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REPORT

Frequent occurrence of the T-loop RNA folding motif in ribosomal RNAs

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ABSTRACT

Analysis of atomic resolution structures of the rRNAs within the context of the 50S and the 30S ribosomal subunits have revealed the presence of nine examples of a recurrent structural motif, first observed in the TΨC loop of tRNAs. The key component of this T-loop motif is a UA *trans* Watson–Crick/Hoogsteen base pair stacked on a Watson–Crick pair on one side. This motif is stabilized by several noncanonical hydrogen bonds, facilitating RNA–RNA as well as RNA–protein interactions. In particular, the sugar edge of the purine on the 3′ side of the pivotal uridine in the UA pair frequently forms a noncanonical base pair with a distant residue. The bulged-out bases, usually seen as part of the motif, also use their Watson–Crick edges to interact with nearby residues via base-specific hydrogen bonds. In certain occurrences, a backbone reversal is stabilized by specific hydrogen bonds as is observed in the U-turn motifs and the adenosine residue of the key UA pair interacts with a third base via its Watson–Crick edge, essentially generating a base triple.

Keywords: ribosomal RNAs; RNA structure; T-loop motif; *trans* Watson-Crick/Hoogsteen pair

INTRODUCTION

Recent studies on RNA structures at atomic resolution have revealed a variety of recurrent folding motifs. These include the kink-turn motif (Klein et al., 2001), the A-minor motif (Nissen et al., 2001), the tetraloops (Woese et al., 1990), U-turn motifs (Gutell et al., 2000), bulged G-motifs (Szewczak et al., 1993; Wimberly et al., 1993; Correll et al., 1998), and cross-strand purine motifs (Wimberly et al., 1993; Correll et al., 1997; Dallas & Moore, 1997; Ban et al., 2000). As is commonly observed in proteins, tertiary structures in larger RNAs are often stabilized by these motifs (Conn & Draper, 1998).

An analysis of the three-dimensional coordinates of the ribosomal RNAs seen in the *Thermus thermophilus* 30S subunit (Wimberly et al., 2000) and the *Haloarcula marismortui* 50S subunit (Ban et al., 2000) structures is reported here. The results reveal the existence of multiple examples of a characteristic fold in the terminal loops of both 23S and 16S rRNAs, which can be formally referred to as the *trans* Watson–Crick/Hoogsteen (WC/HG) motif. This folding motif was first observed in the TΨC loop of $tRNA^{Pe}$ (Quigley & Rich, 1976) and subsequently in other high-resolution tRNA structures and hence will be informally referred to as the T-loop motif. This T-loop-like domain has also been observed in tmRNAs (Barends et al., 2002) and in the 3′ end of the plant viral TYMV RNA genome (Fechter et al., 2001). The prominent interactions seen in the T-loop (Fig. 1) include a UA *trans* WC/HG pair (ΨA in tRNA) stacked on a Watson–Crick pair, a U-turn mediated by a uridine residue 3′ to the pivotal uridine and two to three bulged-out residues 3′ of the adenosine. Base-specific hydrogen bonds stabilize the tertiary interactions between the TΨC and the DHU loops of tRNAs. As reported here, similar interactions are also observed in several terminal loops of ribosomal RNAs.

Because stabilizing interactions similar to those observed in the T-loops are sometimes observed in U-turn motifs, the T-loop has recently been assigned to 1 of 10 different categories of U-turns (Gutell et al., 2000). The additional examples of T-loop-like structures reported here allow a more precise definition of the fold. In particular, if the pivotal U participating in the *trans* WC/HG pair is assigned as position *n*, the $n + 1$ position is typically occupied by a guanine or uridine and the residue at the $n + 3$ position is a purine in most of the examples. A hydrogen bond is formed between the imino hydrogen of the $n + 1$ residue and the phosphate ox-

