Structural Conservation of the Isolated Zinc Site in Archaeal Zinc-containing Ferredoxins as Revealed by X-ray Absorption Spectroscopic Analysis and Its Evolutionary Implications*§}

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The zfx gene encoding a zinc-containing ferredoxin from Thermoplasma acidophilum strain HO-62 was cloned and sequenced. It is located upstream of two genes encoding an archaeal homolog of nascent polypeptide-associated complex α subunit and a tRNA nucleotidyltransferase. This gene organization is not conserved in several euryarchaeoteal genomes. The multiple sequence alignments of the zfx gene product suggest significant sequence similarity of the ferredoxin core fold to that of a low potential 8Fe-containing dicluster ferredoxin without a zinc center. The tightly bound zinc site of zinc-containing ferredoxins from two phylogenetically distantly related Archaea, T. acidophilum HO-62 and Sulfolobus sp. strain 7, was further investigated by x-ray absorption spectroscopy. The zinc K-edge x-ray absorption spectra of both archaeal ferredoxins are strikingly similar, demonstrating that the same zinc site is found in T. acidophilum ferredoxin as in Sulfolobus sp. ferredoxin, which suggests the structural conservation of isolated zinc binding sites among archaeal zinc-containing ferredoxins. The sequence and spectroscopic data provide the common structural features of the archaeal zinc-containing ferredoxin family.

The archaeal domain contains organisms having the most extraordinary optimal growth conditions, with members flourishing at the extremes of pH, temperature, and salinity. As oxygen is often scarce in these conditions, the majority of thermophilic Archaea are anaerobic organisms (1–3). For the more unusual aerobic Archaea, one of the characteristic features in the central metabolic pathways is the involvement in electron transport of small iron-sulfur (FeS) proteins called ferredoxins. Ferredoxins take the place of NAD(P)H, a typical electron carrier in Bacteria and Eucarya (4–7). The physiological significance of bacterial-type ferredoxins in several aerobic and thermooacidophilic Archaea was first recognized by Kerscher et al. (8), when it was demonstrated that ferredoxins are an effective electron acceptor of a coenzyme A-acylating 2-oxoacid: ferredoxin oxidoreductase, which is a key enzyme of the tricarboxylic acid cycle and of coenzyme A-dependent pyruvate oxidation in aerobic Archaea (6–9).

The primary structures of archaeal ferredoxins differ from those of regular bacterial-type monocluster and dicluster ferredoxins in that they contain a central loop region and an N-terminal extension, composed of three β-strands and one α-helix (10–14). An unexpected result from recent x-ray structural analysis of the ferredoxin from the thermoacidophilic archaeon, Sulfolobus sp. strain 7 (optimal growth conditions, pH 2.5–3.0 and 80 °C; Refs. 6 and 15) was that four amino acid residues in the extra regions (His16, His19, His34, and Asp76) serve as ligands to a tetragonally coordinated, novel zinc center (16). The on-line version of this article (available at http://www.jbc.org) contains Tables S1–S3.

The nucleotide sequence reported in this paper has been submitted to the DDBJ/GenBank®/EBI Data Bank with accession number AB023294.

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§ The on-line version of this article (available at http://www.jbc.org) contains Tables S1–S3.
¶ The abbreviation used are: FeS, iron-sulfur; EXAFS, extended x-ray absorption fine structure; FT, Fourier transform; MALDI-TOF MS, matrix-assisted laser desorption ionization-time of flight mass spectrometry; SSRL, Stanford Synchrotron Radiation Laboratory; T. acidophilum, Thermoplasma acidophilum; XAS, x-ray absorption spectroscopy; zfx, zinc-containing ferredoxin; PCR, polymerase chain reaction; bp, base pair(s); α-NAC, nascent polypeptide-associated complex α subunit.

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23160 This paper is available on line at http://www.jbc.org
tion (8, 14) and the other being the membrane-bound aerobic respiratory chain containing multiple b- and d-type cytochromes (21). The pioneering work by Kerscher and co-workers (8) has shown that T. acidophilum strain DSM 1728 contains a bacterial-type ferredoxin functioning as an electron acceptor of the cognate 2-oxidized:ferredoxin oxidoreductase. The amino acid sequence of this ferredoxin was previously determined by Edman degradation of proteolytically generated peptides (10).

