

Local sequence-structure relationships in proteins

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Abstract

We seek to understand the interplay between amino acid sequence and local structure in proteins. Are some amino acids unique in their ability to fit harmoniously into certain local structures? What is the role of sequence in sculpting the putative native state folds from myriad possible conformations? In order to address these questions, we represent the local structure of each C_{α} atom of a protein by just two angles, θ and μ , and we analyze a set of more than 4000 protein structures from the PDB. We use a hierarchical clustering scheme to divide the 20 amino acids into six distinct groups based on their similarity to each other in fitting local structural space. We present the results of a detailed analysis of patterns of amino acid specificity in adopting local structural conformations and show that the sequence-structure correlation is not very strong compared to a random assignment of sequence to

structure. Yet, our analysis may be useful to determine an effective scoring rubric for quantifying the match of an amino acid to its putative local structure.

Keywords: sequence-structure relationship, local structure, amino acid groupings, amino acid propensity

Significance statement: We present a quantitative study of the emergent constraints of sterics, the chain topology, and the quantum chemistry on local protein native state structures measured in a simple representation. We present two main classes of results: the propensity of amino acids to occupy certain local structures and a grouping of amino acids based on their similarity in hosting local structures.

It is known that there are just a few important principles (1-6) that drive the folding process of a protein: the requirement of avoiding steric overlaps in both the folded and unfolded states, the lower conformational entropy in the folded state than in the unfolded state, the hydrophobic effect favoring a compact conformation that is able to expel water from the core of the folded state and the delicate balance of hydrogen bonds with the solvent and within the protein backbone that can tip the energetic balance between the unfolded and folded state. The fundamental issue is how nature has effectively explored the astronomically large sequence space through evolution to make proteins the molecular target of natural selection.

Here we characterize the native state folds within a simple coarse-grained representation and elucidate the role, if any, played by the repertoire of amino acids in fitting into one of these local geometries. We model a chain by just its C_α atoms and follow the coordinate representation shown in Figure 1. With the knowledge of the preceding C_α locations, we specify the position of a given C_α atom by three coordinates (7), the bond length, b , and two angles, θ and μ . θ is the bending angle at the given C_α location, whereas μ is the angle between successive binormals (Figure 1). The binormal associated with a specific consecutive triplet of C_α atoms is the unit vector perpendicular to the plane of the triplets. The tangent, the normal, and the binormal, all at the middle C_α atom, form a right-handed Cartesian coordinate system. This coordinate system was introduced by Rubin and Richardson in a paper describing the Byron bender that allowed for a simple construction of protein C_α models (8,9).

Our analysis is carried out with a set of more than 4000 experimentally determined protein native state structures. Starting from the Top 8000 set proteins of the Richardson laboratory (10,11) with 70% homology level, we excluded all structures with missing atoms in the protein backbone, yielding a set of 4416 protein native state structures that we used for our analysis (the same set was employed in Ref. 7) (see Table S1 in Supplementary Information). We successfully validated our analysis using 478 proteins from the Dunbrack data set (12), this time with a maximum sequence homology level of 20%. There were 205 proteins in common between the Richardson and Dunbrack sets that we employed. We carried out the (θ , μ) analysis for both the Richardson and Dunbrack data sets and obtained virtually identical results with the Dunbrack data being understandably more sparse. We present here the detailed analysis for just the much larger Richardson data set.

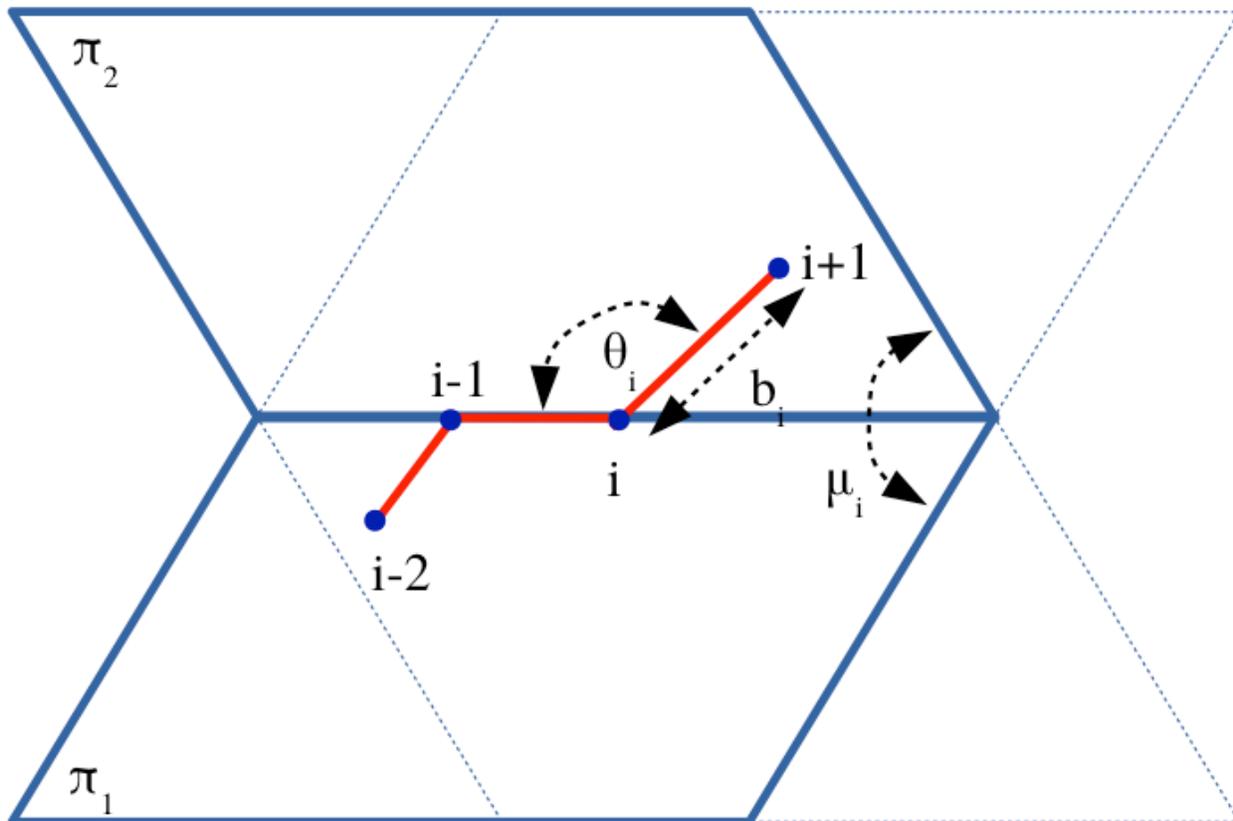


Figure 1: Definition of coordinate system. The bond length b at location i , b_i , is the distance between the points i and $(i+1)$. The angle θ_i is the angle subtended at i by points $(i-1)$ and $(i+1)$ along the chain. The third coordinate μ_i is the dihedral angle between the planes π_1 and π_2 formed by $[(i-2), (i-1), i]$ and $[(i-1), i, (i+1)]$ respectively and is the angle between the binormals at $(i-1)$ and i . Knowledge of the coordinates of the previous three points $(i-2, i-1, i)$ and the three variables (b_i, θ_i, μ_i) are sufficient to uniquely specify the coordinates of the point $(i+1)$.

A simplification arises because the vast majority of bond lengths is nearly constant (Figure 2). Figures 2a and a blown up version, Figure 2b, depict histograms of bond lengths with two peaks centered around 3.81\AA and 2.95\AA . The shorter bonds are associated with a Ramachandran

angle ω (1) around 0 degrees (13) (Figure 2c). Because the fraction of short bonds is relatively small (0.3%), our analysis here is carried out with all C_α positions, each characterized by a bond length, the θ and μ angles and the amino acid identity. An analysis of the amino acids associated with just the short bonds shows the preponderance of glycine in the first position and proline in the second position (because of the low barrier for transitioning between its cis and trans conformations).

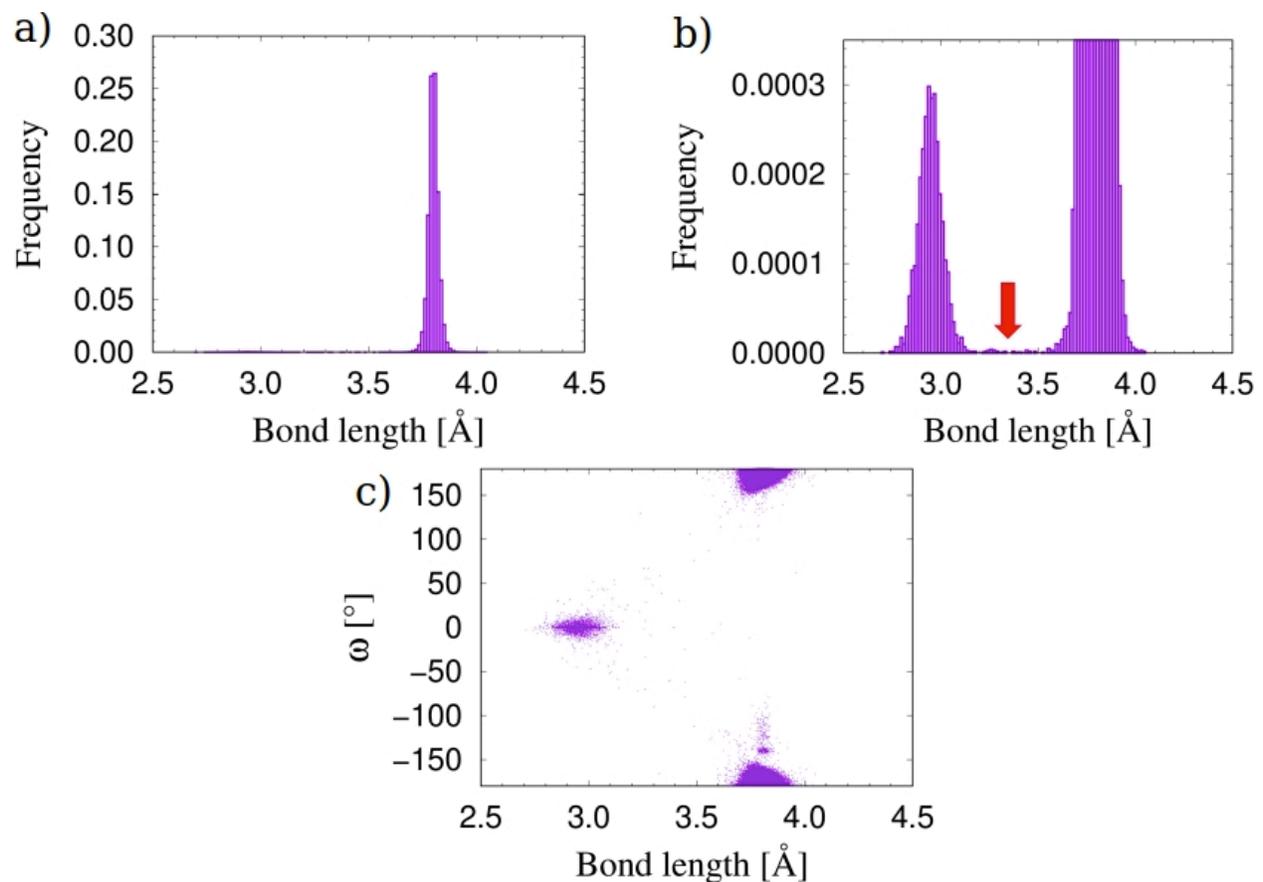


Figure 2: Distribution of bond lengths. Figure 2a shows a histogram of bond lengths in our data set. A blown up version in Fig 2b shows that the distribution is bimodal with short bonds (centered around 2.95Å) and long bonds (centered around 3.81Å). The red arrow is the length

we use for partitioning the bonds into the short and long categories. Figure 2c shows the link between the Ramachandran ω angle (1,13) and the bond length.

For a non-interacting phantom chain, one obtains a uniform distribution of points in the (θ, μ) plane (not shown as a figure). As a benchmark, we studied, using Wang-Landau Monte Carlo simulations (14), a simple self-avoiding polymer chain model comprised of 40 unit diameter tangent spheres (tethered hard spheres) subject to a self-attraction between sphere centers located within a distance of 2 units of each other. Figure 3a and 3b show a cross plot in the (θ, μ) plane of 17 conformations in the coil phase adopted by the chain at high temperatures and for 17 low energy conformations, respectively. The situation is dramatically different for proteins compared to a standard self-avoiding polymer model. Figure 3c is the (θ, μ) cross plot for the protein data set with a highly selective occupancy of (θ, μ) space (a version of this graph was presented earlier in Ref. 7).