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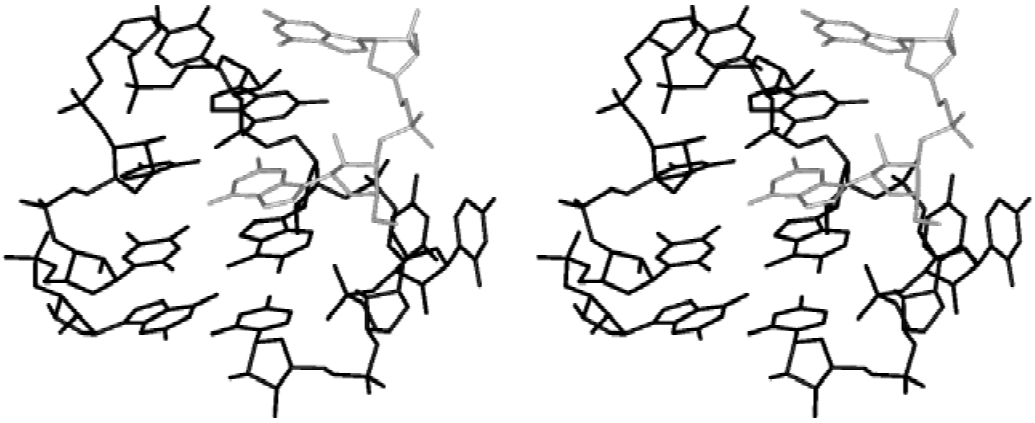

FIGURE 1. Stereo view of the TΨC loop of $tRNA^{Phe}$ (IEHZ). The tertiary interaction between T- and the D-loops is shown. The D-loop residues are colored gray for the sake of clarity.

ygen of the $n + 4$ residue. This central interaction facilitates the reversal of the phosphodiester backbone. In addition, the sugar hydroxyl of the $n + 1$ residue hydrogen bonds with N7 of the purine at the $n + 3$ position and the $n + 1$ residue hydrogen bonds with a distant residue via its sugar edge (SE). Although most of these features are observed in at least some U-turns, examples of the T-loop fold have additional structural interactions that are not observed in the U-turn motif. Given this and the new evidence presented here that the T-loop structure is far more common than previously realized, it is appropriate to consider it to be a motif in its own right. Herein, we discuss the structural features of two T-loop families and their variants and also provide a detailed summary of the tertiary interactions associated with each example.

RESULTS AND DISCUSSION

We have developed a database that summarizes all the known occurrences of noncanonical base–base interactions (Nagaswamy et al., 2002). In particular, examples of the UA *trans* WC/HG base pair were examined. It was found that a number of the occurrences in the large (Ban et al., 2000) and the small (Wimberly et al., 2000) subunit ribosomal RNAs were in very similar structural contexts (Fig. 2). In all the examples, the key UA pair is always stacked on a Watson–Crick pair and the nucleotides 3′ to the adenine base are bulged out. Examination of additional interactions in the loops revealed the similarity of these structures to the tRNA T-loop. Two distinct families of these T-loop motifs were identified in ribosomal RNAs.

Type I family

The canonical Type I T-loop (Fig. 3) is observed in three loops defined by positions 313–317 (23S), 1388–1392 (23S), and 1315–1319 (16S). The common interactions observed in these three terminal loops include the key *trans* WC/HG pair, the backbone reversal stabilized by specific base-sugar and base-phosphate hydrogen bonds, and long range tertiary base pairing involving the sugar edge of the $n + 1$ residue. The presence or absence of each of these features is indicated in Table 1. The secondary structures, two-dimensional summary of noncanonical interactions (Leontis & Westhof, 2001), and a stereo drawing of each example of the Type I motif are shown Figure 3. The interactions seen are strikingly similar to those observed in the TΨC loops of tRNAs. For instance, in the 313–317 loop, the $n + 1$ G314 residue forms a *trans* SE/WC pair with A337. In the 1388–1392 loop, G1389 forms a *cis* SE/WC pair with U1435. Residue G1316 of the 1315–1319 loop forms a *trans* SE/WC pair with A978. These interactions are similar to that observed between residues Ψ55 and G18 (*trans* SE/WC) in the T-loop of $tRNA^{Phe}$ (Shi & Moore, 2000). Additionally, C1394 of the 1388–1392 loop forms a *trans* WC/SE pair with U1432. Similar pairing is observed between the bulged U59 of the TΨC and D16 of the DHU loops in $tRNA^{Phe}$ (1EHZ). These geometric similarities are clearly depicted in the two-dimensional annotation scheme (Leontis & Westhof, 2001) on Figure 3.