Recently, we purified the functionally equivalent ferredoxin from T. acidophilum strain HO-62 (20). Through chemical analysis, electron paramagnetic resonance (EPR) and low temperature resonance Raman spectroscopy, it was demonstrated that the ferredoxin contains one [3Fe-4S]1+ cluster, one [4Fe-4S]2+ cluster, and one tightly bound zinc center (14), thus indicating the existence of “zinc-containing ferredoxins” among phylogenetically diverse members of several thermoacidophilic Archaea (14). Although the presence of a tightly bound zinc center is one of the most unique properties of the archaeal zinc-containing ferredoxins, the structural details of the zinc site have been characterized only for ferredoxin from Sulfolobus sp. strain 7, which was analyzed by x-ray diffraction (16).

X-ray absorption spectroscopy (XAS) is ideally suited for the investigation of the metric structural environment of specific metal sites in biomolecules (22). Herein, we report the XAS analysis of zinc-containing ferredoxins from these two phylogenetically distantly related Archaea, Thermoplasma acidophilum strain HO-62 and Sulfolobus sp. strain 7 (6, 14, 15), to characterize the structural properties of the zinc and iron coordination environments. We also report cloning and sequencing of the zfx gene encoding zinc-containing ferredoxin of T. acidophilum strain HO-62 (zfx for zinc-containing ferredoxin) and its flanking regions, to clarify its gene organization and the distribution of zinc-containing ferredoxin homologs in thermophilic organisms. The gene sequence and spectroscopic data provide the basis for comparison of the structural features among the archaeal zinc-containing ferredoxin family.

**EXPERIMENTAL PROCEDURES**

DEAE-Sepacel, DEAE-Sepharose Fast Flow, and Sephadex G-50 were purchased from Amersham Pharmacia Biotech. Water was purified by the Milli-Q purification system (Millipore). Other chemicals used in this study were purchased commercially and were of analytical grade.

Thermoplasma acidophilum strain HO-62 cells, originally isolated from hot sulfur springs at Ohwakudani solfataric field in Hakone, Japan, were routinely cultivated at pH 1.8 and at 56°C in 10- and 30-liter acid-resistant fermenters as described by Yasuda et al. (20), and zinc-containing ferredoxin was purified as described previously (14). Sulfolobus sp. strain 7 cells, originally isolated from Beppu Hot Springs, Japan, were cultured aerobically and chemoheterotrophically at pH 2.5–3 and 75–80°C (23), and the 7Fe form of the cognate ferredoxin was purified as described previously (6, 15). Escherichia coli strain DH5α, used for cloning, was grown in LB or TB medium, with 50 mg/ml ampicillin when required. Plasmids pGEMT and pGEM3ZF(+) (Promega) were used for cloning and sequencing. DNA was manipulated by standard procedures (24).

The N-terminal 15 amino acid residues of T. acidophilum HO-62 ferredoxin (VKLNLDFKPKPIDE) (14) have been confirmed in the previous work to be identical to the amino acid sequence of a different strain (DSM 1728) of T. acidophilum determined by Edman degradation of proteolytically generated peptides (accession number P00218). A DNA fragment encoding the zfx gene was obtained by PCR from template genomic DNA of T. acidophilum strain HO-62, using the following two oligonucleotide primers: TFP1 (corresponding to the N-terminal KPKPIDE sequence (10, 14)), 5′-AA(A/G) CC(A/G/C/T) AA(A/G) CC(A/G/C/T) AA(A/G) CC(A/G/C/T) GA(A/G/C/T) GA(A/G) CA(T/C) TT-3′, and TFP2 (corresponding to the DCIFCMAC sequence at the cluster-binding site; Ref. 10), 5′-TC(A/G) CA(A/G/C/T) GCC AT(A/G) CA(A/G) AA(A/G) CA(A/G) GA(A/G) CC(A/G)/