We binned the data in Figure 3c into squares of width 5° along θ (24 bins in the range 60° - 180°) and 5° along μ (72 bins spanning the range from 0° to 360°) to determine the three highest density regions. These density peaks are shown in the figure as black X's along with three larger squares of size $10^\circ \times 10^\circ$ around them. They are identified as helices (blue region with black X at $\theta = 92.5^\circ$ and $\mu = 47.5^\circ$), β -strands (red region with black X at $\theta = 122.5^\circ$ and $\mu = 192.5^\circ$), and loops (green region with black X at $\theta = 92.5^\circ$ and $\mu = 242.5^\circ$) with 184382, 16372, and 10974 points respectively. The density of points in the α -helix peak is approximately 20 times that of loops and β -strands but the loop and β -strand regions are more spread out than the helical

region. The other populated regions in the (θ, μ) plane correspond to variants of helices and β -strands and the loops that link them together in the native state structure.

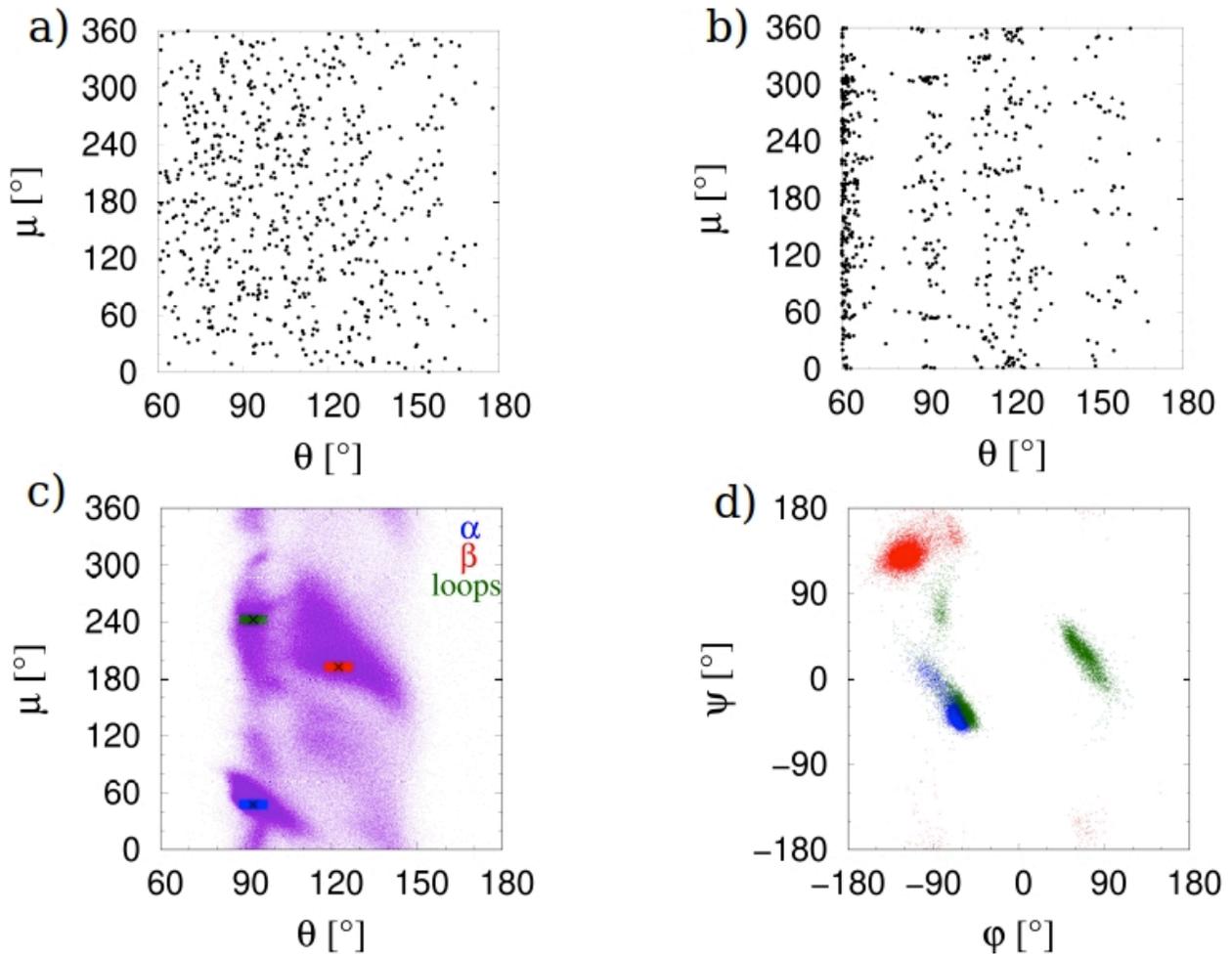


Figure 3: Local structure representation. a) (θ, μ) cross plot for the high temperature coil phase of tethered hard spheres. The only constraint here is the requirement of self-avoidance of the spheres. The points are scattered across the plane with no θ angle less than 60° (a steric constraint) and few almost straight line triplets with a θ near 180° . b) (θ, μ) cross plot for low energy states of tethered hard spheres. Here again one observes no θ angles below 60° and favored θ angles of $60^\circ, 90^\circ, 120^\circ$, and 150° showing that the order favors a face-centered-cubic packing locally, which would be appropriate for the close packing of untethered spheres. c) (θ, μ)

plot for the Richardson data set comprising 4416 proteins and 972519 residues (purple points). The three highlighted regions correspond to density peaks related to α -helices (blue region $\theta = 92.5^\circ$ and $\mu = 47.5^\circ$), β -strands (red region $\theta = 122.5^\circ$ and $\mu = 192.5^\circ$), and loops (green region $\theta = 92.5^\circ$ and $\mu = 242.5^\circ$) (d) Plot of the Ramachandran (φ, ψ) angles for the highlighted regions in Figure (c).

It is important to note that the angles θ and μ are distinct from the Ramachandran (1) angles, which require the knowledge of the locations of backbone atoms besides those of the C_α atoms. The (θ, μ) pair is a coarse grained representation of the Ramachandran angles and can be useful to describe a generic chain conformation and employed in models of statistical mechanics (15). In fact, knowing a sequence of Ramachandran angles, one can derive the values of θ and μ . The inverse process of determining the Ramachandran angles from the (θ, μ) values does not have a unique solution. For the C_α atoms in the interior of all 4416 proteins, we measured the (θ, μ) as well as the Ramachandran (φ, ψ) angles. We illustrate the relationship between the two coordinate systems in Figure 3d. We plot the three colored regions (blue, red and green) of dense points in Figure 3c, but this time expressed as the (φ, ψ) Ramachandran angles color coded in the same manner as in the (θ, μ) plot. Note that the closely packed points in the (θ, μ) plot are more dispersed in the Ramachandran plot sometimes occupying non-contiguous regions. This is because θ and μ depend on more than one set of Ramachandran angles and the relationship is complicated and non-linear.

There are four important earlier papers that our work builds on. Rackovsky and Scheraga (16) considered a torsion-curvature plot (distinct from but related to the plot we studied) for 22 protein structures for two different structural groups (helices + bends and extended strands) and the amino acids present therein. Levitt (17) analyzed 13 proteins and considered a (θ, μ) plot similar to ours except that the definition of μ was shifted by one C_α position in the backward direction compared to our definition. Our own definition was motivated by defining θ and μ at a given site i that would determine the coordinates of the $(i+1)$ -th C_α coordinate. Importantly, Levitt determined an approximate empirical relationship between his θ and μ to elucidate approximate potentials for folding simulations.

Oldfield and Hubbard (18) considered two successive θ angles and one μ angle (defined for a bond joining the two C_α atoms) for a set of 83 protein structures and carried out a comprehensive study of local conformational space (but not amino acid preferences) recognizing that the two major building blocks of protein native state structures, helices and strands, are repetitive conformations. DeWitte and Shakhnovich (19) considered 87 protein structures with a goal of deducing the pairwise potentials, in the spirit of Miyazawa and Jernigan, for the formation of secondary structures in protein simulations based on a cross-plot of two successive μ angles (this time again defined as bond variables rather than at a site) and employing Levitt's empirical relationship. Finally, the approach of Bahar, Kaplan, and Jernigan (20) is most similar to ours. They do have a (θ, μ) plot just like ours except that their μ definition is shifted by one position compared to ours. They employed 302 protein structures for their

analysis, they carried out an amino acid propensity estimate like we do, and they successfully developed short-ranged (along the sequence) rotational potentials for single amino acids.

In essence, our work here builds on these earlier advances. The principal distinctions are the definition of μ - our μ is defined at a site not at a bond, it is shifted with respect to other definitions, and the number of protein structures we employ, many decades after the earliest work, is understandably larger and comprises over 4000 experimentally determined and curated protein structures. Our goal in this paper is not to extract effective potentials but rather analyze, more generally, sequence-local structure relationships. Furthermore, we seek to group the 20 amino acids into distinct groups in terms of their similarity to substitute for each other in local conformational space.

Figure 4 shows histograms of θ and μ values and evidence for a clear correlation between the average values of θ and the average value of μ among all proteins. Table 1 presents data on the amino acid occurrence probability and the degree of localization in (θ, μ) space. For each amino acid, we measured the inverse participation ratio (IPR) defined as

$$IPR = \frac{(\sum_{i=1}^N x_i^2)^2}{\sum_{i=1}^N x_i^4} \quad (1)$$

where x_i denotes the normalized density of occupancy of the i -th bin in (θ, μ) space and the total number of bins $N=1728$. An IPR value of 1 indicates perfect localization in just one bin whereas the largest possible value of the IPR is $N=1728$ for a uniform occupancy of all 1728 bins.

A perfect localization (IPR=1) is indicative of an amino acid that is always associated with the same local structure leading to a perfect sequence-structure relationship. The most localized amino acid is LEU (IPR=2.70) while the least localized is PRO (IPR=83.28). Figure 5 shows the occupancies of the (θ, μ) space of amino acids LEU and PRO. Interestingly, even the most localized amino acid, while being largely concentrated in just a few squares, is yet spread out over many squares indicating that there is no strong selection of local structure by amino acid identity.

We carried out an analysis of triplet amino acids identities of all the 324 tight bends with θ angles less than 80° . The smallest θ angle in the data set has a value of 59.98° and the corresponding amino acid triplet is GLY-GLN-ASP. These tight turns $(i-1, i, i+1)$ have no selectivity in μ angles. However, there is indeed a sequence-structure relationship with (GLY or SER) accounting for a total of 34% occupancy in the $i-1$ position, (PRO or SER) having 31% residency in site i , and (ALA or SER) accounting for 21% in site $(i+1)$.

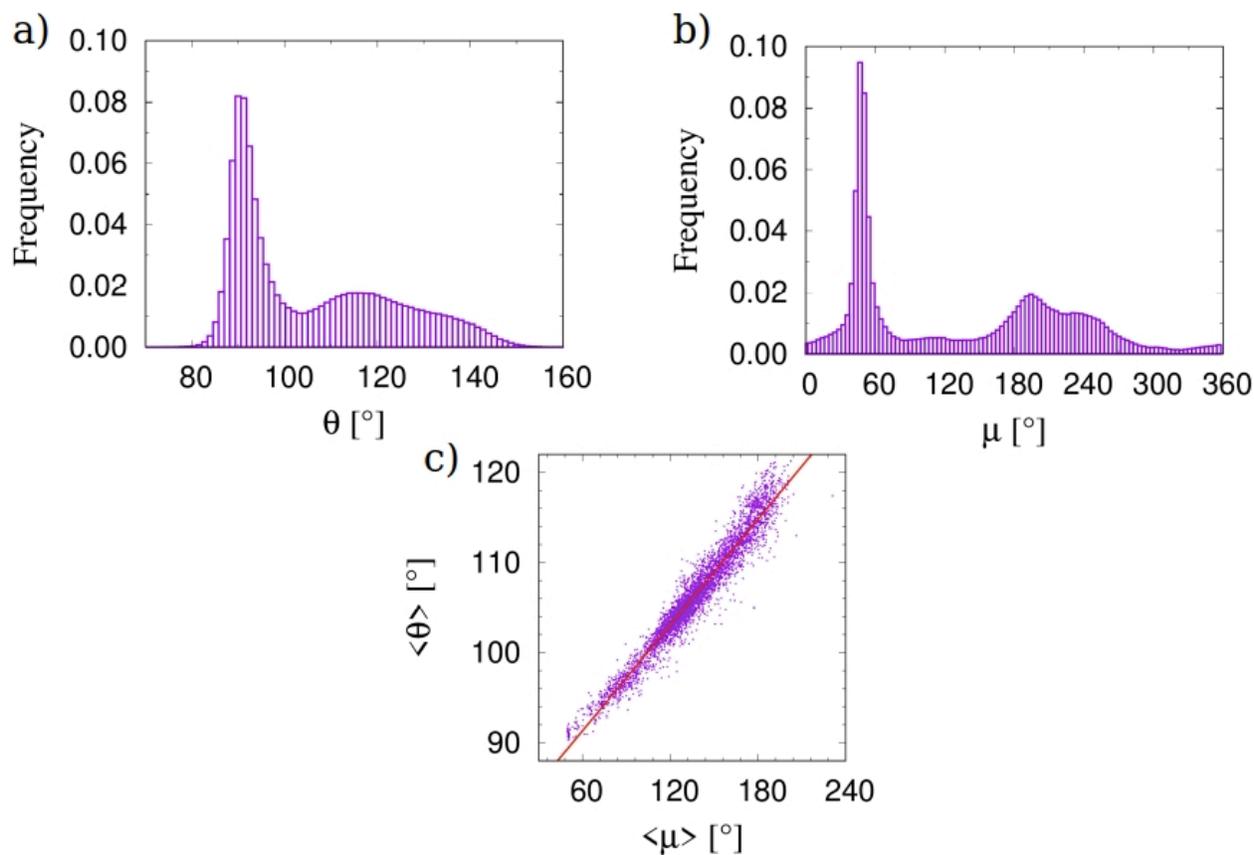


Figure 4: a) and b). Histograms of θ and μ values showing a multi-peaked structure. c). A plot of the average value of θ versus the average value of μ for all 4416 proteins showing a tight correlation with a Pearson correlation coefficient of 0.97. This may be readily understood by noting that a protein structure is primarily composed of helices and sheets with varying fractions depending on the protein being considered. The θ - μ values for an α -helix are both smaller than those of a β -strand leading to the correlation. Note that the standard deviations (not shown) are large because of the relatively large width in angle space of the regions.