The ribosomal RNAs also contain three obvious variants of the canonical type I T-loop motif (Fig. 4). In the case of the terminal loop defined by positions 322–329 of *T. thermophilus* 16S rRNA, a CA *trans* WC/HG pair is stacked on a GA *cis* WC/WC pair with a *trans* WC/HG UA pair on the other side. The two bulged residues C330 and G331 both hydrogen bond with residue G111 along their Watson–Crick edges in the *cis* orientation. The other characteristic hydrogen bonds stabilizing the backbone reversal are all observed in this loop. Two other variants of the type I family are the loops defined by 23S rRNA Positions 624–628 and 1499–1504. In both examples, position $n + 1$ is occupied by a uridine

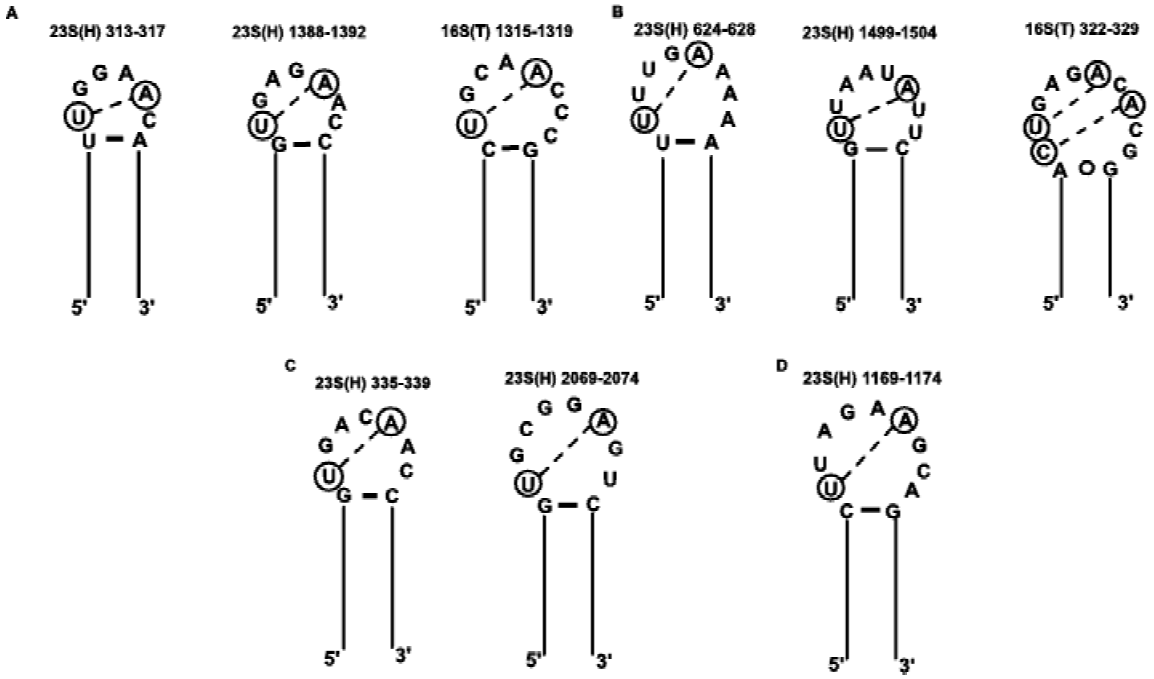

FIGURE 2. Secondary structures of the nine terminal loops satisfying the sequence constraints for the T-loop motif in *H. marismortui* 23S rRNA(H) and *T. thermophilus* 16S rRNA(T). **A**: Type I T-loop sequences. **B**: Type I variants. **C**: Type II T-loop sequences. **D:** Terminal loop in 23S rRNA that satisfies T-loop sequence constraint. The numbering system used is that of *H. marismortui* for 23S rRNA and *E. coli* for 16S rRNA. The solid lines represent Watson–Crick hydrogen bonds, the dashed lines represent the key *trans* WC/HG pair defining the T-loop motif.

instead of a guanine. In the 624–628 loop, one of the hydrogen bonds in the key UA pair is likely to be water mediated. Except for the sugar edge hydrogen bond observed in the type I family, the other characteristic hydrogen bonds are observed in the 1499–1504 loop.

Type II family

The terminal loops in 23S rRNA defined by the pairs 335–339 and 2069–2074 constitute the type II family (Fig. 5). In this family, the two bulged-out nucleotides 3′ of the key adenosine participate in Watson–Crick pairing with nearby residues. In addition, the adenosine of the key UA pair interacts with a distant uridine via its Watson–Crick edge, essentially generating a UAU base triple. The 335–339 loop does not make a U-turn, and, hence, none of the characteristic hydrogen bonds associated with the backbone reversal are observed (Fig. 5A). The two $n+1$ residues (G336 and G2070) of the type II loops use their sugar edges to pair with an $n+2$ residue (G315) and an $n+5$ residue (A629) of type I T-loops in the *trans* orientation. In addition, the two $n+2$ residues (A337 and C2071) form *trans* WC/SE pairs with the two $n+1$ residues (G314 and U625) of type I T-loops. The terminal loop defined by positions 2069–2074 also has some features of the type I family (Fig. 5B). These include backbone reversal stabilized by specific hydrogen bonds and the sugar edge pairing of the $n+1$ residue.

