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Prediction of the determinants of thermal stability by linear discriminant analysis: The case of the glutamate dehydrogenase protein family

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HIGHLIGHTS

• A novel method for predicting the determinants of thermostability in a protein family.

- It is a multivariate statistical method based on the linear discriminant analysis.
- It was applied to a set of 69 glutamate dehydrogenases from Archaea and Bacteria.
- Three amino acid clusters were predicted to be the determinants of thermostability.
- Analysis within the clusters led to identification of 8 critical amino acid sites.

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ABSTRACT

Little is known about the determinants of thermal stability in individual protein families. Most of the knowledge on thermostability comes, in fact, from comparative analyses between large, and heterogeneous, sets of thermo- and mesophilic proteins. Here, we present a multivariate statistical approach aimed to detect signature sequences for thermostability in a single protein family. It was applied to the glutamate dehydrogenase (GDH) family, which is a good model for investigating this peculiar process. The structure of GDH consists of six subunits, each of them organized into two domains. Formation of ion-pair networks on the surface of the protein subunits, or increase in the inter-subunit hydrophobic interactions, have been suggested as important factors for explaining stability at high temperatures. However, identification of the amino acid changes that are involved in this process still remains elusive. Our approach consisted of a linear discriminant analysis on a set of GDH sequences from Archaea and Bacteria (33 thermo- and 36 mesophilic GDHs). It led to detection of 3 amino acid clusters as the putative determinants of thermal stability. They were localized at the subunit interface or in close proximity to the binding site of the NAD(P)⁺ coenzyme. Analysis within the clusters led to prediction of 8 critical amino acid sites. This approach could have a wide utility, in the light of the notion that each protein family seems to adopt its own strategy for achieving thermostability.

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1. Introduction

Glutamate dehydrogenase (GDH) catalyzes the reversible oxidative deamination of L-glutamate to 2-oxoglutarate and ammonia using NAD(P)⁺ as coenzyme. The structure of GDH consists of six identical subunits of 48 kDa, each of them organized into two domains separated by a deep cleft. Domain I is responsible for directing the self-assembly of the subunits into hexamer, while domain II forms the dinucleotide-binding domain (Baker et al., 1992). The broad characterization of GDH in prokaryotes has led to its adoption as a paradigm for investigating adaptation to temperatures around 100 °C. Comparison between the 3D structure of the thermophilic GDH from *Pyrococcus furiosus* and that of the mesophilic homolog from *Clostridium symbiosum* has revealed one major difference, consisting of a series of ion-pair networks on the surface of the protein subunits and buried at inter-domain and inter-subunit interfaces (Yip et al., 1995). This finding has been supported by mutational studies on the GDHs of *Thermococcus litoralis* (Vetriani et al., 1998) and *Thermotoga maritima* (Lebbink et al., 1999). Determination of the 3D structure of the hyperthermostable GDH from *Pyrobaculum islandicum* has revealed that oligomerization is also affected by an increase in the inter-subunit hydrophobic interactions (Bhuiya et al., 2005).

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Analysis of the amino acid composition has shown that thermophilic GDHs have a lower content of glycine, methionine, and cysteine with respect to mesophilic GDHs (Knapp et al., 1997). Bhuiya et al. (2005) have found that the hyperthermostable GDHs of *P. islandicum* and *P. furiosus* show a similar content of alanine and β -branched residues (Val, Thr, and Ile). Comparison of the mesophilic GDH from *C. symbiosum* with the thermophilic homologs from *P. furiosus* and *T. litoralis* has pointed out that the most frequent substitutions are Val/Ile, Val/Lys, Leu/Ile, and Gly/Ala, though no solid conclusions about their functional role have been reached (Britton et al., 1995).