Amino acid type	Fraction [%]	Inverse Participation Ratio (IPR)
ALA	8.53	3.28
ARG	4.84	3.24
ASN	4.42	4.53
ASP	5.96	4.60
CYS	1.36	3.69
GLU	6.48	3.25
GLN	3.61	3.30
GLY	7.90	11.61
HIS	2.32	4.31
ILE	5.62	2.93
LEU	8.79	2.70
LYS	5.70	3.43
MET	2.02	2.95
PHE	4.04	4.06
PRO	4.59	83.28
SER	5.88	5.14
THR	5.58	4.75
TRP	1.52	3.99
TYR	3.61	4.25
VAL	7.23	3.77

Table 1: Frequency of 20 amino acids in the set of 4416 proteins (second column) and a measure of the localization of each amino acid in (θ, μ) space (third column).

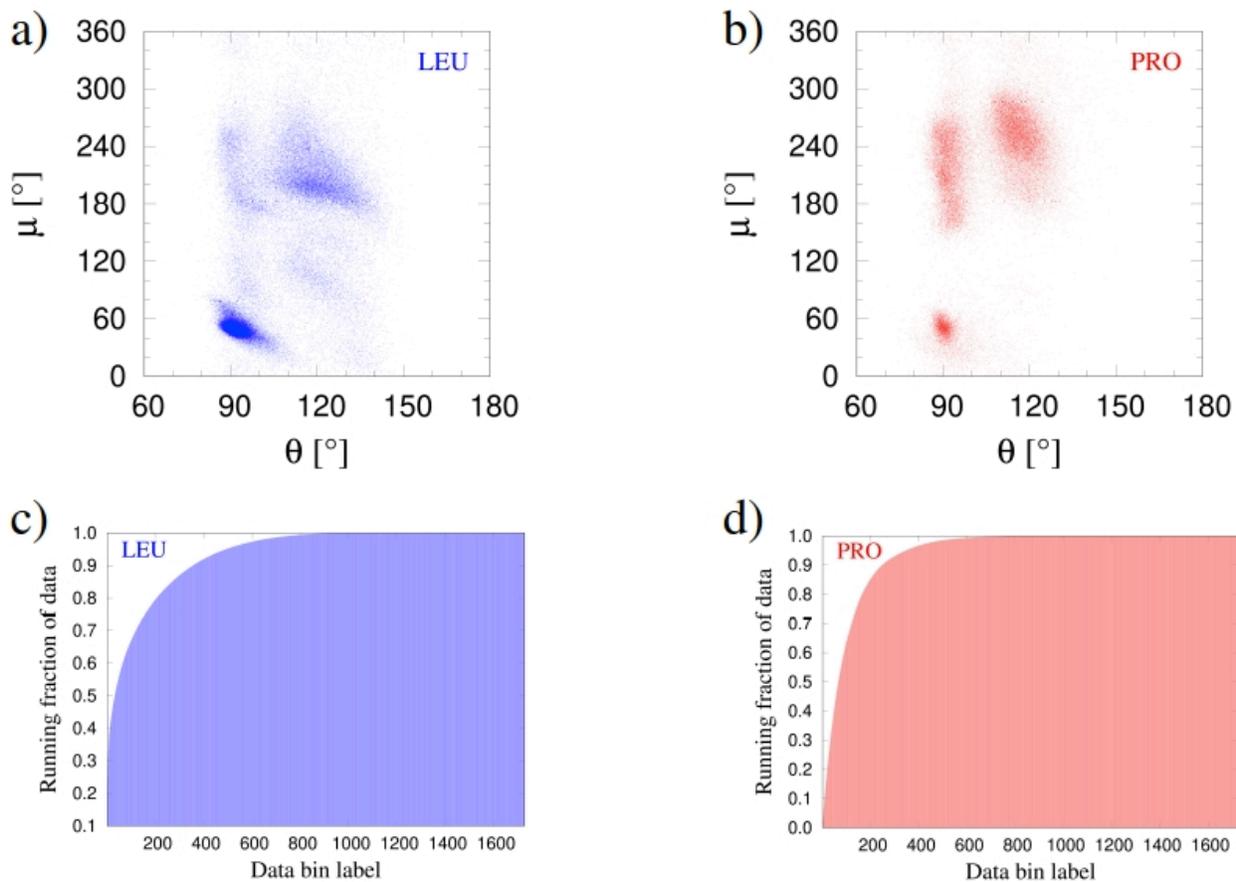


Figure 5: Occupancy pattern of amino acids LEU and PRO in (θ, μ) space. a) and b) depict the locations of the two amino acids. LEU is the most localized amino acid (IPR=2.70) whereas PRO has the largest IPR=83.28 value among the amino acids and is spread out the most. A rank ordered normalized occupancy fraction of the two amino acids is shown in c), and d). The number of bins needed to account for 50% and 90% occupancy for the two amino acids are LEU – 33 and 356, and PRO – 66 and 248, respectively.

We studied histograms of the θ and μ values associated with each of the twenty amino acids. The distributions are roughly equally wide and substantially independent of amino acid identity (see Figures 6 and 7).

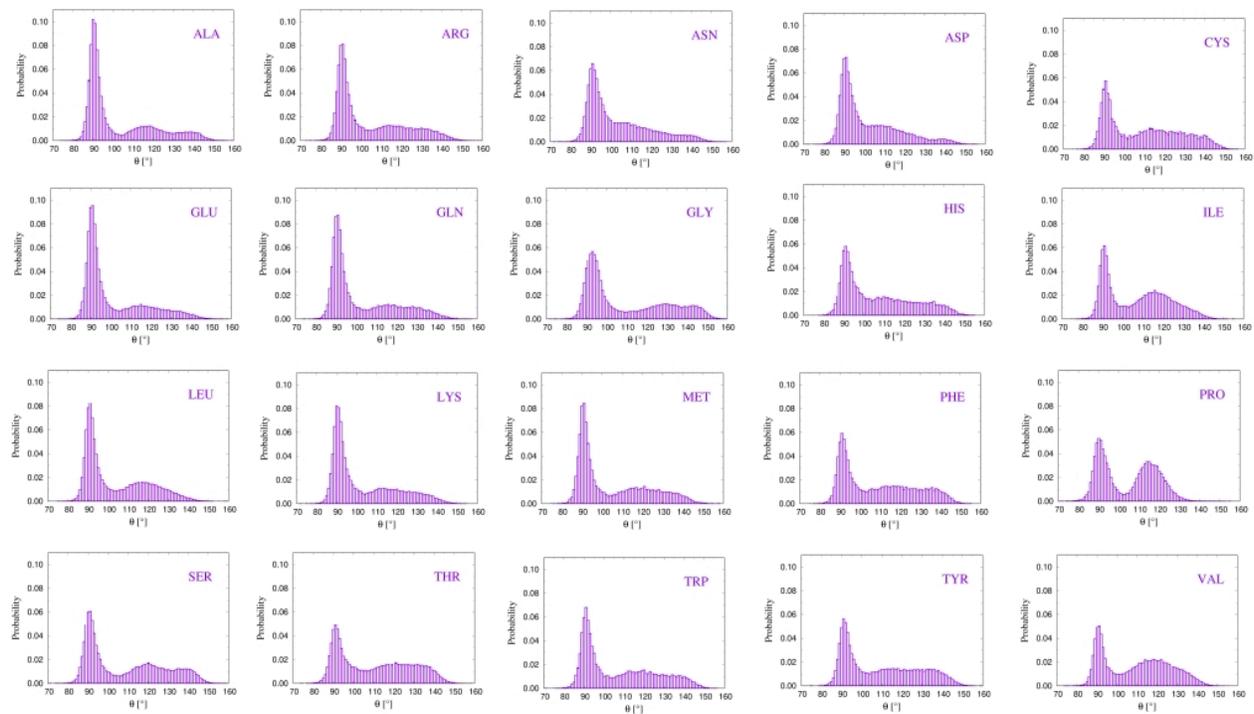


Figure 6: Histograms of the θ values for each of the twenty amino acids. While the shapes of the histograms vary from amino acid to amino acid, the ranges are mostly independent of amino acid identity. PRO is a bit of an outlier with a somewhat lower upper cut-off value of θ .

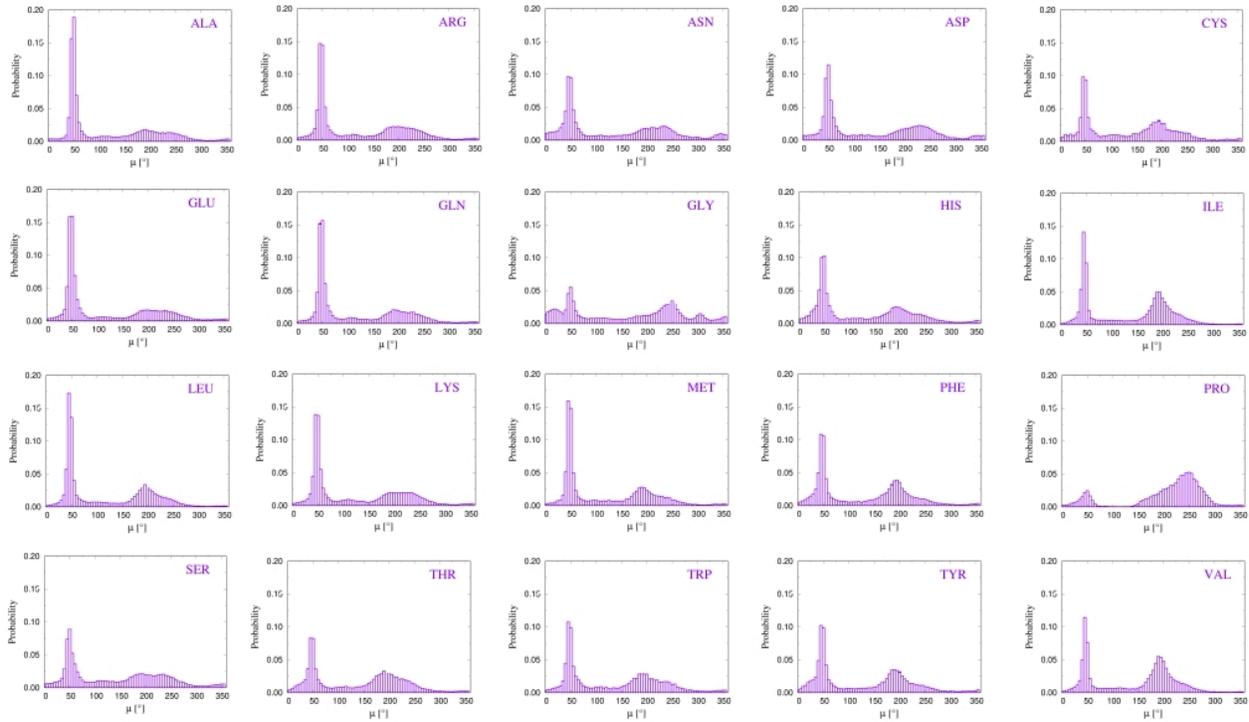


Figure 7: Histograms of the μ values for each of the twenty amino acids. Even though the shapes of the histograms vary from amino acid to amino acid, the ranges are mostly independent of amino acid identity.