The 1169–1174 loop

The 1169–1174 loop of 23S rRNA also satisfies the sequence requirements of a typical T-loop motif. However, this region is not resolved in the 50S subunit and hence its detailed folding in the ribosome is not yet known. In an independent study of the *Thermotoga maritima* L11-RNA complex (Conn et al., 1999), the anticipated UA *trans* WC/HG pair was not found. However, the loop residues do interact with a nearby loop region (1092–1099), in a manner similar to what is seen with the 313–317 and 335–339 loops.

Tertiary interactions stabilized by the T-loop motif

In tRNA structures, the hinge region is stabilized by two specific base–base interactions between the TΨC loop and the DHU loop. Analogous interactions are observed in the ribosomal RNAs, where the T-loop motif interacts with distant strands, essentially mimicking the tRNA hinge. Tables 2 and 3 summarize the tertiary interactions associated with all the occurrences of the T-loop motif found in the ribosomal RNAs. It is noteworthy that both type II examples interact with a type I T-loop (335–339/313–317 and 2069–2074/624–628), using the same mode of hydrogen bonding. T-loop 1388–1392 interacts with the terminal loop defined by positions 1430–1436 via base-specific hydrogen bonds

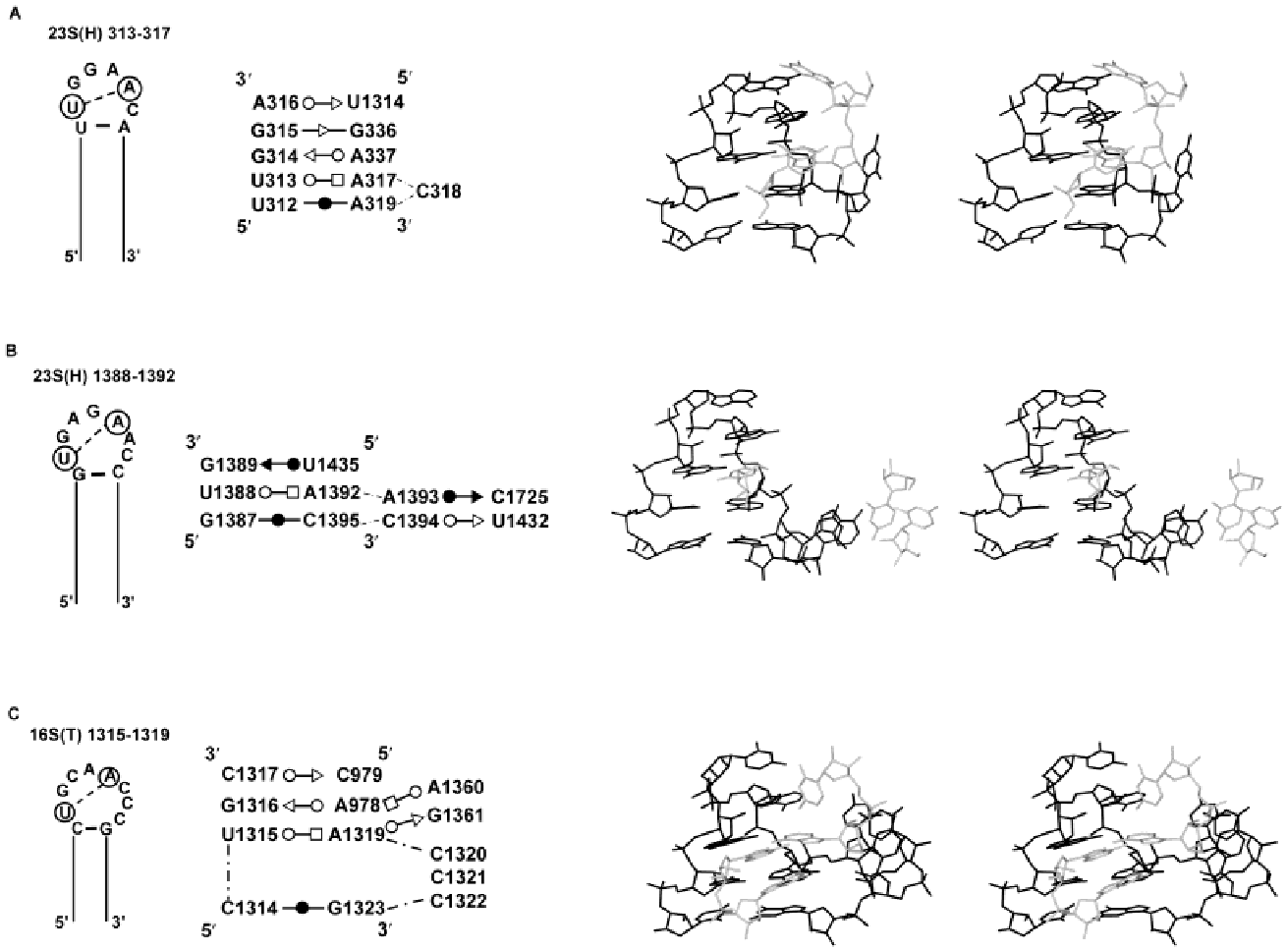

FIGURE 3. Type I family. **A:** T-loop 313–317 of 23S rRNA (H). **B:** T-loop 1388–1392 of 23S rRNA (H). **C**: T-loop 1315–1319 of 16S rRNA (T). Left panel: Secondary structures. Central panel: Two-dimensional annotations representing the key noncanonical interactions stabilizing these T-loop motifs. Symbols: (—●—) *cis* WC/WC, (○—□) *trans* WC/HG, (◀—●) *cis* SE/WC, (—▷—) *trans* SE/SE, (○—▷) *trans* WC/SE, (- — - —) backbone extension. Right panel: Stereo view of the three-dimensional loop structures. For the sake of clarity, the hydrogen bonds between interacting bases are not indicated. The loop residues are indicated in black and the off-loop residues are colored gray.