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**TABLE I**

| Facility | Fe EXAFS | Zn EXAFS |
|----------|----------|----------|
| SR       | SSRL     | SSRL     |
| Beamline | 7–3      | 7–3      |
| Current in storage ring | 80–100 mA | 50–60 mA |
| Monochromator crystal | Si[220] | Si[220] |
| Detection method | Fluorescence | Fluorescence |
| Detector type | Solid state array | Solid state array |
| Scan length (min) | 28 | 25 |
| Scans in average | 16 | 10 |
| Temperature (K) | 10 | 10 |
| Energy standard | Fe foil, first | Zn foil, first |
| Energy calibration (eV) | 7111.3 | 9670 |
| E₀ (eV) | 7120 | 9670 |
| Pre-edge background | Energy range (eV) | 6789–7075 | 8657–9625 |
| | Gaussian center (eV) | 6403 | 8638 |
| | Width (eV) | 750 | 750 |
| | Spline background | Energy range (eV) | 7354–7599 (4) | 9902–10134 (4) |
| | (Polynomial order) | 7589–7822 (4) | 10134–10366 (4) |

**RESULTS**

**Sequence Analysis of the zfx Gene and Flanking Regions**—The zfx gene utilizes a translational start codon, GTG (posi-

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2. T. Iwasaki, unpublished results.

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tions 121–123, Fig. 1), and the corresponding valine residue is absent in zinc-containing ferredoxin isolated from the *T. acidophilum* HO-62 cells (Fig. 1), indicating post-translational modification. The single open reading frame encodes a protein with a deduced molecular mass of 15,955 Da (excluding the initial residue), which is in agreement with the average mass \[M_1^1\] of 15,961 Da (estimated error, \(6 \times 10^3\) Da) for purified apoferredoxin by MALDI-TOF mass spectrometry. The *zfx* gene sequence predicts an amino acid sequence containing the three consensus histidine residues, His\(_{30}\), His\(_{33}\), and His\(_{57}\), and a remote Asp\(_{116}\) (doubly-underlined in Fig. 1). The equivalent residues in *Sulfolobus* sp. ferredoxin (Fig. 2) serve as ligands to the isolated zinc center (14). The deduced amino acid sequence is essentially identical to the reported sequence of *T. acidophilum* DSM 1728 ferredoxin determined by Edman degradation of proteolytically generated peptides (accession number P00218) (10). The two discrepancies, Glu\(_{101}\) and Ala\(_{105}\), located in the central loop region (underlined residues in Fig. 1), most likely reflects the difference in strains used (strain HO-62 versus DSM 1728). Similarity searches against available data bases (GenEMBL, PIR, and SWISS-PROT) indicate a high sequence homology of the *zfx* gene product with other zinc-containing ferredoxins of several fast-clock crenarchaeotes (*Sulfolobales*, Fig. 2), which are distantly related to the euryarchaeote *T. acidophilum* on the basis of the universal 16 S rRNA sequence tree (2, 3, 19). On the other hand, no *zfx* gene homolog with the consensus N-terminal extension sequence could be identified in the genomes of hyperthermophilic euryarchaeotes such as *Methanococcus jannaschii* (31), *Methanobacterium thermoautotrophicum* (32), *Pyrococcus horikoshii* (shinkaj) (33), *Archaeoglobus fulgidus* (34), and a hyperthermophilic bacterium *Aquifex ae-
oicus (35) by either amino acid or nucleotide sequence similarity searches (data not shown). Clearly, distribution of zinc-containing ferredoxins in hyperthermophilic and thermophilic organisms is limited even in the archaeal domain. A promoter-like element (box A) (36) was found immediately upstream of the zfx gene at positions 81–86 (Fig. 1), and a putative ribosome binding sequence (5'-GGTGAG-3') complementary to the 3' end of the 16 S rRNA (19) at positions 109–114 (underlined in Fig. 1). Because the zfx gene product is abundantly produced in T. acidophilum (8, 14), the proximal promoter region of the zfx gene might be useful to express a foreign gene efficiently in this euryarchaeote. A T-rich terminator-like element (37) was found shortly after the stop codon at positions 565–573 (underlined in Fig. 1). Apparently, the zfx gene of T. acidophilum strain HO-62 does not have an operonic structure.

Two open reading frames were found shortly after the zfx gene (Fig. 1). The first structural gene, orf1, encodes a 13.9-kDa protein with a relatively high methionine content in the N-terminal region. The Orf1 protein is strictly conserved in several thermophilic Archaea (as unknown open reading frame in Refs. 31–34; 31) (data not shown). The similarity of the Orf1 protein of T. acidophilum to eucaryal α-NAC homologs suggests that the archaeal protein might also serve as a putative transcriptional coactivator.