A criticism to this approach is that discrimination between the amino acid changes responsible for thermal adaptation and those affected by other evolutionary pressures is very difficult to achieve. For example, the GDH of *P. furiosus* (optimal growth temperature at 98 °C) shows an amino acid difference of 60% with respect to that of *C. symbiosum* (optimal growth temperature at 37 °C). It is obvious to expect that only a small fraction of such amino acid diversity is due to positive selection in response to high temperature. Another criticism concerns the assumption that all amino acid positions are equivalent and independent with respect to the substitution process, thus underestimating the importance of the local environment of a residue and the effects of amino acid substitutions at neighboring sites.

A better understanding of this process could be achieved by using predictive methods. As demonstrated by a series of recent publications (Chen et al., 2012a, 2013; Min et al., 2013; Xu et al., 2013a, 2013b; Xiao et al., 2013) and summarized in a comprehensive review (Chou, 2011), to develop an useful prediction method we need to consider the following procedures: i) construct a valid benchmark dataset to train and test the predictor; ii) consider a number of properties correlated with the attribute to be predicted; iii) introduce a powerful algorithm to operate the prediction; iv) perform a cross-validation test to evaluate the accuracy of the prediction.

Accordingly, we first constructed a training set of 33 thermo- and 36 mesophilic GDHs from Archaea and Bacteria. We then selected a number of physico-chemical properties of amino acids, some of them correlated to protein stability. We introduced the linear discriminant function (Fisher, 1936; Lachenbruch and Goldstein, 1979) as predictor of the determinants of thermostability. This choice was based on the ability of linear discriminant analysis to distinguish adaptive from neutral amino acid changes in protein evolution (Horimoto et al., 1990; Otsuka et al., 1993). Finally, we evaluated the accuracy of the prediction by using the Kolmogorov-Smirnov permutation test. This approach led to detection of 3 amino acid clusters as the putative determinants of thermal adaptation in GDH.

2. Materials and methods

2.1. Sequence data

We selected from the UniProt Knowledgebase (http://www.ebi. ac.uk/uniprot/) a training set of 69 GDH sequences. As shown in Table 1, it was subdivided into four groups: I) 17 GDHs from thermophilic Archaea with an optimal growth temperature (OGT) ranging from 55° to 98 °C II) 17 GDHs from mesophilic Archaea (OGT from 22° to 37 °C) III) 16 GDHs from thermophilic Bacteria (OGT from 55° to 80 °C) IV) 19 GDHs from mesophilic Bacteria (OGT from 27° to 37 °C). The training set included 7 GDHs encoded by paralogous genes: 2 from *Halobacterium salinarium*, 2 from *Haloarcula marismortui*, 1 from *Halogeometricum borinquense*, *Natronomas pharaonis*, and *Thermanaerovibrio acidaminovorans*, respectively. Information about OGT was taken from the German Collection of Microorganisms and Cell Culture (http://www.dsmz.de).

Table 1

List of the 69 GDH sequences of the training set.