(see Type I family). T-loop 1499–1504 interacts with 1445–1448 region via backbone packing. Similar tertiary interactions have been proposed between the T- and the D-loop-like domains observed in the tmRNA and the 3′ end of some plant viral RNA genome. The overwhelming similarity of these long-range interactions observed in both tRNAs and ribosomal RNAs leads us to believe that the T-loop-derived motif is a very important building unit in large RNA structures.

T-loop motifs and U-turns

The type I T-loop motif shares some of the structural features observed in the category of U-turn motifs that are flanked by a Y:R-type base pair (Gutell et al., 2000). The tRNA TΨC loops (Fig. 1), are a typical example where structural features of both motifs are observed. Although the U-turn has analogous hydrogen bonds to those seen in the T-loop motif, the location of the pivotal residues actually differs by one position. Nevertheless, given the similarity, it is not surprising that of the nine examples discussed here, five (16S: 322–329, 16S: 1315–1319, 23S: 313–317, 23S: 624–628, and 23S: 1169–1174) were actually predicted to fold into the U-turn motifs (Gutell et al., 2000). Despite the similarities, there are also important differences. In particular, the key interactions including the sugar edge pair formed by the $n + 1$ residue in T-loops of type I, the UAU triple, and the Watson–Crick pairs involving the bulged-out nucleotides observed in type II T-loops are not observed in all U-turn motifs.

TABLE 1. Terminal loops in ribosomal RNAs stabilized by a UA pair *trans* WC/HG pairs.

Positions	Family	$n+1$	$n+3$	5′ base pair	3′ base pair	Core hydrogen bonds		Base triple[c]	Bulged-out nucleotides	
						1[a]	2[b]		Number	Base pairing edges[d]
322–329 (16S)	Type I[e]	G[j]	G[k]	GA-WC	UA[f]	Yes	Yes	None	2	*cis* WC/WC, *cis* WC/WC
1315–1319 (16S)	Type I	G	A	CG-WC	GA[g]	Yes	Yes	GAU	3	None
313–317 (23S)	Type I	G	A	UA-WC	GA[g]	Yes	Yes	None	1	None
335–339 (23S)	Type II	G	C	GC-WC	None	No	No	UAU	2	*cis* WC/WC, *cis* WC/WC
624–628 (23S)	Type I[e]	U	G	UA-WC	UC[h]	Yes	Yes	None	3	*trans* WC/SE, none, none
1388–1392 (23S)	Type I	G	A	GC-WC	GU[i]	Yes	Yes	None	2	*cis* SE/WC, *trans* SE/WC
1499–1504 (23S)	Type I[e]	U	A	GC-WC	None	Yes	Yes	None	2	None
2069–2074 (23S)	Type II	G	G	GC-WC	GA[g]	Yes	No	UAU	2	*cis* WC/WC, *cis* WC/WC