The second gene, cca, was found immediately downstream of orf1, and was partially sequenced in this study (Fig. 1). It predicts the N-terminal half of a T. acidophilum homolog of class I tRNA nucleotidyltransferase (Fig. 3B), which repairs the 3'-terminal CCA sequence of all tRNAs (45, 46). Interestingly, the archaeal tRNA nucleotidyltransferases are similar to eucaryal poly(A) polymerases and DNA polymerase β, but distantly related to either the bacterial or eucaryal CCA-adding enzymes (45–47). The unique feature of the cca gene of T. acidophilum is its one-base pair overlap with the orf1 gene, implying an operonic structure; this gene organization is not observed for other hyperthermophilic euryarchaeotes with known genome sequences (31–34) (data not shown). The two structural genes downstream of the zfx gene are likely involved in translation or tRNA modification system, and apparently unrelated to the zfx gene, which is involved in cytoplasmic electron transport.

**Zinc K-edge XAS Analysis—**The zinc K-edge x-ray absorption spectra of the 7Fe form of zinc-containing ferredoxins purified from the two phylogenetically different Archaea, T. acidophilum strain HO-62 and Sulfolobus sp. strain 7, are very similar (Fig. 4, trace a). The absorption edge position (9663.3 eV for T. acidophilum; 9663.2 eV for Sulfolobus) for both spectra fall at the expected energy for Zn(II) with all light elements (nitrogen or oxygen) in the coordination sphere (48, 49). The intensity of the edge is most reminiscent of four-coordinate compounds and the peak area of the second XANES peak is not as

![Image](72x511 to 532x729)
intense as expected for tetra-imidazole coordination, nor is it as weak as seen in a ZnO$_4$ compound (48). Curve-fitting analyses of zinc EXAFS of each of the two archaeal zinc-containing ferredoxins suggest the presence of three or four imidazoles. However, such Zn(imid)$_3$,4(N,O)$_1$ fits simulate Fourier transform (FT) peaks of about the same height at 3 and 4 Å, while the observed data have a much larger FT peak at 4 Å (Fig. 5, traces a and b). This suggests that some other scatterer interferes destructively with the 3-Å imidazole contribution, resulting in an absence of FT intensity. This interference can be modeled with a carboxylate group, in which the average Zn-N and Zn-O bond distances are 2.01 and 1.90 Å, respectively. The data were modeled with a Zn-O-C angle of either $180^\circ$ (data not shown) or $126^\circ$ (Fits 3 and 4 and 7 and 8, Table II), the two most common conformations found for zinc-carboxylate coordination in the Cambridge Structural Data base. The latter provides better fits of the data. Thus, the zinc K-edge EXAFS spectra of both archaeal zinc-containing ferredoxins can be best fit, assuming a Zn(imid)$_3$,4(COO$_2$)$_1$ coordination environment (Fig. 5, traces a and b). The zinc XAS results clearly show that the zinc site found in the zfx gene product of *T. acidophilum* strain HO-62 is very similar to that of *Sulfolobus* sp. ferredoxin. The XAS-determined bond distances and bond angles are also in agreement with the crystallographically determined Zn-N and Zn-O bond distances (1.96 and 1.90 Å, respectively) and Zn-O-C angle ($126^\circ$) (16).

Fig. 3. Multiple amino acid sequence alignments of orf1 (a) and cca (b) with homologous proteins. Conserved amino acid residues are shaded. The amino acid sequences used are: *A. fulgidus*, O30024 (AF2015); *P. horikoshii*, O2879 (MTH177); *T. acidophilum*, this work; *YeastEGD2* (Saccharomyces cerevisiae EGD2 protein), P38879; *Dros. alphaNAC* (Drosophila melanogaster nascent polypeptide-associated complex protein α subunit (oxen)), Q84518; *mouse alphanAC* (mouse α NAC/1.9.2 protein), U22151; *human alphanAC* (human nascent polypeptide-associated complex α subunit), S49326; and b, *T. acidophilum*, this work; *M. jannaschii*, Q58511 (MJ1111); *A. fulgidus*, O28126 (AF2156); *P. horikoshii*, D1030113 (PH0101); *M. thermoautotrophicum*, O26684 (MTH584); *S. shibatae* (Sulfolobus shibatae RNA nucleotidytranferase (cca)), P77976.
Iron K-edge XAS Analysis—The iron K-edge x-ray absorption spectra for zinc-containing ferredoxin from *T. acidophilum* strain HO-62 are almost identical to that from *Sulfolobus* sp. strain 7 (Fig. 4, trace b). The integrated peak area (0.206 eV for *T. acidophilum* and 0.289 eV for *Sulfolobus*), for the 1 s → 3 d transition at ~7113 eV, falls in the range expected for tetrahedral compounds (50–52).