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Methanocellula paludicola International parkeri Methanosarcina barkeri International parkeri Jncultured methanogenic archaeon RC-1 International parkeri Chermophilic Bacteria (16 GDHs) International parkeri Soprothermobacter proteolyticus International parkeri Geobacillus thermodenitrificans International parkeri Sphaerobacter thermophilus International parkeri Suffuritydrogenibium azorense International parkeris Symbiobacterium thermophilum International parkeris Thermoanaerobacter sp. International parkeris Fermoanaerobacter tengcongensis International parkeris Thermoanaerobio acidaminovorans International parkeris Thermosicrobium roseum International parkeris Thermosipho africanus Internosipho africanus Thermosipho africanus International parkeris Thermosipho melanesiensis International parkeris Mesophilic Bacteria (19 GDHs) Acienetobacter baumanii Aciellus cereus International parkeris	Q3IS94	37	
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Methanosarcina barkeri Incultured methanogenic archaeon RC-1 Incultured methanogenic archaeon RC-1 Incultured methanogenic archaeon RC-1 Incuntured methanogenic archaeon RC-1 Incultured methanogenic archaeon RC-1 Incuntured methanogenic archaeon RC-1 Incuntured methanogenic archaeon RC-1 Incuntured methanogenic archae	D1YWP3	37	411
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Thermophilic Bacteria (16 GDHs) Coprothermobacter proteolyticus Seobacillus thermodenitrificans Seobacillus thermodenitrificans Suphaerobacter thermophilus Sulfurihydrogenibium azorense Symbiobacterium thermophilum Thermoanaerobacter sp. Termoanaerobacter rengcongensis Thermanaerovibrio acidaminovorans Thermanaerovibrio acidaminovorans Thermonicrobium roseum Thermosinus carboxydivorans Thermosipho africanus Thermosipho melanesiensis Thermotoga maritima Thermotoga createria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	Q467V9	35	419
Coprothermobacter proteolyticus Eobacillus thermodenitrificans Sphaerobacter thermophilus Sulfurihydrogenibium azorense Symbiobacterium thermophilum Thermoanaerobacter sp. Termoanaerobacter tengcongensis Thermanaerovibrio acidaminovorans Thermoanaerovibrio acidaminovorans Thermoaculum terrenum Thermosicrobium roseum Thermosipho africanus Thermosipho africanus Thermosipho melanesiensis Thermostoga maritima Thermoster baumanii Acinetobacter baumanii Bacillus cereus Bacillus pumilus	Q0W8B2	30	417
Coprothermobacter proteolyticus Geobacillus thermodenitrificans phaerobacter thermophilus ulfurihydrogenibium azorense ymbiobacterium thermophilum hermoanaerobacter sp. ermoanaerobacter tengcongensis hermanaerovibrio acidaminovorans hermoanaerobacter tengcongensis hermoanaerovibrio acidaminovorans hermosino cardaminovorans hermosinus carboxydivorans hermosipho africanus hermosipho melanesiensis hermotoga maritima hermostermotilus Aesophilic Bacteria (19 CDHs) kcinetobacter baumanii iacillus cereus Bacillus pumilus			
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ulfurihydrogenibium azorense ymbiobacterium thermophilum 'hermoanaerobacter sp. 'ermoanaerobacter tengcongensis 'hermanaerovibrio acidaminovorans 'hermanaerovibrio acidaminovorans 'hermonacerovibrio acidaminovorans 'hermonicrobium terrenum 'hermosinus carboxydivorans 'hermosipho africanus 'hermosipho melanesiensis 'hermotoga maritima 'hermostile Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	D1C4B5	55	425
Symbiobacterium thermophilum Image: Symbolic Constant Symbol Thermoanaerobacter tengcongensis Image: Symbol Thermanaerovibrio acidaminovorans Image: Symbol Thermanaerovibrio acidaminovorans Image: Symbol Thermonaerovibrio acidaminovorans Image: Symbol Thermonaerovibrio acidaminovorans Image: Symbol Thermosinus carboxydivorans Image: Symbol Thermosipho africanus Image: Symbol Thermosipho melanesiensis Image: Symbol <td< td=""><td>C1DWD7</td><td>68</td><td>418</td></td<>	C1DWD7	68	418