WC: Watson-Crick edge, HG: Hoogsteen edge, SE: sugar edge.
[a]Hydrogen bond between imino proton of residue at $n+1$ position and the phosphate oxygen of $n+4$ residue.
[b]Hydrogen bond between the sugar hydroxyl of $n+1$ residue and the N7 of $n+3$ purine.
[c]Base triple involving the adenosine in the key UA pair.
[d]Interacting edges of pairs involving bulged nucleotides.
[e]Variant
[f]UA *trans* WC/HG
[g]GA *trans* SE/WC
[h]UC *trans* SE/WC
[i]GU cis SE/WC
[j]$n+2$ residue
[k]$n+4$ residue

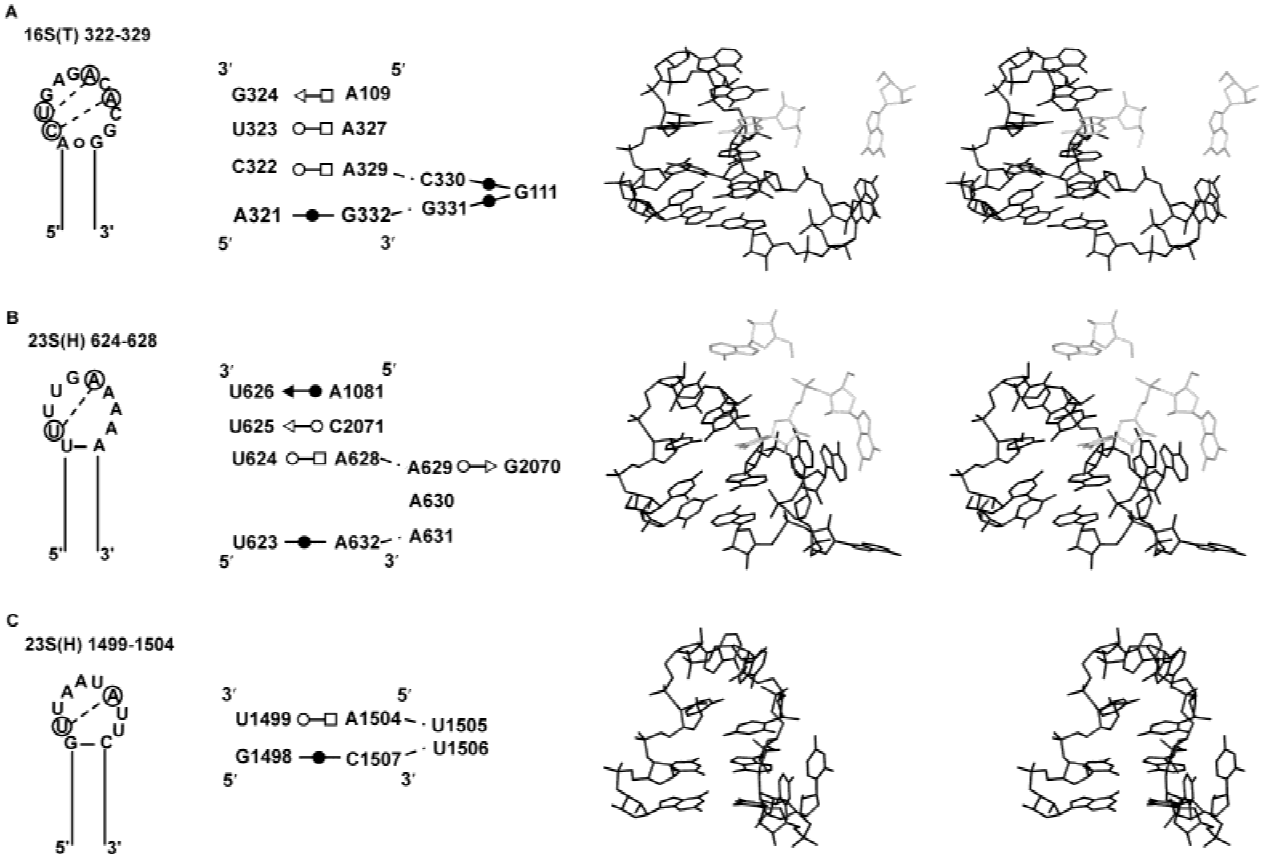

FIGURE 4. Variants of the Type I structure. **A**: T-loop variant 322–329 of 16S rRNA (T). **B**: T-loop variant 624–628 of 23S rRNA (H). **C**: T-loop variant 1499–1504 of 23S rRNA (H). Left panel: Secondary structures. Central panel: Two-dimensional annotations representing the key noncanonical interactions stabilizing these T-loop motifs. Symbols: (—●—) *cis* WC/WC, (○—□) *trans* WC/HG, (◀—●) *cis* SE/WC, (—▷—) *trans* SE/SE, (○—▷) *trans* WC/SE, (- —— - ——) backbone extension. Right panel: Stereo view of the three-dimensional loop structures. For the sake of clarity, the hydrogen bonds between interacting bases are not indicated. The loop residues are indicated in black and the off-loop residues are colored gray.

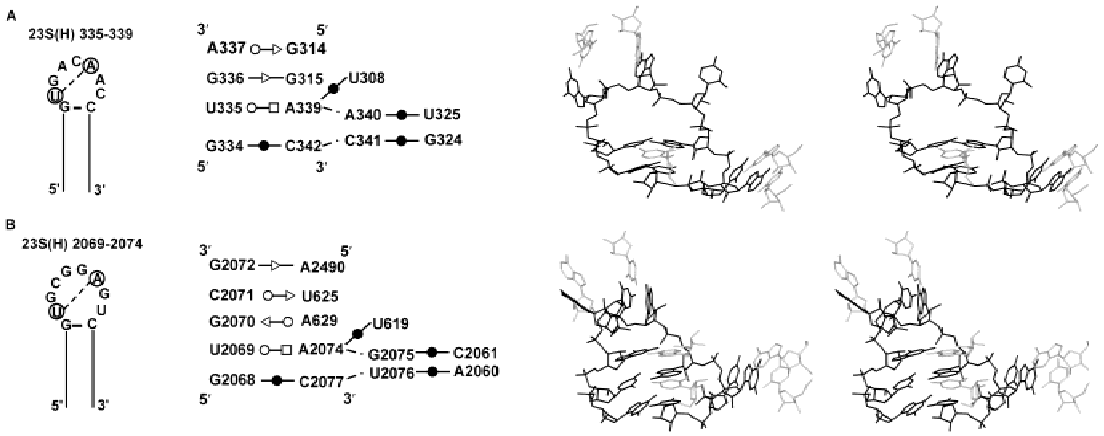

FIGURE 5. Type II family. **A:** T-loop 335–339 of 23S rRNA (H). **B**: T-loop 2069–2074 of 23S rRNA (H). Left panel: Secondary structures. Central panel: Two-dimensional annotations representing the key noncanonical interactions stabilizing these T-loop motifs. Symbols: (—●—) *cis* WC/WC, (○—□) *trans* WC/HG, (◀—●) *cis* SE/WC, (—▷—) *trans* SE/SE, (○—▷) *trans* WC/SE, (-·····-) backbone extension. Right panel: Stereo diagrams of the three-dimensional loop structures. For the sake of clarity, the hydrogen bonds between interacting bases are not indicated. The loop residues are indicated in black and the off-loop residues are colored gray.