Curve-fitting analysis of both archaeal ferredoxins reveals the presence of a 2.25–2.26 Å Fe-S and a 2.71–2.72 Å Fe-Fe interaction. The best fit (by goodness-of-fit values) is obtained from calculated EXAFS for FeS$_4$Fe$_2$ (Fits 9 and 11, Table II; Fig. 5, traces c and d). However, the data can also be fit assuming FeS$_4$Fe$_{2.5}$ (Fits 10 and 12, Table II), as expected for one 3Fe and one 4Fe cluster.

**EPR Spectroscopy**—The air-oxidized form of both ferredoxins (*Sulfolobus* sp. strain 7 and *T. acidophilum* strain HO-62) elicited the sharp g = 2.02 EPR signals with slightly different lineshapes (0.9–1.0 spin/mol), which are attributable to a [3Fe-4S]$^{1-}$ cluster as reported previously (6, 14) (Fig. 6, A and C). Upon reduction of these ferredoxins by excess dithionite under anaerobic conditions, the sharp g = 2.02 EPR signals disappeared, and a broad low field resonance at g ~ 12 appeared; this signal is characteristic of the reduced S = 2 [3Fe-4S]$^{0}$ cluster (data not shown). In addition, rhombic EPR signals at g = 2.06, 1.94, and 1.88 (Fig. 6B) and g = 2.06, 1.94, and 1.90 (Fig. 6D), both attributed to a reduced S = 1/2 [4Fe-4S]$^{1+}$ cluster, were detected up to 30 K for *T. acidophilum* and *Sulfolobus* sp. ferredoxins, respectively, together with additional wings on the high and low field sides of the main EPR signals due to magnetic interactions with the reduced S = 2 [3Fe-4S]$^{0}$ cluster (Fig. 6, B and D).

Taken together, the XAS and EPR results indicate that the two archaeal zinc-containing ferredoxins contain one [3Fe-4S]$^{1+}$ cluster and one [4Fe-4S]$^{2+}$ cluster, and that the average iron environments are nearly identical in the two proteins (Figs. 5 and 6 and Table II). The zfx gene product of *T. acidophilum* contains three cysteine residues arranged in a Cys$^{67}$-Cys$^{68}$-Ile-Ala-Asp$^{71}$-Gly-Ala-Cys$^{74}$, and remote Cys$^{133}$-Pro motif, which could serve as ligands to a [3Fe-4S]$_{2}$ cluster, and four cysteine residues in another motif, Cys$^{129}$-Ile-Phe-Cys$^{136}$-Met-Ala-Cys$^{129}$, and remote Cys$^{75}$-Pro, which are likely ligands to a [4Fe-4S]$_{2}$ cluster (dotted cysteines in Fig. 1). The same spacing of consensus cysteine residues was found in other zinc-containing ferredoxin sequences (6, 10, 11, 13, 53), and was proposed to be attributed to the similarity of the pattern of hyperfine-shifted resonances of $^{1}$H-NMR spectra of the 7Fe form of zinc-containing ferredoxins$^{5}$ to those of the 3Fe-, 4Fe-, and 8Fe-containing ferredoxins (53, 54). In the *Azotobacter* type 7Fe-containing ferredoxins with a long C-terminal region, the cysteine ligand residues are arranged more asymmetrically due to the insertion of a short amino acid sequence stretch at the cluster binding motif (54–58). The zfx sequence also shows the presence of two additional cysteine residues, Cys$^{66}$ and Cys$^{115}$ (bold residues in Fig. 1), which are not present in the *Sulfolobus* ferredoxin sequence (Fig. 2), and hence most likely do not serve as ligands to the clusters.