Unlike the α -helix region associated with tight local packing and hence a relatively small variation in the θ angle, there is a range of θ values associated with the β -strand region. We carried out sequence analyses of the β -strands to understand whether there is an amino acid selection principle for θ . We selected the (θ, μ) subspace consisting of μ values in the range from 175° to 185° ($\pm 5^\circ$ degree interval around the ideal value of 180°) and of θ angles in the range from 105° to 145° . We divided up the relevant range of θ angles into 40 bins of width 1° . Again, we measure the IPR defined in Eq.(1) with $N=40$ in this case. The extreme values of the IPR are 16.08 for the most localized amino acid, PRO, and 31.46 for the most spread out amino

acid, ASP (see Figure 8). The average θ value and its standard deviation for all amino acids in the β -region is 128.0° and 9.5° respectively.

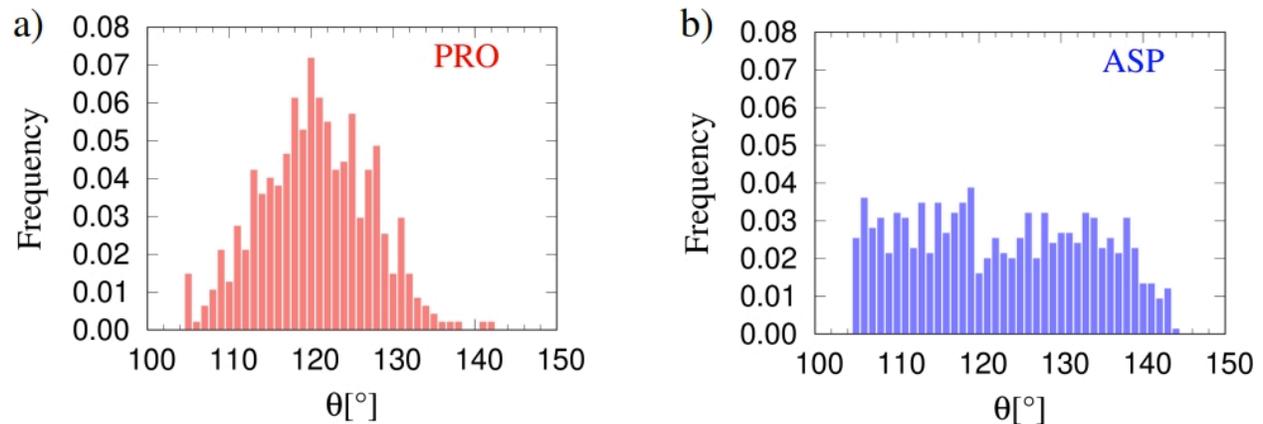


Figure 8: Distribution of θ angles in the β - region for PRO (a) and ASP (b). PRO is the most localized amino acid, yet exhibits some spread of θ angles.

We also studied the identities of the 210 pairs of amino acids (and their associated side chain sizes) located at sites $i-1$ and $i+1$ (these side chains stick out in roughly the same direction with a possibility of steric clashes) flanking site i in the β -region. We considered only those statistically significant pairs ($i-1, i+1$) which occurred at least 162 times (estimated as the total number of pairs divided by 210) with beads $i-1, i, i+1$ all lying in the β -strand region and divided the θ range again into 40 equally spaced bins. The number of amino acid pairs that met the 162 threshold was 52 out of the 210 pairs. We find that all pairs are spread out in θ values. The most localized pair among these was ALA-THR with an IPR of 10.51 and the most spread out pair was PHE-PRO with an IPR of 22.77 (see Figure 9 for histograms of θ values associated with these pairs). A cross plot of the mean van der Waals diameter of a pair and its average θ value (not shown) results in a weak correlation and an overall negative trend. All these results indicate that

the sequence does not play a significant role in determining the θ angle associated with a β -strand.

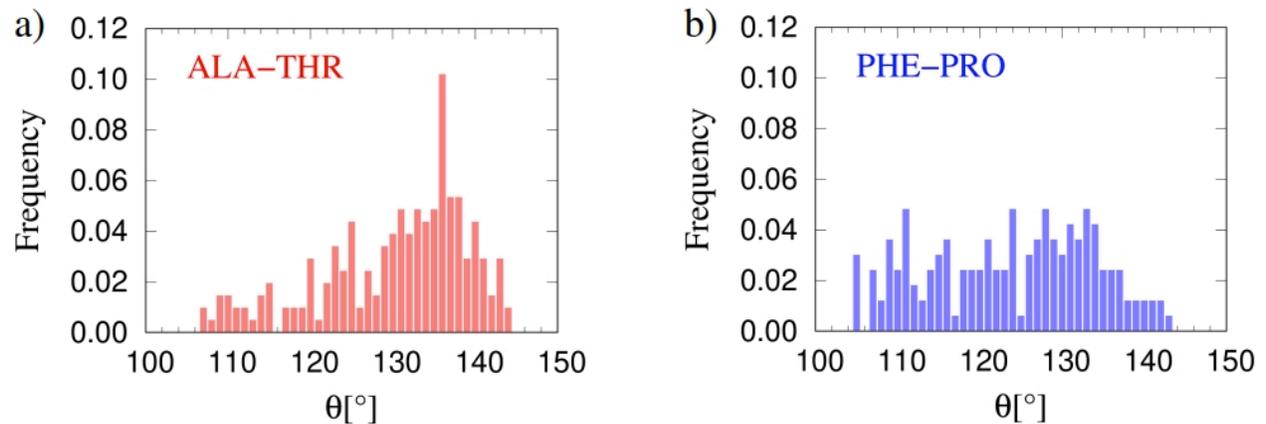


Figure 9: Distribution of θ angles in the β -region for (ALA-THR) and (PHE-PRO) amino acid pairs in positions (i-1,i+1) respectively. ALA-THR is the most localized pair in θ space, yet is spread out. PHE-PRO is the most spread out pair.

We carried out simple sequence analyses of the loop region as well, to understand whether there is a selection principle for the value of the μ angle. We select the (θ, μ) subspace consisting of θ angles in the range from 87.5° to 97.5° ($\pm 5^\circ$ interval around the value 92.5° , identified as the peak density green region in Figure 3c) and μ values in the range from 90° to 360° to ensure that there is no overlap with the α -helix region. We divided up the range of μ angles into 54 bins of width 5° . We measured the IPR value for the 20 amino acids and we find that the most localized amino acid is GLY with a value of 8.49, whereas the most delocalized amino acid is PHE with an IPR equal to 28.42 (see Figure 10). Note that $\mu=180^\circ$ and 360° correspond to planar configurations of 4 consecutive C_α atoms, with the former corresponding to zig-zagging and the latter to rotation in the same sense.

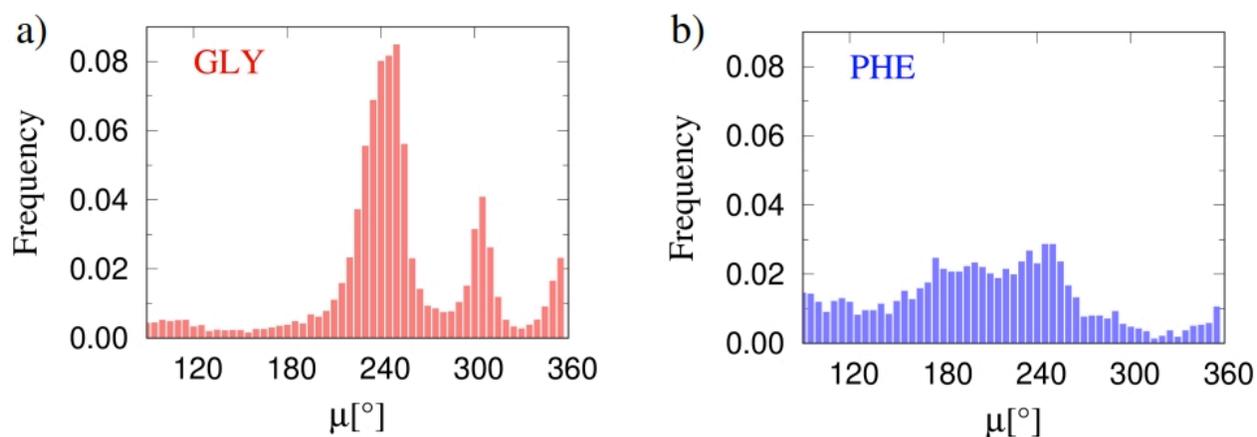


Figure 10: Distribution of μ angles in the loop region for GLY and PHE. GLY is the most localized amino acid, yet exhibits a spread of angles.

Based on the normalized density of occupancy of the amino acids in (θ, μ) space, one can assess the mutual similarity of the 20 amino acids by measuring the Cartesian distance between the 190 pairs of amino acids, which serves as a proxy of similarity. We have employed the Bhattacharyya coefficient (21) in order to calculate the degree of closeness of the (θ, μ) distributions of amino acids. We carried out hierarchical clustering by rank-ordering the closeness – the two closest amino acids were placed into a single group thereby now having effectively 19 groups of amino acids. This procedure was repeated recursively to reduce the effective groups of amino acids by one each time. A natural stopping point for this hierarchical clustering is when there is a relatively large jump in the measure of closeness of the remaining groups. The result of this analysis is shown in Figure 11 and yields 6 different groups comprising 7, 7, 2, 2, 1, and 1 amino acids each. Figure 12 shows the occupancy in (θ, μ) space of the six amino acid groups.

Group A: **ALA - ARG - GLN - GLU - LEU - LYS - MET**
 Group B: **CYS - HIS - PHE - SER - THR - TRP - TYR**
 Group C: **ILE - VAL**
 Group D: **ASN - ASP**
 Group E: **GLY**
 Group F: **PRO**

ARG — LYS	PHE — TYR	ILE — VAL
(ARG, LYS) — GLN	HIS — (PHE, TYR)	ASN — ASP
(ARG, GLN, LYS) — GLU	(HIS, PHE, TYR) — THR	
ALA — (ARG, GLN, GLU, LYS)	(HIS, PHE, THR, TYR) — TRP	
(ALA, ARG, GLN, GLU, LYS) — MET	CYS — (HIS, PHE, THR, TRP, TYR)	
(ALA, ARG, GLN, GLU, LYS, MET) — LEU	(CYS, HIS, PHE, THR, TRP, TYR) — SER	

Figure 11: Clustering of amino acids into groups. The 6 amino acid groups obtained based on their similarity in occupying the local structural (θ, μ) space are shown. 6 is a natural choice because the closeness for the next collapse into five groups is approximately twice as large as the previous closeness measure. A 5 member group would result in the merger of the two largest groups, Group A and Group B. If one were to retain seven groups, SER would detach from Group B and remain isolated as its own group. The sequences of hierarchical clustering for the first four groups A (blue), B (red), C (purple) and D (green) is shown with the link thickness quantitatively representing the closeness measure.

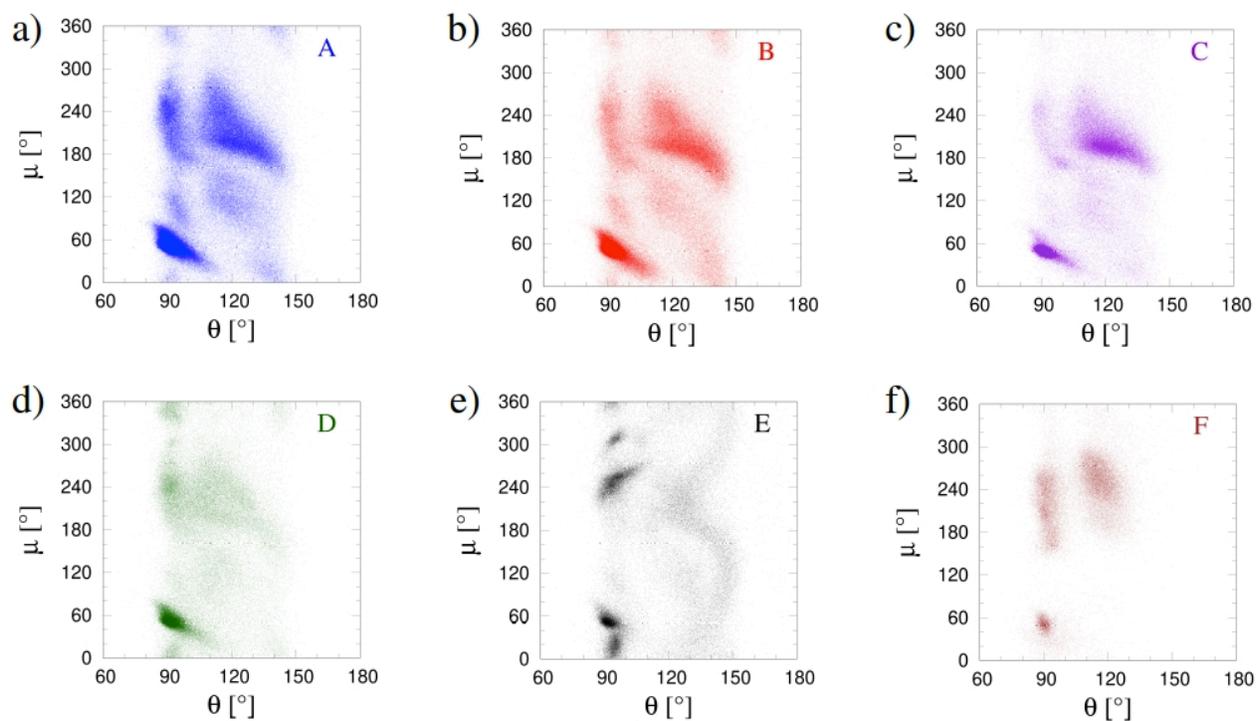


Figure 12: Occupancy of the six amino acid groups in (θ, μ) space. Groups A and B are somewhat similar with the main difference being the relative weights of the α -helix and β -strand regions. The most distinctive groups are E and F corresponding to GLY and PRO respectively. We remind the reader (see Figure 3c) that the density peaks occur at $(\theta = 92.5^\circ$ and $\mu = 47.5^\circ)$ for α -helices, $(\theta = 122.5^\circ$ and $\mu = 192.5^\circ)$ for β -strands, and $(\theta = 92.5^\circ$ and $\mu = 242.5^\circ)$ for loops.