Although some examples of the T-loop motif are clearly similar to the U-turn, it is in our view not useful to consider them to be simply a type of U-turn. To do so would add further to the ambiguity of what is meant by the term U-turn and would obscure the similarity between the non-U-turn-like type II example of the T-loop motif and the U-turn-like type I examples. In contrast, when these structures are considered to comprise a

TABLE 2. Tertiary interactions associated with type I T-loops and their variants.

Type I			Type I variants		
	Tertiary base	Hydrogen bonding		Tertiary base	Hydrogen bonding
313–317 (23S)			322–329 (16S)		
U313	None	None	C322	None	None
G314	A337	*trans* SE/WC	U323	None	None
G315	G336	*trans* SE/SE	G324	A109	*trans* SE/HG
A316	U1314	*trans* WC/SE	A325	None	None
A317	None	None	G326	None	None
C318	None	None	A327	None	None
			C330	G111	*cis* WC/WC
1388–1392 (23S)			G331	G111	*cis* WC/WC
U1388	None	None			
G1389	U1435	*cis* SE/WC	624–628 (23S)		
A1390	None	None	U624	None	None
G1391	None	None	U625	C2071	*trans* SE/WC
A1392	None	None	U626	A1081	*cis* SE/WC
A1393	C1725	*cis* WC/SE	G627	None	None
C1394	U1432	*trans* WC/SE	A628	None	None
			A629	G2070	*trans* WC/SE
1315–1319 (16S)			A630	None	None
U1315	None	None	A631	None	None
G1316	A978	*trans* SE/WC			
C1317	C979	*trans* WC/SE	1499–1504 (23S)		
A1318	None	None	U1499	None	None
A1319	G1361	*trans* WC/SE	U1500	None	None
C1320	None	None	A1501	None	None
C1321	None	None	A1502	G1444	*trans* SE/SE
C1322	None	None	U1503	None	None
			A1504	None	None
			U1505	None	None
			U1506	None	None

