0.3       0     0.30     0.3       1     0.30     0.3       1     1     1       1     1     1       1     1     1       1     1     1       1     1     1       1     1     1   
   
   
  | 3 0.53<br>3 0.52<br>4 0.51<br>0.53<br>3 - 0.53<br>7 154<br>7 154<br>7 153  
   
   | 0.49 0<br>0.50 0<br>0.48 0<br>0.47 0<br>0.47 0<br>0.38 0<br>0.38 0<br>1.42 1<br>1.42  
   
  | 0.59 0.5<br>58 0.5<br>0.55 0.5<br>0.57 0.5<br>0.47 0.4<br>0.41 0.4<br>0.41 0.4<br>95 -   
  | 59 0.58<br>54 0.58<br>57 0.57<br>46 0.46<br>46 0.40<br>29 0.30<br>29 0.30   | 0.52<br>0.52<br>0.49<br>0.49<br>0.43<br>0.43<br>0.43  | 0.55 0.54 0.55 0.54 0.55 0.54 0.53 0.54 0.53 0.53 0.53 0.53 0.54 0.54 0.54 0.54 0.54 0.54 0.54 0.54  
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Fig. 3. Pairwise distance between taxa. Absolute distances (below diagonal) and mean distances (above diagonal) were calculated for unordered characters using PAUP. Bold boxes correspond to the major clades resolved by both parsimony and distance analysis, being from top to bottom, the archaea, plastid, and cytosolic.

The position of *G. polyedra* GAPCp within the cytosolic clade raises the question of its origin. It is possible that, as in *Pinus* GAPCp, it arose by targeting a cytosolic-type isoform to the chloroplast, with amino acid changes allowing catalysis using both NAD<sup>+</sup> and NADP<sup>+</sup>. This is unlikely because gene duplication followed by an extremely rapid divergence would be necessary to explain the distance between the GAPC and the GAPCp sequences. Also, the similarity between cryptomonad and dinoflagellate GAPCp sequences argues against both being derived independently from their respective GAPC homologs.

The origin of GAPCp in cryptomonads is proposed to be proteobacterial, while that of their chloroplasts is evidently cyanobacterial, as indicated by sequences of several plastid-encoded genes, including 16S rRNAs and *tuf*A (Delwiche et al. 1995; Douglas 1993; Giovannoni et al. 1993). In dinoflagellates RuBisCO is also reported to be proteobacterial in origin (Morse et al. 1995; Rowan et al. 1996; Watson and Tabita 1997), while the intrinsic peridinin–chlorophyll binding protein (iPCP) is of cyanobacterial origin [part of a larger gene family encompassing the fucoxanthin–chlorophyll proteins of the chromophytes and the chlorophyll a/b-binding proteins of the land plants (Durnford et al. 1996)]. What could explain the presence of proteobacterial-type isoforms in plastids of cyanobacterial origin?

For cryptomonads it was proposed that the GAPCp gene was laterally transferred from a proteobacterialtype cell to the nucleus during a primary endosymbiosis (Liaud et al. 1997). GAPCp was then targeted to the cyanobacterial-type plastid of a red algal eukaryote acquired during a second endosymbiotic event. It is also possible that the primary endosymbiont was a cyanobacterium that harbored two (or more) GAPDH isoforms. As reported by Martin et al. (1993), and is evident from our phylogenetic analysis, a GAPC isoform, which could be the GAPCp ancestor, occurs within the cyanobacteria (*Anabaena* 1 in Fig. 2).

While either mechanism (or any similar one) could also explain the presence of a proteobacterial GAPCp in dinoflagellates, it is unlikely to have occurred independently in both, given the sequence similarities. In addition, GAPC isoforms and rDNA phylogenies (Bhattacharya et al. 1992) indicate that dinoflagellates and cryptomonads are only distantly related, thus ruling out a common ancestral origin of the two groups as an explanation for the similarity between the GAPCp forms. A more likely possibility is that the *G. polyedra* GAPCp gene was acquired from a cryptomonad symbiont through lateral transfer.

Lateral gene transfer should be favored in situations where two genomes are closely associated. Such associations are commonly found in both heterotrophic and phototrophic dinoflagellates, many members of which are known to ingest and retain cells of other species. Peridinium balticum and P. foliaceum, for example, harbor diatoms with distinct nuclei and chloroplasts in a stable association (Chesnick et al. 1997). A more common, if more transient, association occurs in kleptochloroplasty, in which chloroplasts of an ingested cell are retained and used as temporary photosynthetic organelles by the dinoflagellate after endocytotic engulfment of prey. Indeed, in the dinoflagellates Amphidinium poecilochroum, Gymnodinium aeruginosum, and Amphidinium wigrense, the kleptochloroplasts are thought to be of cryptomonad origin (Larsen 1988; Schnepf 1992; Wilcox and Wedemayer 1985). We postulate that the GAPCp gene in the phototroph G. polyedra is derived from such an association, in which the integration of a cryptomonad-like cell or chloroplast into a heterotrophic dinoflagellate led to the transfer of a cryptomonad gene(s) to the dinoflagellate nucleus. However, our data are also consistent with such a transfer from a dinoflagellate to a cryptomonad.

Phylogenetic analysis of the three dinoflagellate nuclear-encoded chloroplast-targeted proteins so far examined, RuBisCO, iPCP, and GAPCp, suggests that the genome may be more chimeric than previously anticipated (Morse et al. 1995; Rowan et al. 1996; Watson and Tabita 1997). Lateral transfer from a cryptomonad in the course of an ancestral association with a dinoflagellate would account for the acquisition of two of these genes, GAPCp and iPCP, which have homologues in the cryptomonads, as the consequence of a single endosymbiosis.

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