hermoanaerobacter sp. ermoanaerobacter tengcongensis hermanaerovibrio acidaminovorans hermobaculum terrenum hermosicrobium roseum hermosipho africanus hermosipho melanesiensis hermosopho melanesiensis hermosopho melanesiensis hermostermophilus Mesophilic Bacteria (19 CDHs) kcinetobacter baumanii lacillus cereus Bacillus gumilus	Q67Q62	60	417
Fermoanaerobacter tengcongensis Thermanaerovibrio acidaminovorans Thermobaculum terrenum Thermosinus carboxydivorans Thermosipho africanus Thermosipho africanus Thermosipho melanesiensis Thermosipho melanesiensis Thermosipho Exteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	BOK183	67	416
Thermanaerovibrio acidaminovorans Thermanaerovibrio acidaminovorans Thermobaculum terrenum Thermosinus carboxydivorans Thermosipho africanus Thermosipho melanesiensis Thermosipho melanesiensis Thermosta maritima Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	Q8RAK8	75	413
Chermanaerovibrio acidaminovorans I Chermobaculum terrenum I Chermosinus carboxydivorans I Chermosipho africanus I Chermosipho africanus I Chermosipho melanesiensis I Chermotoga maritima I Chermotoga thermophilus I Mesophilic Bacteria (19 GDHs) I Acinetobacter baumanii I Bacillus cereus I Bacillus pumilus I	D1B825	55	414
Thermobaculum terrenum Thermomicrobium roseum Thermosipho africanus Thermosipho melanesiensis Thermotoga maritima Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	D1B8F3	55	414
Thermomicrobium roseum Thermosinus carboxydivorans Thermosipho africanus Thermosipho melanesiensis Thermotoga maritima Thermus thermophilus Mesophilic Bacteria (19 CDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	D168F5 D1CFL6	55 67	424 419
Thermosinus carboxydivorans Thermosipho africanus Thermosipho melanesiensis Thermotoga maritima Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	B9KZK6	70	419
Thermosipho africanus Thermosipho melanesiensis Thermotoga maritima Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus			
Thermosipho melanesiensis Thermotoga maritima Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	A1HSF6	60 75	412
Thermotoga maritima Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	B7IG24	75	427
Thermus thermophilus Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	A6LKL9	70	412
Mesophilic Bacteria (19 GDHs) Acinetobacter baumanii Bacillus cereus Bacillus pumilus	P96110	80	416
Acinetobacter baumanii Bacillus cereus Bacillus pumilus	OOCDOC	75	419
Bacillus cereus Bacillus pumilus	Q8GR86		
Bacillus pumilus		30	423
	B0VQ84	30	428
Racillus subtilis	BOVQ84 Q63DP1	30	424
	B0VQ84	30	424
	B0VQ84 Q63DP1 A8FEN2 P39633		429
	BOVQ84 Q63DP1 A8FEN2	37	428
	B0VQ84 Q63DP1 A8FEN2 P39633	37 27	421
Frankia sp.	BOVQ84 Q63DP1 A8FEN2 P39633 Q7VXC5		110
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667	27	418
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1YI38	27 28	418 424
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1YI38 A8LCL1	27 28 28	
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1YI38 A8LCL1 A6T8K3	27 28 28 37	424
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1YI38 A8LCL1 A6T8K3 B1HXF2 A1ZDU1	27 28 28 37 30	424 414
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98	27 28 28 37 30 22 28	424 414 424 426
-	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98 A1APQ5	27 28 28 37 30 22 28 30	424 414 424 426 420
-	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98 A1APQ5 Q0RY06	27 28 28 37 30 22 28 30 28	424 414 424 426 420 423
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98 A1APQ5 Q0RY06 B4SUI7	27 28 28 37 30 22 28 30 28 34	424 414 424 426 420 423 424
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98 A1APQ5 Q0RY06 B4SUI7 Q6GID0	27 28 28 37 30 22 28 30 28 34 37	424 414 424 426 420 423 424 414
	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98 A1APQ5 Q0RY06 B4SU17 Q6GID0 A8GEN4	27 28 28 37 30 22 28 30 28 34 37 30	424 414 424 426 420 423 424 414 424
Sporosarcina halophila	B0VQ84 Q63DP1 A8FEN2 P39633 Q7VXC5 Q6J667 B1Y138 A8LCL1 A6T8K3 B1HXF2 A1ZDU1 Q8EQ98 A1APQ5 Q0RY06 B4SUI7 Q6GID0	27 28 28 37 30 22 28 30 28 34 37	424 414 424 426 420 423 424 414

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