We alert the reader that this grouping is distinct from the more familiar groupings of amino acids based on their non-local interactions (22-29). Here, instead, it is entirely based on the similarity of their propensity to adopt specific local conformations.

We defined three significantly occupied regions of (θ, μ) space corresponding to α -helix ($\theta \in [90^\circ, 95^\circ]$, $\mu \in [45^\circ, 50^\circ]$), β -strand ($\theta \in [105^\circ, 145^\circ]$, $\mu \in [175^\circ, 185^\circ]$), and loop ($\theta \in [87.5^\circ, 97.5^\circ]$, $\mu \in [90^\circ, 360^\circ]$). The amino acid occupancies of the three regions are normalized by their frequencies in the entire (θ, μ) space of all 4416 proteins and they are shown in Table 2. Amino acids having a normalized occupancy greater than 1 are over-represented in a given region and vice versa compared to the expectation from random considerations. The over-represented amino acids in the α -helix region (second column of Table 2) are all members of Groups A and C of amino acids with the top four being LEU (1.56), MET (1.46) and ALA/GLU both having 1.42 normalized occupancy. The amino acids over-represented in the β -strand region (third column of Table 2) are all members of amino acid Groups B and C, the top three being VAL (1.93), ILE (1.55) and TYR (1.51). Finally, the most over-represented amino acids in the loop region correspond to those that are the most under-represented in both the α -helix and β -strand regions: PRO (2.49), GLY (1.76), ASP (1.33) and ASN (1.31). These four amino acids are members of the amino acid groups D (ASN and ASP), E (GLY), and F (PRO) – see amino acid grouping analysis and Figure 11. The strong correlation observed between the values of normalized occupancies of amino acids in the three regions and the results of the amino acid groupings suggests that amino acid Group A can be interpreted as the “ α -helical” group, amino acid Group B as the “ β -strand” group, while Group C is over-represented in both α -helix and β -strand regions. Finally, amino acid Groups D, E, and F can be described as “loop” groups, since they are strongly over-represented in loops and under-represented in both α -helix and β -strand regions. These findings are in a good accord with the observed amino acid propensities in proteins previously reported in the literature (3,5,31-33).

Amino acid type	Normalized occupancy in the α -helix region	Normalized occupancy in the β -strand region	Normalized occupancy in the loop region
ALA	1.42	0.85	0.89
ARG	1.29	1.02	0.89
ASN	0.77	0.60	1.31
ASP	0.77	0.48	1.33
CYS	0.87	1.41	0.67
GLU	1.42	0.63	0.97
GLN	1.38	0.78	0.88
GLY	0.34	0.60	1.76
HIS	0.80	0.98	0.81
ILE	1.26	1.55	0.51
LEU	1.56	0.94	0.70
LYS	1.21	0.75	1.08
MET	1.46	1.21	0.69
PHE	0.88	1.38	0.64
PRO	0.14	0.40	2.49
SER	0.61	1.05	1.04
THR	0.67	1.43	0.76
TRP	0.89	1.23	0.89
TYR	0.80	1.51	0.63
VAL	1.00	1.93	0.50

Table 2: Propensity of the 20 amino acids to occupy the α -helix, β -strand, and loop regions in (θ, μ) space. The numbers shown have been normalized by the amino acid occurrences in all of the (θ, μ) space.

With the identification of just six groups, we proceeded to an analysis of correlating the local structure (θ, μ) at bead i to the identity of the triplet of amino acid groups at positions $(i-1, i, i+1)$. The simplicity now is that the total number of distinct triplets is 216 instead of 8000. We considered each of these triplets and studied the number of times these occurred. Obviously,

one would expect that triplets containing the amino acids in groups C, D, E and F would be fewer than those occurring in Groups A and B. Indeed, the number of triplets which occurred more than 4461 times (deduced by dividing the total number of triplets = 963681 and the total number of types of triplets = 216) was just 57 and we used these for our analysis because of their statistical significance. The results are summarized in Figure 13.

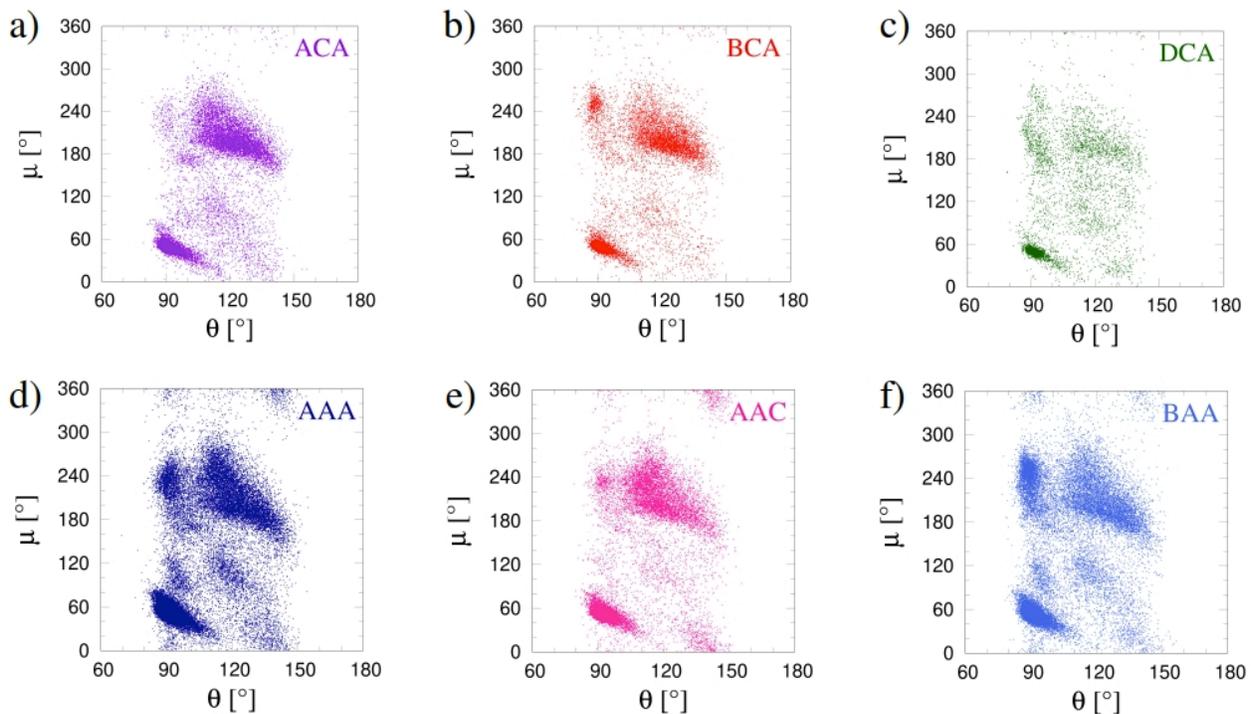


Figure 13: The six panels show the distributions of the 6 most localized triplets in the (θ, μ) plane. They all occupy the α -helix region predominantly. But they are spread out considerably underscoring the weak role of the amino acid sequence in matching with the local structure. We remind the reader (see Figure 3c) that the density peaks occur at $(\theta = 92.5^\circ$ and $\mu = 47.5^\circ)$ for α -helices, $(\theta = 122.5^\circ$ and $\mu = 192.5^\circ)$ for β -strands, and $(\theta = 92.5^\circ$ and $\mu = 242.5^\circ)$ for loops.

We conclude with the lessons learned from our analysis. Our goal here was to characterize the local structures associated with protein native state folds using the simple representation of just two angles (θ and μ) for each C_α position (Figure 1). This simplification is made possible because the vast majority of bond lengths is substantially constant (Figure 2). The (θ , μ) variables are a coarse-grained representation of successive Ramachandran angles. The local structures adopted by proteins are captured by simple patterns of points in the (θ , μ) plane. This reveals that protein native state structures (even at the local level) are highly structured unlike the behavior of a generic chain. Even though there is a great deal of spread in the θ and μ values, there is a tight correlation in the plot of the mean θ versus mean μ for the 4416 proteins (Figure 4).

Armed with insights on the local structural pattern, we explored a potential sequence-structure relationship in multiple ways. We considered the propensity of the 20 amino acids to occupy certain regions of local structural space. We also divided the 20 amino acids into 6 groups based on their similarity to each other in being associated with regions in the (θ , μ) space. We explored singlets and triplets based on grouping. The basic result of our analysis is that any sequence-local structure relationship is not very strong and there is flexibility in the ability of the amino acids to adapt to the local structure. This is consistent with the prevalence of neutral evolution where neither the native state fold nor the ability to function changes under many amino acid substitutions. It serves to underscore the pioneering results of Brian Matthews (34,35) and his team who “used the lysozyme from bacteriophage T4 to define the contributions that different types of interaction make to the stability of proteins”. One of their key findings was that “the protein is, in general, very tolerant of amino acid replacement”. Our findings also

are in accord with more recent experimental studies on proteins (36,37) which showed that, while protein structures are highly tolerant of amino acid substitutions, a small number of key alterations can yield distinct structure and function. An interesting challenge is to be able to predict, in a transparent and reliable manner, the identity of these key amino acids.

We conclude by revisiting a seminal paper by Levitt (38) more than four decades ago in which he very carefully measured the Chou-Fasman propensity (39) of the twenty amino acids to be housed in three secondary structures. He noted that, generally, the preferences of the individual amino acids for secondary structure are rather weak. He provided a physical interpretation of his results by noting that “the chemical structure and stereochemistry of the amino acid plays a major part in determining its preference and dislike for secondary structure..... Bulky amino acids, namely, those that are branched at the β -carbon or have a large aromatic side chain, prefer β -sheet. The shorter polar side chains prefer reverse turns, as do Gly and Pro, the special side chains. All other side chains prefer α -helix, except Arg which has no preference.” Table 3 shows a side-by-side comparison of the results of Levitt obtained with less than a hundred protein structures and our findings with entirely different methods and more than 4000 protein structures. Our results match those of Levitt (38) confirming the adage – *old is gold*.

α -helix propensity		β -sheet propensity		Loop propensity	
Our study	Levitt [38]	Our study	Levitt [38]	Our study	Levitt [38]
LEU (1.56)	MET (1.47)	VAL (1.93)	VAL (1.49)	PRO (2.49)	PRO (1.91)
MET (1.46)	GLU (1.44)	ILE (1.55)	ILE (1.45)	GLY (1.76)	GLY (1.64)
GLU (1.42)	LEU (1.30)	TYR (1.51)	PHE (1.32)	ASP (1.33)	ASP (1.41)

Table 3: Identities of three amino acids with the highest propensities to occupy the α -helix, β -strand, and loop regions in (θ, μ) space (taken from Table 2). The Table also shows the winning amino acids from Levitt’s analysis of 1978 (38). There is excellent accord between our results and those of Levitt. The key difference is the identity of one of the top three amino acids in the β -sheet propensity group. PHE scores third in Levitt’s analysis with a normalized probability of 1.32 whereas PHE scores fifth in our analysis with a similar probability score of 1.38. TYR scores third in our study and fourth in Levitt’s analysis.

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Supplementary Information for the manuscript

“Local sequence-structure relationships in proteins”

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Table S1: PDB codes of the 4416 proteins used in our analysis.