TABLE 3. Tertiary interactions associated with type II T-loops.

	Type II			
	Tertiary base	Hydrogen bonding	Tertiary base	Hydrogen bonding
335–339 (23S)				
U335	None	None		
G336	G315	*trans* SE/SE		
A337	G314	*trans* WC/SE		
C338	None	None		
A339	U308	*cis* WC/WC		
A340	U325	*cis* WC/WC	A306	*trans* SE/SE
C341	G324	*cis* WC/WC		
2069–2074 (23S)				
U2069	None	None		
G2070	A629	*trans* SE/WC		
C2071	U625	*trans* WC/SE		
G2072	A2490	*trans* SE/SE		
G2073	None	None		
A2074	U619	*cis* WC/WC		
G2075	C2061	*cis* WC/WC	A536	*trans* SE/SE
U2076	A2060	*cis* WC/WC		

motif in their own right, the potential presence of that motif is readily recognizable in secondary structure representations, and the relationship between type I and II is not lost. Moreover, it is now clear that these folds are sufficiently common that it will be useful to be able to alert investigators to their presence by the use of the unique designation of T-loop motif.

Protein–T-loop interactions

As is seen in the kink-turn motif, the T-loop motifs seen in the ribosome structures sometimes interact with amino acid residues of nearby proteins. For example, ribosomal protein L24 interacts with the 313–317 loop. In particular, residue Arg52 packs against the backbone and Asp54 hydrogen bonds with the sugar of G315. Ribosomal proteins L24 and L4 both interact extensively with the 336–339 loop. In this case, residues Tyr186 of L4 and Arg8 of L24 interact with the RNA backbone. Asn95 of L24 packs against the UAU base triple. Arg11 and Lys19 of ribosomal protein L15 pack against the backbone of 624–628 loop of 23S rRNA. Residues Arg41, Arg8, and Arg37 of L19E protein pack against the backbone of 1499–1504 loop. Glu12 and Lys13 of L23 protein hydrogen bond with A1501 and U1503, respectively. The only T-loop that does not interact with any of the large subunit proteins is the 2069–2074 loop. Finally, residue Arg22 of S20 hydrogen bonds with the phosphate oxygen connecting U323 and G324 in the 322–329 loop. Asn26 and Ser70 of S20 also pack against the backbone of this loop. Ribosomal proteins S19 and S14 interact with the 1315–1319 loop.

CONCLUSIONS

The fact that the T-loop motif has been found to exist not only in tRNAs but in some viral RNAs, tmRNAs, and local regions of the ribosomal RNAs suggest that this frequent loop motif is an important RNA structural building block, particularly stabilizing RNA–RNA tertiary interactions. Indeed, the T-loop motif may have a special role in the history of the translation machinery by facilitating the transition from an early one-domain tRNA to the modern two-domain tRNA (Schimmel & de Paupiana, 1995). It is also likely to be identified in as yet uncharacterized RNAs as well.

MATERIALS AND METHODS

All noncanonical interactions connected by at least two hydrogen bonds observed in the 50S (1JJ2) and the 30S (1J5E) ribosomal subunits were analyzed using the Swiss PDB Viewer Program (Guex & Peitsch, 1997). The nomenclature for noncanonical interactions was based on a recent proposal by Leontis and Westhof (2001). The UA *trans* WC/HG pairs occurring in terminal loops of the ribosomal RNAs were classified into two families according to their three-dimensional structure. The secondary structures of the terminal loops were obtained from the CRW website (http://www.rna.icmb.utexas.edu/). The loop numbers correspond to the key *trans* WC/HG UA pair. The figures representing the three-dimensional drawings of the terminal loops were generated from the pdb files using the Viewerpro software (Accelrys) and processed using the Adobe illustrator software (Version 9.0).

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