**DISCUSSION**

The sequence and spectroscopic data reported herein provide detailed structural information of the metal binding sites in *T. acidophilum* zinc-containing ferredoxin. The tightly bound zinc atom of archaeal zinc-containing ferredoxins constitutes an isolated and structurally conserved zinc center. The zinc is tetrahedrally coordinated with (most likely) three histidine imidazoles and one carboxylate, with average Zn-N and Zn-O bond distances of 2.01 and 1.90 Å, respectively. The sequence comparisons suggest that the three conserved histidine residues in the N-terminal extension region and one conserved aspartate in the ferredoxin core fold (Fig 2) serve as ligands to the zinc. The similarity search for zinc-containing ferredoxin 5 T. Iwasaki, E. Watanabe, D. Ohmori, T. Imai, A. Urushiyama, M. Akiyama, C. M. V. Stålhandske, N. J. Cosper, and R. A. Scott, manuscript in preparation.
homologs with these consensus sequence motifs against nucleotide and amino acid sequence data bases indicated their limited distribution among hyperthermophilic organisms, even within the archaeal domain (Fig. 2). This implies that early zinc-containing ferredoxins might have appeared shortly after divergence of the early Archaea, which is also in line with previous phylogenetic analysis (14).

The overall protein fold of archaeal zinc-containing ferredoxins is largely asymmetric due to the presence of a long N-terminal extension and the insertion of central loop region, as

| Sample filename | Fit | Shell | $R_{\text{max}}$ | $\sigma_{\text{max}}^2$ | $f'$ |
|-----------------|-----|-------|-----------------|-----------------|-----|
| $\Delta k^3 |\chi = 13.05$ |
| 1 Zn-O | 1.91 | 0.0007 | 0.069 | 7 | 1 Zn-O | 1.91 | 0.0002 | 0.070 |
| 1 Zn-C | 2.82 | 0.0010 | | 1 Zn-C | 2.82 | 0.0030 | |
| 1 Zn-O | 3.08 | 0.0011 | | 1 Zn-O | 3.08 | 0.0032 | |
| 3 Zn-(N/O) | 2.01 | -0.0002 | | 3 Zn-(N/O) | 2.01 | -0.0001 | |
| 3 Zn-C | 2.94 | -0.0002 | | 3 Zn-C | 2.93 | 0.0001 | |
| 3 Zn-C | 3.07 | -0.0003 | | 3 Zn-C | 3.07 | 0.0002 | |
| 3 Zn-C | 4.10 | -0.0004 | | 3 Zn-C | 4.10 | 0.0003 | |
| 3 Zn-N | 4.18 | -0.0004 | | 3 Zn-N | 4.18 | 0.0003 | |
| 4 Zn-(N/O) | 2.01 | 0.0009 | | 4 Zn-(N/O) | 2.01 | 0.0013 | |
| 4 Zn-C | 2.93 | 0.0011 | | 4 Zn-C | 2.93 | 0.0013 | |
| 4 Zn-C | 3.06 | 0.0017 | | 4 Zn-C | 3.07 | 0.0019 | |
| 4 Zn-C | 4.09 | 0.0022 | | 4 Zn-C | 4.09 | 0.0025 | |

$^a$ $R_{\text{max}}$ is the metal-scatterer distance. $\sigma_{\text{max}}^2$ is a mean square deviation in $R_{\text{max}}$. The shift in $E_0$ for the theoretical scattering functions was optimized, but did not vary more than 1.5 eV. Numbers in square brackets were constrained to be either a multiple of the above value ($\sigma_{\text{max}}^2$) or to maintain a constant difference from the above value ($R_{\text{max}}$). $f'$ is a normalized error (chi-squared).

$$f' = \frac{\left| \sum_i \left( k \chi_{\text{calc}}(i) - \chi_{\text{exp}}(i) \right)^2 \right|}{\left( k \chi_{\text{calc}}^{\text{abs}} \right)_{\text{max}}^2 - \left( k \chi_{\text{calc}}^{\text{abs}} \right)_{\text{min}}^2}$$

![Fig. 6. EPR spectra of zinc-containing ferredoxin from *T. acidophilum* strain HO-62 (a and b) and *Sulfolobus* sp. strain 7 (c and d) in the air-oxidized (a and c) and dithionite-reduced (b and d) states at pH = 9.3.](image-url)

The overall protein fold of archaeal zinc-containing ferredoxins is largely asymmetric due to the presence of a long N-terminal extension and the insertion of central loop region, as
Sequence and XAS of Archaeal Zinc-containing Ferredoxin

1. PFAM database.

2. MASS spectrometry.

3. REFERENCES

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