16pk_A	1iqc_C	1pnc_A	1w0p_A	2buw_B	2hwn_D	2rc3_A	2zk9_X	3euf_D	3kl0_B
1a1i_A	1iqq_A	1pnd_A	1w0u_A	2bv2_B	2hxm_A	2rc8_B	2zkd_B	3eul_A	3kl6_B
1a2p_B	1iqz_A	1pp0_C	1w1h_C	2bv4_A	2hxp_A	2rci_A	2zl6_B	3eun_A	3klq_A
1a2y_A	1irq_A	1psr_A	1w2c_A	2bw0_A	2hxs_A	2rcq_A	2znd_A	3eup_B	3klr_A
1a2y_B	1isp_A	1ptq_A	1w2i_B	2bw8_A	2hxt_A	2rcv_E	2znr_A	3evf_A	3kmt_C
1a2z_C	1isu_A	1puc_A	1w3i_A	2bwf_A	2hy5_A	2rcz_B	2zoo_A	3evk_D	3kmv_D
1a34_A	1it2_B	1puf_B	1w3w_A	2bwl_A	2hy5_B	2rdh_C	2zpd_A	3evy_B	3knb_B
1a3a_A	1itw_D	1pvm_A	1w3y_A	2bwr_B	2hy7_A	2rdq_A	2zpo_A	3ew0_A	3knv_A
1a4i_B	1itx_A	1pvx_A	1w4s_A	2c0c_A	2hyk_A	2rdu_A	2zpu_A	3ew1_D	3kp8_A
1a73_A	1iu8_B	1pxv_B	1w4t_A	2c0h_A	2hyv_A	2rdz_A	2zqe_A	3ewi_A	3kpb_D
1a7d_A	1iue_B	1pyo_B	1w4v_B	2c0r_B	2hzi_B	2ree_A	2zqm_A	3exe_D	3kq0_A
1a7t_B	1iuz_A	1pzs_A	1w4x_A	2c0z_A	2hzy_B	2reg_A	2zqn_B	3exr_A	3kqi_A
1a88_A	1iv3_D	1q08_B	1w53_A	2c1d_D	2i0q_A	2rem_B	2zs0_A	3ey6_A	3kqr_A
1a8q_A	1iv9_A	1q0q_A	1w5r_B	2c1s_A	2i1n_A	2rer_A	2zs0_D	3eye_A	3kre_A
1a8s_A	1iwd_A	1q0r_A	1w66_A	2c1v_B	2i24_N	2rfg_A	2zs1_B	3eyi_A	3krs_A
1a92_C	1ix1_B	1q1r_B	1w6s_C	2c29_F	2i2q_A	2rfm_B	2zs1_C	3eyp_B	3kru_A
1ab1_A	1ixg_A	1q1u_A	1w6s_D	2c2n_A	2i3f_A	2rh2_A	2zsi_A	3ezi_B	3kse_D
1aba_A	1iy8_C	1q2h_A	1w70_A	2c2p_A	2i49_A	2rh3_A	2ztl_C	3f0y_C	3ksh_A
1afb_3	1iyb_A	1q4u_B	1w8o_A	2c2u_A	2i4a_A	2rhi_A	2zu1_B	3f17_A	3ksv_A
1ag9_B	1iye_C	1q5m_B	1w8u_A	2c3n_C	2i5r_B	2rhk_C	2zu2_A	3f1l_A	3ksx_A
1agy_A	1iyn_A	1q5z_A	1w99_A	2c41_F	2i5v_O	2ri0_B	2zux_B	3f1p_A	3kt9_A
1ah7_A	1izc_A	1q6o_A	1w9p_A	2c42_B	2i61_A	2ri7_A	2zuy_A	3f1p_B	3ktz_A
1aho_A	1ize_A	1q7l_A	1w9s_A	2c4e_A	2i62_D	2ri9_A	2zw2_A	3f2e_A	3ku3_B
1aii_A	1j05_B	1q7l_B	1wa3_A	2c4f_T	2i6v_A	2rik_A	2zwd_A	3f2u_A	3kus_B
1ako_A	1j0h_B	1q8f_A	1wb0_A	2c4j_D	2i7c_C	2riq_A	2zww_A	3f3q_A	3kuv_A
1aky_A	1j0p_A	1qau_A	1wb6_B	2c4n_A	2i7d_A	2rji_A	2zwn_A	3f3x_A	3kwe_A
1aoh_B	1j1y_A	1qav_A	1wba_A	2c53_A	2i7f_B	2rjw_A	2zww_A	3f47_A	3kxt_A
1aoz_A	1j24_A	1qaz_A	1wbe_A	2c6q_B	2i8t_B	2rk3_A	2zx2_A	3f4m_A	3kyj_A
1arb_A	1j27_A	1qb5_E	1wbh_B	2c6u_A	2i9a_D	2rk5_A	2zxj_B	3f4s_A	3kz5_A
1ast_A	1j2j_B	1qb7_A	1wbi_H	2c6z_A	2i9i_A	2rkl_A	2zxy_A	3f52_A	3kz7_A
1atg_A	1j2r_A	1qba_A	1wbj_A	2c78_A	2iax_A	2rkq_A	2zya_B	3f5l_B	3kzj_A
1atl_B	1j30_B	1qcx_A	1wbj_B	2c7p_A	2ib8_A	2rku_A	2zyh_B	3f5o_G	3kzu_B
1atz_B	1j34_A	1qd1_B	1wc2_A	2c81_A	2ibj_A	2rky_C	2zyo_A	3f6o_A	3l07_B
1aun_A	1j34_B	1qd2_A	1wc9_A	2c82_B	2ibl_A	2sak_A	2zdd_E	3f6q_A	3l0f_A
1avb_A	1j3w_C	1qd9_C	1wcf_A	2c8h_D	2ibp_B	2sec_I	2zdd_J	3f6q_B	3l0l_B
1awd_A	1j48_A	1qdd_A	1wcf_B	2c92_D	2ic6_A	2sga_A	2zdz_A	3f6y_A	3l18_A

1aye_A	1j71_A	1qfv_B	1wck_A	2c95_B	2ic7_B	2sn3_A	2zrz_A	3f74_B	3l1e_A
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1b16_A	1j77_A	1qgj_A	1wdd_S	2cal_A	2if6_A	2uuy_B	2zzv_B	3f75_P	3l32_A
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1b2s_F	1j7g_A	1qh5_B	1wf3_A	2cb5_A	2ig8_A	2uvj_A	3a03_A	3f7q_A	3l3u_A
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1b3a_B	1j8u_A	1qho_A	1wka_A	2cbz_A	2igp_A	2uw1_A	3a07_A	3f97_A	3l42_A
1b4f_B	1j9l_A	1qhq_A	1wko_A	2cc6_A	2igv_A	2uwa_A	3a09_A	3f9b_A	3l46_A
1b5e_A	1ja9_A	1qhv_A	1wkq_B	2ccch_B	2igx_A	2uyt_A	3a0y_B	3f9r_A	3l4p_A
1b63_A	1jae_A	1qj5_B	1wkr_A	2ccq_A	2ih5_A	2uyw_A	3a16_C	3fas_B	3l4r_A
1b66_A	1jak_A	1qjc_B	1wku_B	2ccw_A	2ihd_A	2uyz_A	3a1c_A	3fb9_A	3l5l_A
1b67_A	1jat_A	1qjw_B	1wkx_A	2cdn_A	2ii2_A	2uyz_B	3a21_A	3fbg_A	3l6g_A
1b8a_B	1jay_B	1qkk_A	1wld_A	2cf7_C	2iid_A	2uz1_D	3a2q_A	3fbl_A	3l6n_A
1b8d_K	1jcd_A	1ql0_B	1wlg_B	2cfe_A	2ijh_A	2uzc_C	3a2v_I	3fd7_B	3l77_A
1b8p_A	1jcv_A	1ql3_B	1wlz_C	2cg7_A	2ijq_A	2v09_A	3a2z_A	3fde_B	3l7h_B
1b93_A	1jd0_B	1qlw_A	1wm2_A	2cgq_A	2ijx_D	2v0h_A	3a39_A	3fdl_A	3l7t_B
1bas_A	1jd1_C	1qmy_C	1wma_A	2chc_B	2imf_A	2v0s_A	3a3d_B	3fdq_A	3l8e_B
1baz_A	1jd5_A	1qnj_A	1wmd_A	2cia_A	2imi_B	2v0u_A	3a3v_A	3fdr_A	3l8w_A
1bdo_A	1jdh_B	1qnn_C	1wmh_A	2ciu_A	2imq_X	2v1o_B	3a40_X	3fe0_A	3l91_A
1beh_A	1jdl_A	1qnp_A	1wmw_A	2ciw_A	2in8_A	2v1q_A	3a4r_A	3fe7_A	3l91_B
1bf6_A	1jek_A	1qnx_A	1wmz_D	2cj3_A	2inc_A	2v1w_B	3a4u_A	3fev_A	3l9a_X
1bgf_A	1jev_A	1qoz_B	1wn2_A	2cj4_A	2inc_B	2v25_A	3a4w_B	3ff5_B	3l9f_D
1bgp_A	1jf8_A	1qre_A	1wny_A	2cjj_A	2ior_A	2v27_A	3a57_A	3ff7_C	3l9s_A
1bhp_A	1jfl_B	1qrp_E	1wo8_D	2cjl_B	2ioy_B	2v2g_C	3a5p_D	3ff9_B	3l9u_A
1bj7_A	1jfr_A	1qs1_A	1wod_A	2cjp_A	2ip2_B	2v33_B	3a5r_A	3fg0_F	3l9y_B
1bkp_A	1jfu_A	1qsa_A	1wog_E	2cjs_C	2ip6_A	2v36_D	3a6r_B	3fgd_A	3las_B
1bn8_A	1jfx_A	1qsg_A	1woq_B	2ckf_D	2ipr_B	2v3g_A	3a72_A	3fh2_A	3lat_A
1bq8_A	1jg1_A	1qt9_A	1wor_A	2ckk_A	2iq7_A	2v3s_A	3a7l_A	3fhg_A	3lbe_D
1bqb_A	1jhd_A	1qtn_A	1wpa_A	2cks_A	2iqj_A	2v4n_A	3a7n_A	3fid_A	3lbf_C
1bqk_A	1jhf_A	1qtw_A	1wpm_B	2cm4_A	2iru_B	2v4v_A	3a8g_B	3fil_B	3lbl_A
1brt_A	1jhg_A	1qu1_D	1wpu_A	2cmj_B	2is8_A	2v5i_A	3a8u_X	3fiq_A	3lbn_B
1bs3_B	1jhj_A	1qve_B	1wq8_A	2cmt_A	2is9_A	2v5j_A	3a9b_A	3fju_B	3lcc_A
1bs9_A	1jhs_A	1qw9_B	1wqj_B	2cn3_B	2it1_A	2v5z_A	3a9f_A	3fkb_E	3lcm_A
1bsg_A	1ji1_A	1qwd_A	1wqj_I	2cnz_A	2iu5_A	2v6a_O	3a9j_A	3fkc_A	3ld3_A
1bue_A	1jid_A	1qwg_A	1wr8_B	2cov_I	2ium_A	2v6k_B	3a9l_B	3fke_A	3ldd_A
1bx4_A	1jif_A	1qwk_A	1wrdr_A	2cs7_A	2ivf_A	2v6u_A	3a9q_N	3flg_A	3le0_A
1bx7_A	1jke_C	1qwmm_B	1wri_A	2cu5_A	2ivf_B	2v7w_C	3a9s_B	3flv_A	3le3_A
1bxu_A	1jkg_A	1qwz_A	1wrm_A	2cvd_D	2ivn_A	2v84_A	3aa0_A	3fn5_A	3le4_A
1bxy_A	1jkx_A	1qxy_A	1ws8_A	2cve_A	2ivx_A	2v89_A	3aa6_B	3fp5_A	3let_A
1byi_A	1jl1_A	1qy6_A	1wst_A	2cvi_B	2ivy_A	2v8i_A	3aaf_B	3fpc_A	3lf6_B
1c02_A	1jl7_A	1qz9_A	1wt6_A	2cwd_A	2iw0_A	2v8u_A	3aal_A	3fpf_A	3lfh_F
1c0p_A	1jll_A	1r0r_E	1wta_A	2cwi_B	2iw1_A	2v9m_A	3aam_A	3fpk_B	3lfj_B
1c1d_A	1jlt_A	1r12_A	1wte_A	2cwr_A	2iw2_B	2v9t_B	3ab6_A	3fpr_D	3lfk_C
1c1k_A	1jlt_B	1r17_A	1wtj_A	2cws_A	2iwk_A	2v9v_A	3aba_A	3fpu_B	3lg5_A
1c1l_A	1jm1_A	1r1p_A	1wto_A	2cxn_B	2iwz_A	2vac_A	3abf_E	3fpw_A	3lgi_A
1c1y_A	1jnr_C	1r1t_B	1wu9_B	2cyg_A	2ix4_B	2vap_A	3aci_A	3fq3_C	3lgn_A
1c1y_B	1jnr_D	1r26_A	1wui_S	2cz4_A	2ixc_A	2vb1_A	3act_B	3fqm_A	3lhq_A
1c4q_B	1jo0_A	1r29_A	1wur_B	2czd_A	2ixd_B	2vba_D	3acx_A	3frq_A	3lhr_B
1c52_A	1jo8_A	1r2m_A	1wve_D	2czq_B	2ixk_A	2vbk_A	3adg_A	3frr_A	3lid_B
1c5e_A	1jpe_A	1r2r_B	1wvf_A	2d0i_B	2ixm_A	2vc3_A	3ado_A	3fs7_A	3lim_D
1c75_A	1jq5_A	1r3q_A	1wwz_B	2d16_A	2izz_B	2vc8_A	3aey_A	3ft1_C	3liy_A
1c7j_A	1jqe_A	1r45_B	1wy1_A	2d1c_A	2j1s_A	2ve8_E	3afm_A	3ftd_A	3lijw_B
1c7k_A	1jr8_A	1r55_A	1wy2_B	2d1x_A	2j23_A	2veb_A	3afv_A	3fv3_G	3lke_A

1c7n_F	1jsd_B	1r6d_A	1wyx_B	2d1y_C	2j27_A	2vfk_A	3ag3_C	3fv9_G	3lkt_B
1cc8_A	1jt2_A	1r6j_A	1wz3_A	2d29_A	2j2j_F	2vfq_A	3ag3_E	3fvb_B	3lkt_Q
1ccw_B	1ju2_A	1r6x_A	1wz8_A	2d37_A	2j3x_A	2vg1_B	3ag7_A	3fvh_A	3llb_A
1cf3_A	1jub_B	1r77_B	1wzd_B	2d3d_A	2j5g_A	2vg3_C	3agn_A	3fwa_A	3llu_A
1cg5_A	1juv_A	1r7j_A	1x0c_A	2d3n_A	2j5i_F	2vgp_D	3ah2_A	3fwy_A	3lny_A
1cg5_B	1jvw_A	1r87_A	1x0l_A	2d4n_A	2j5y_A	2vha_B	3ahc_A	3fx4_A	3log_C
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1cip_A	1jy2_N	1r89_A	1x1n_A	2d4v_C	2j6a_A	2vig_A	3ahx_D	3fy1_B	3lpc_A
1cjc_A	1jy2_R	1r8h_D	1x1o_B	2d5b_A	2j6b_A	2vj0_A	3ahy_A	3fy3_A	3lpe_B
1cjw_A	1jy3_P	1r8s_A	1x2i_A	2d5c_A	2j6f_A	2vjpb_B	3ahz_A	3fym_A	3lpe_G
1cka_A	1jyh_A	1r9d_A	1x2t_C	2d5k_C	2j6i_A	2vjv_B	3ai3_C	3fza_A	3lpw_B
1clc_A	1jyo_B	1r9h_A	1x38_A	2d5w_B	2j6l_F	2vk8_C	3aia_A	3fzy_B	3lqw_A
1cnv_A	1k07_A	1r9l_A	1x3o_A	2d5z_B	2j73_B	2vkj_A	3aj7_A	3g00_A	3lr4_A
1cnz_B	1k0i_A	1ra0_A	1x3x_B	2d68_B	2j7j_A	2vkl_A	3ajo_A	3g0e_A	3lrt_A
1coj_A	1k0m_A	1rc9_A	1x46_A	2d69_A	2j7z_A	2vkv_A	3ajx_C	3g0m_A	3ls0_A
1cpq_A	1k1e_K	1rdo_2	1x54_A	2d6m_A	2j8b_A	2vla_A	3ak2_B	3g1l_A	3ls9_A
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1cs6_A	1k4i_A	1rg8_B	1x8d_C	2d7t_L	2j8k_A	2vmc_A	3akh_A	3g20_B	3lum_D
1ctj_A	1k4m_C	1rgx_C	1x91_A	2d81_A	2j8m_A	2vn4_A	3alf_A	3g21_A	3lvf_P
1cuo_A	1k5c_A	1rgz_A	1x9i_A	2d8d_B	2j8w_A	2vn6_A	3alu_A	3g2b_A	3lw6_A
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1d02_B	1k9u_B	1rkq_A	1xg0_B	2de6_F	2jba_B	2vo9_B	3b4u_B	3g7w_A	3ly7_A
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1d2n_A	1kaf_A	1rl0_A	1xg2_B	2dfb_A	2jc4_A	2voz_A	3b51_X	3g98_B	3lzo_B
1d4o_A	1kao_A	1rlh_A	1xg4_A	2dfd_C	2jc5_A	2vpg_A	3b5g_B	3g9m_B	3lzw_A
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1d5l_B	1kaz_A	1rm6_A	1xgs_A	2dga_A	2jcb_A	2vq4_A	3b5m_B	3ga3_A	3m0f_A
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1dbf_A	1keq_B	1rp0_B	1xk4_H	2dkj_A	2jdk_D	2vsv_A	3b5n_K	3gbe_A	3m21_D
1dbw_B	1kew_A	1rqj_A	1xk4_I	2dko_A	2je6_B	2vte_B	3b64_A	3gbs_A	3m3g_A
1dci_C	1kfw_A	1rro_A	1xky_B	2dm9_B	2je8_B	2vuj_A	3b6i_A	3gc6_A	3m4d_A
1deu_A	1kg2_A	1rtq_A	1xkz_B	2dp6_A	2jek_A	2vun_B	3b76_A	3gc7_A	3m5l_A
1dfu_P	1kgc_D	1rtt_A	1xlq_C	2dp9_A	2jep_B	2vuo_A	3b7e_A	3gd6_A	3m5q_A
1dgd_A	1khi_A	1ru0_B	1xm8_A	2dpf_D	2jft_A	2vv6_D	3b7s_A	3gd8_A	3m66_A
1dhn_A	1khq_A	1ru4_A	1xmk_A	2dqa_A	2jg6_A	2vve_A	3b84_A	3gdc_A	3m6b_A
1dj0_B	1kid_A	1rv9_A	1xmp_B	2dql_A	2jh1_A	2vvp_B	3b8f_C	3gdl_B	3m6z_A
1djr_G	1kjj_A	1rwh_A	1xmt_A	2dr1_B	2jhf_B	2vvt_B	3b8i_E	3ge3_A	3m73_A
1dk8_A	1klx_A	1rwj_A	1xng_B	2dri_A	2jhq_A	2vww_A	3b8z_B	3ge3_E	3m7o_A
1dl5_B	1km9_A	1rwr_A	1xnk_A	2drm_B	2ji7_A	2vw8_A	3b9c_C	3gfu_A	3m7q_B
1dlf_H	1kms_A	1rwy_B	1xo7_B	2ds2_D	2jik_A	2vwf_A	3b9d_A	3gg7_A	3m8j_A
1dlf_L	1kmt_A	1rwz_A	1xoc_A	2ds5_A	2jjc_A	2vwr_A	3b9w_A	3gg9_B	3m8o_H
1dlj_A	1kng_A	1rx0_C	1xov_A	2dsj_B	2jjf_A	2vws_C	3ba1_A	3ggw_C	3m8o_L
1dlw_A	1knt_A	1ry9_C	1xph_A	2dsn_B	2jjn_A	2vx5_A	3baa_A	3ggy_A	3m8t_B
1dly_A	1koe_A	1ryi_B	1xpp_C	2dsx_A	2jjs_C	2vxn_A	3bal_B	3gh6_A	3m8u_A

1dm1_A	1kol_B	1ryo_A	1xqo_A	2dt4_A	2jk9_A	2vxq_A	3bbb_D	3gha_A	3m91_C
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1dp7_P	1kpt_A	1ryp_K	1xs5_A	2dur_A	2jkh_A	2vxy_A	3bd1_A	3gk7_B	3mao_A
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1dqg_A	1kq3_A	1rzh_L	1xt5_A	2dwu_A	2jllq_A	2vyw_A	3beo_A	3gkm_A	3mb5_A
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1dqp_A	1kqr_A	1s1d_B	1xty_B	2dy0_A	2mnr_A	2vzc_A	3bex_A	3gkt_A	3mbk_B
1dqz_A	1krh_A	1s2o_A	1xu1_D	2dy1_A	2nml_A	2vzm_A	3bf7_B	3gkv_B	3mbx_H
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1dsz_A	1ku1_A	1s5m_A	1xvg_E	2dyu_A	2nnr_A	2w1j_B	3bfq_G	3glv_B	3md7_A
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1dx_e_B	1kve_D	1s9r_A	1xw6_A	2e0t_A	2npt_D	2w1v_A	3bgo_P	3gmi_A	3mds_B
1dxj_A	1kw6_B	1sa3_A	1xwt_A	2e11_B	2nql_B	2w20_A	3bh4_A	3gms_A	3mdu_A
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1e29_A	1l3p_A	1sds_A	1y0h_A	2e3z_B	2nug_B	2w3g_A	3bkj_H	3go2_A	3mhy_C
1e2w_B	1l5o_A	1seg_A	1y0m_A	2e42_A	2nuh_A	2w3j_A	3bkr_A	3go6_A	3mi4_A
1e3d_B	1l5w_B	1sen_A	1y1p_A	2e4t_A	2nuk_A	2w3p_B	3bkt_A	3goc_B	3mil_A
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1e6i_A	1lc3_A	1sh8_B	1y4w_A	2e85_A	2nz7_A	2w4f_A	3bo6_B	3gqh_A	3mmg_A
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1eao_A	1lj5_A	1stm_B	1y7p_B	2ebb_A	2o20_F	2w7w_B	3bov_A	3gt5_A	3mpc_A
1ear_A	1lj9_B	1svb_A	1y7t_B	2ebo_C	2o28_A	2w83_C	3bp5_A	3gv6_A	3mpz_B
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1ejb_A	1lqx_A	1szn_A	1yb0_B	2eh6_A	2o5u_A	2wb6_A	3bsy_B	3gwm_A	3muj_B
1ekj_C	1lr7_A	1szo_K	1yb5_A	2ehg_A	2o6f_A	2wbf_X	3buv_B	3gwn_A	3muz_3
1ekx_A	1lrh_A	1t00_A	1ybi_B	2ehq_A	2o6p_A	2wbs_A	3bv6_D	3gx8_A	3mwc_A
1elk_A	1ls6_A	1t06_A	1ybk_D	2eht_A	2o6s_A	2wc8_B	3bvk_F	3gxb_A	3mwf_A
1elr_A	1ls9_A	1t0b_D	1ybz_A	2ehz_A	2o74_F	2wci_A	3bwh_A	3gxr_B	3mwj_A

1elu_A	1lst_A	1tof_B	1yd3_A	2ei5_B	2o7i_A	2wcj_A	3bwu_D	3gzg_A	3mx6_B
1elw_A	1lt1_H	1tof_C	1ydy_A	2eiq_B	2o90_A	2wco_A	3bx4_A	3gzh_A	3mxn_A
1enf_A	1lua_C	1top_B	1yfn_C	2eix_A	2o9c_A	2wcr_A	3bx4_B	3gzk_A	3mxn_B
1eo6_B	1lvw_B	1tot_X	1yfu_A	2eiy_B	2o9s_A	2wcu_A	3bx4_C	3gzx_A	3mxu_A
1ep0_A	1lw6_E	1t1g_A	1yif_A	2eja_B	2oaa_B	2wdc_A	3by4_A	3gzx_B	3myb_A
1eq9_B	1lw6_I	1t1j_B	1yii_A	2ejn_B	2obi_A	2wds_A	3byb_B	3h01_A	3mzv_B
1es5_A	1lwb_A	1t1v_B	1ykd_A	2ejw_A	2obl_A	2wdu_B	3byp_A	3h04_A	3n08_A
1esw_A	1lwd_B	1t2d_A	1yki_B	2ejx_A	2ocg_A	2we5_C	3bzz_B	3h09_B	3n0i_B
1eu3_A	1ly2_A	1t2h_B	1yn3_B	2ekp_A	2ode_D	2wei_A	3c05_A	3h0o_A	3n10_B
1euh_C	1m0d_C	1t2w_C	1yn8_E	2eky_C	2odf_E	2wf6_A	3c05_D	3h0u_C	3n11_A
1euv_A	1m0s_B	1t3q_A	1yn9_A	2elc_B	2odk_C	2wfc_C	3c0i_A	3h12_B	3n1e_B
1euv_B	1m0u_A	1t3q_B	1ynb_C	2end_A	2oe3_A	2wfh_B	3c1o_A	3h1g_A	3n1f_D
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1ex2_B	1m1n_E	1t4b_B	1ynp_B	2eq6_B	2ofc_A	2wfo_A	3c3y_B	3h34_A	3n22_A
1ext_A	1m1n_F	1t61_C	1yo3_A	2erf_A	2ofk_A	2wfz_A	3c4s_A	3h3n_X	3n2n_E
1eyh_A	1m1r_A	1t61_E	1yoa_A	2erw_A	2og1_A	2wge_A	3c5a_A	3h4n_A	3n37_A
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1f08_B	1m40_A	1t7r_A	1yq2_C	2eu7_X	2okl_B	2wj5_A	3c70_A	3h62_B	3n72_B
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1f0y_B	1m4j_A	1t8k_A	1yqe_A	2ev1_A	2okq_A	2wjn_C	3c7t_A	3h6p_C	3n98_A
1f1m_C	1m55_A	1t8t_B	1yqw_B	2evb_A	2ol1_B	2wjn_L	3c7x_A	3h78_A	3n9g_H
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1f3u_G	1m70_D	1t9i_B	1yrk_A	2ex0_B	2olp_A	2wkk_C	3c8o_A	3h7i_A	3n9u_C
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1f60_A	1m8s_A	1taw_B	1yu0_A	2f0c_A	2oo1_B	2wmf_A	3c9u_B	3h87_D	3ndj_A
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1fob_A	1mj5_A	1tjy_A	1z2a_A	2fba_A	2ox4_H	2wsb_C	3chm_A	3hef_B	3no7_A
1fp2_A	1mk0_A	1tke_A	1z2n_X	2fbd_A	2ox6_B	2wt1_A	3ci7_A	3hf5_C	3noj_A
1fpo_B	1mkk_A	1tn4_A	1z2u_A	2fbn_A	2oxc_A	2wta_A	3cij_A	3hfo_A	3nok_A
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1gk7_A	1nep_A	1uai_A	1zs4_D	2fuk_A	2pg0_B	2x7k_A	3czz_B	3i2z_A	3oaj_A
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1gl2_D	1nh2_B	1ucr_B	1zuu_A	2fyx_A	2piy_B	2x96_A	3d1k_A	3i3g_A	3ofk_C
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1gug_D	1ntv_A	1ukm_A	2a4v_A	2gbw_E	2pqr_D	2xfv_A	3dan_A	3iav_A	3ose_A
1gui_A	1nty_A	1ukm_B	2a4x_A	2gc4_L	2pqx_A	2xh2_C	3daq_A	3ib7_A	3osm_A
1gv5_A	1nvm_C	1uku_A	2a53_C	2gdq_B	2pr5_A	2xhi_A	3dau_A	3ich_A	3oti_B
1gvj_A	1nvm_F	1ukz_A	2a5d_A	2gdz_A	2psd_A	2xhn_A	3dc5_C	3id1_A	3ouf_B
1gvn_D	1nw2_H	1ulk_A	2a61_C	2gec_A	2psp_B	2xi8_A	3dcn_A	3id7_A	3ovp_B
1gwe_A	1nwa_A	1ulr_A	2a6s_B	2gey_D	2pst_X	2xij_A	3del_B	3ida_A	3oyy_B
1gwi_B	1nwp_A	1umd_C	2a6x_A	2gf3_B	2pth_A	2xio_A	3deo_A	3idw_A	3p0t_A
1gwu_A	1nww_A	1umd_D	2a70_A	2gf9_A	2ptt_B	2xkg_A	3dfg_A	3ie4_A	3p1f_A
1gxn_A	1nwz_A	1umk_A	2a7l_B	2gg6_A	2ptz_A	2xkr_A	3dgb_A	3ie5_A	3p1g_A
1gxu_A	1nxc_A	1umz_A	2a8n_A	2gh0_B	2pu3_A	2xla_A	3dgp_A	3iei_C	3p2n_A
1gxy_A	1nxj_A	1uow_A	2a9i_A	2gh0_D	2pu9_A	2xlk_A	3dgp_B	3iev_A	3p2t_A
1gy6_A	1nxm_A	1uoy_A	2a9s_A	2gh9_A	2pu9_B	2xm5_A	3dgt_A	3iez_B	3p3c_A
1gy7_C	1nyk_B	1uqx_A	2aa1_B	2gha_A	2pv2_A	2xmx_A	3dha_A	3ife_A	3p3e_A
1gyh_C	1nyt_C	1uqz_A	2aa1_C	2gia_B	2pvb_A	2xn4_A	3dhi_B	3ig9_C	3p3g_A
1gyo_A	1nza_A	1urn_C	2aan_A	2gib_B	2pve_B	2xn6_A	3dhi_C	3igz_B	3p3o_A
1gyv_A	1o04_E	1urr_A	2ab0_A	2giy_A	2pvq_A	2xov_A	3dho_C	3ihw_A	3p48_A
1gyy_B	1o0e_B	1urs_A	2abk_A	2gj3_A	2pwy_A	2xpp_A	3die_A	3ihz_B	3p4t_A
1gzc_A	1o1z_A	1us5_A	2abw_B	2gjd_C	2pxx_A	2xqu_A	3dj9_A	3ii7_A	3p5h_A
1gzw_B	1o26_C	1use_A	2acf_D	2gke_A	2py4_A	2xs4_A	3djh_C	3iij_A	3p73_A
1h03_P	1o4k_A	1usf_B	2ad6_A	2gkm_B	2pyw_A	2xsu_A	3djl_A	3iiu_M	3p73_B
1h0h_B	1o4s_A	1usg_A	2ad6_D	2gkr_I	2pz0_B	2xt2_A	3djo_A	3ij3_A	3p7y_A
1h16_A	1o4t_A	1uso_A	2ae2_A	2gl5_A	2pze_B	2xts_A	3dk9_A	3ijl_A	3p97_C
1h1n_A	1o4v_A	1usq_B	2aen_E	2gmy_E	2pzh_B	2xts_B	3dkc_A	3ik7_D	3p9c_A
1h1y_A	1o4y_A	1uti_A	2aex_A	2gn4_B	2q0l_A	2xtt_B	3dkm_A	3ilo_A	3p9p_A
1h2b_B	1o5u_A	1uu4_A	2ag4_B	2gnc_A	2q20_B	2xu3_A	3dkr_A	3ils_A	3p9x_A
1h2c_A	1o5x_A	1uuq_A	2ag5_B	2gok_A	2q28_A	2xu8_B	3dl0_A	3ilw_A	3pb6_X
1h2e_A	1o7e_B	1uuy_A	2agd_B	2gom_A	2q2a_D	2xvm_B	3dlm_A	3im1_A	3pbf_A
1h2s_A	1o7i_A	1uv4_A	2ahf_A	2gou_A	2q2h_A	2xvs_A	3dm8_A	3im9_A	3pc3_A
1h2s_B	1o7j_C	1uvq_A	2ahn_A	2gpe_B	2q35_A	2xvx_A	3dme_B	3imh_A	3pcv_A
1h4a_X	1o7q_B	1uw4_C	2aib_A	2gqt_A	2q5c_A	2xws_A	3dmg_A	3inz_B	3pd2_B

1h4g_A	1o7z_B	1uw4_D	2akz_B	2gqw_A	2q62_G	2xwt_C	3dmi_A	3iof_A	3pd7_A
1h4p_A	1o82_A	1uwc_A	2anv_A	2grc_A	2q73_C	2xxj_D	3dmo_A	3ioh_A	3pdn_A
1h4r_A	1o8s_A	1uwf_A	2any_A	2grr_B	2q86_B	2xxl_B	3dnf_B	3ioq_A	3pel_B
1h5b_B	1o8x_A	1uwk_B	2ap1_A	2gsd_A	2q87_A	2xy2_A	3dpg_B	3iox_A	3pew_A
1h5q_L	1o91_C	1uwz_A	2apg_A	2gso_B	2q88_A	2xz2_A	3dqg_A	3ip4_A	3pf2_A
1h5v_A	1o98_A	1uxx_X	2aqm_A	2gte_A	2q8n_C	2xzi_A	3dr0_C	3ip8_A	3pfg_A
1h64_Q	1o9i_D	1uxy_A	2aqp_A	2gtr_A	2q8r_G	2y2z_A	3dr4_B	3ipc_A	3pfs_A
1h6f_A	1o9r_E	1uy1_A	2ar1_A	2gu3_A	2q9u_A	2y39_A	3dra_A	3ipf_A	3pg6_C
1h6l_A	1oa2_C	1uyx_A	2arc_B	2gud_B	2qa9_E	2y3q_B	3drf_A	3ipw_A	3pgx_A
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1h72_C	1oai_A	1v08_B	2at8_X	2guy_A	2qb7_A	2y5p_C	3ds4_B	3irp_X	3pjp_B
1h75_A	1oal_A	1v0z_B	2atb_A	2gw4_D	2qc5_A	2y7b_A	3dsk_A	3irs_A	3pk0_A
1h7e_B	1oao_A	1v2z_A	2atv_A	2gwm_A	2qd6_A	2y88_A	3dso_A	3irv_A	3pkv_A
1h8p_B	1oaq_H	1v30_A	2au7_A	2gxg_A	2qdx_A	2y8m_A	3dt9_A	3is3_A	3plf_D
1h8u_A	1oaq_L	1v33_A	2avd_B	2gyq_B	2qed_A	2yay_A	3dtb_A	3isa_B	3plw_A
1h97_B	1obo_A	1v37_A	2avk_A	2gz1_B	2qee_F	2ygs_A	3dvw_A	3iso_A	3plx_B
1h98_A	1oc2_B	1v4p_C	2axq_A	2gz4_A	2qev_A	2yqu_B	3dwg_A	3isq_A	3pmc_B
1h9m_A	1oc8_A	1v4x_B	2axw_B	2gze_A	2qf4_B	2yrr_B	3dwg_C	3it4_B	3pmd_A
1h9s_B	1ock_A	1v54_A	2ayd_A	2gze_B	2qfa_A	2ysk_A	3dvw_B	3it4_C	3pms_A
1hbn_C	1ocy_A	1v54_J	2b0a_A	2gzg_B	2qfa_B	2yva_B	3dxt_A	3iu5_A	3pmt_A
1hbn_E	1odm_A	1v54_V	2b0t_A	2h17_A	2qfa_C	2yve_A	3dy0_A	3iu7_A	3pna_A
1hc9_B	1odt_H	1v55_D	2b1k_A	2h1c_A	2qfe_A	2yvi_A	3dzw_A	3iux_A	3po0_A
1hd2_A	1oe2_A	1v55_L	2b3f_D	2h1v_A	2qg1_A	2yvo_A	3e05_B	3iwt_A	3po8_A
1hdo_A	1off_A	1v58_B	2b3h_A	2h2b_A	2qgy_B	2yvt_A	3e0i_A	3ix3_B	3pqa_B
1hfe_L	1ofl_A	1v5d_A	2b49_A	2h2r_B	2qhl_B	2yw2_A	3e13_X	3ixq_D	3pr9_A
1hfe_T	1ofs_C	1v5f_A	2b4z_A	2h2z_A	2qho_B	2yw3_A	3e17_B	3jpz_B	3prp_A
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1hl7_B	1oh0_A	1v7z_F	2b82_A	2h6f_A	2qkh_A	2yxo_B	3e6j_A	3js4_B	3q12_C
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1hml_A	1oi6_B	1v93_A	2bba_A	2h88_A	2qmc_D	2yyy_A	3e7h_A	3jsy_B	3q2e_A
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1hnj_A	1ojq_A	1v98_A	2bcg_G	2h88_D	2qmq_A	2yzc_D	3e8m_B	3jtm_A	3q49_B
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1hxr_B	1oqv_C	1vef_B	2bgs_A	2hbc8_A	2qsk_A	2z38_A	3ee4_A	3k1h_A	3qby_A
1hz4_A	1orn_A	1vf1_A	2bh8_B	2hc9_A	2qsq_B	2z3g_D	3eeh_A	3k26_A	3qc7_A
1hz6_C	1orr_A	1vfr_B	2bii_B	2hd9_A	2qt7_B	2z3v_A	3ees_A	3k2w_E	3qds_B
1hzj_A	1os6_A	1vfy_A	2bjd_B	2hda_A	2qub_I	2z4u_A	3ef4_A	3k31_A	3qe1_A

1hzo_A	1osy_B	1vg8_C	2bjf_A	2he0_A	2qud_A	2z66_B	3ef6_A	3k3c_D	3qgz_A
1hzt_A	1oth_A	1vh5_A	2bji_A	2he2_A	2qul_C	2z6n_A	3efy_A	3k3k_A	3qh4_A
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1i77_A	1oz9_A	1vke_F	2bky_B	2h jv_A	2qx8_B	2z8l_A	3ej9_C	3k89_A	3qxc_A
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1ig3_A	1p99_A	1vp2_A	2bo1_A	2hqs_H	2r37_A	2zdo_B	3enb_A	3kda_A	4ubp_A
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1iq6_B	1pl8_D	1w0n_A	2buu_A	2hvw_C	2rbk_A	2zjd_C	3eu9_C	3kkq_A	