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**ON SOME FORBIDDEN CONFIGURATIONS
FOR SELF-COMPLEMENTARY
TRINUCLEOTIDE CIRCULAR CODES**

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Abstract

A self-complementary trinucleotide circular code has two permuted sets which are either both circular codes or both not circular codes.

Key words: trinucleotide circular codes; self-complementary property; permuted circular sets.

1. Introduction

We continue our study of the combinatorial properties of maximum trinucleotide circular codes, i.e. circular codes with 20 trinucleotides. A trinucleotide is a word of three letters on the 4-letter alphabet $\{A, C, G, T\}$. The set of $4^3 = 64$ trinucleotides is a code in the sense of language theory, more precisely a uniform code, but not a circular code. In order to have an intuitive meaning of these notions, codes are written on a straight line while circular codes are written on a circle, but, in both cases, unique decipherability is required.

In the past 50 years, circular codes have been studied in theoretical biology, mainly to understand the structure and the origin of the genetic code as well as the reading frame (construction) of genes, e.g. [6, 9, 10, 14]. In 1996, a circular code of 20 trinucleotides was identified statistically on two large and different gene populations, eukaryotes and prokaryotes [1]. Furthermore, this code has two properties: it is self-complementary and its two permuted sets are also circular codes. During the last years, circular codes are mathematical objects studied in discrete mathematics, theoretical computer science and theoretical biology, e.g. [2, 13, 4, 3, 25, 11, 7, 19, 16, 24, 8, 15, 20, 17, 18, 21, 12, 22, 23].

Among the 12,964,440 trinucleotide circular codes, only 528 of them are self-complementary [1, 24, 18]. New propositions are identified here with these 528 self-complementary trinucleotide circular codes.

The 528 self-complementary trinucleotide circular codes are divided into two classes: a class of 216 circular codes where each code has two permuted sets X_1 and X_2 which are circular codes [1, 18] and a class containing the remaining 312 circular codes, denoted $\overline{C^3}$, for which the circularity of the permuted sets X_1 and of X_2 were not investigated so far.

For the $\overline{C^3}$ class, three cases are possible:

- (i) X_1 is a circular code and X_2 is not a circular code;
- (ii) X_1 is not a circular code and X_2 is a circular code;
- (iii) X_1 and X_2 are not circular codes.

The main proposition of this paper will prove that only the case (iii) is verified. This result was obtained with a detailed identification of 51 “forbidden configurations” corresponding to 51 propositions which are collected in three groups (section Results). Thus, the 528 self-complementary trinucleotide circular codes are divided into two classes for which a certain symmetry holds. Indeed, even if these two classes have different cardinality (216 and 312), the first class contains 216 circular codes where X_1 and X_2 are both circular codes while the second class contains 312 circular codes where X_1 and X_2 are both non-circular codes.

2. Definitions

For the classical notions of *alphabet*, *empty word*, *length*, *factor*, *proper factor*, *prefix*, *proper prefix*, *suffix*, *proper suffix*, *alphabetical order*, we refer to [5]. Let $\mathcal{A}_4 = \{A, C, G, T\}$ denote the genetic alphabet, lexicographically ordered with $A < C < G < T$. We use the following notation:

- \mathcal{A}_4^* (respectively \mathcal{A}_4^+) is the set of words (respectively nonempty words) over \mathcal{A}_4 ;
- \mathcal{A}_4^2 is the set of the 16 words of length 2 (or *diletters* or *dinucleotides*) and
- \mathcal{A}_4^3 the set of the 64 words of length 3 (or *triletters* or *trinucleotides*).

We now recall two important genetic maps, the definitions of code and circular code [14, 5], and the C^3 self-complementary property of a circular code [1].

4.

Definition 2.1. The complementary map $\mathcal{C}: \mathcal{A}_4^+ \rightarrow \mathcal{A}_4^+$ is defined by $\mathcal{C}(A) = T$, $\mathcal{C}(T) = A$, $\mathcal{C}(C) = G$ and $\mathcal{C}(G) = C$ and by $\mathcal{C}(uv) = \mathcal{C}(v)\mathcal{C}(u)$ for all $u, v \in \mathcal{A}_4^+$, e.g. $\mathcal{C}(AAC) = GTT$. This map on words is naturally extended to word sets: a complementary trinucleotide set is obtained by applying the complementary map \mathcal{C} to all its trinucleotides.

Definition 2.2. The circular permutation map $\mathcal{P}: \mathcal{A}_4^3 \rightarrow \mathcal{A}_4^3$ permutes circularly each trinucleotide $l_1l_2l_3$ as follows $\mathcal{P}(l_1l_2l_3) = l_2l_3l_1$. The k -th iterate of \mathcal{P} is denoted \mathcal{P}^k . This map on words is also naturally extended to word sets: a permuted trinucleotide set is obtained by applying the circular permutation map \mathcal{P} (or the k -th iterate of \mathcal{P}) to all its trinucleotides.

Definition 2.3. Code: A set X_0 of words is a code if, for each $x_1, \dots, x_n, x'_1, \dots, x'_m \in X$, $n, m \geq 1$, the condition $x_1 \cdots x_n = x'_1 \cdots x'_m$ implies $n = m$ and $x_i = x'_i$ for $i = 1, \dots, n$.

We consider in this paper only codes consisting of trinucleotides.

Definition 2.4. Trinucleotide circular code: A set X_0 of trinucleotides is a trinucleotide circular code if, for each $x_1, \dots, x_n, x'_1, \dots, x'_m \in X_0$, $n, m \geq 1$, $p \in \mathcal{A}_4^*$, $s \in \mathcal{A}_4^+$, the conditions $sx_2 \cdots x_np = x'_1 \cdots x'_m$ and $x_1 = ps$ imply $n = m$, $p = \varepsilon$ (empty word) and $x_i = x'_i$ for $i = 1, \dots, n$.

Definition 2.5. A trinucleotide circular code X_0 is self-complementary if, for each $y \in X_0$, $\mathcal{C}(y) \in X_0$.

Definition 2.6. If X_0 is a trinucleotide circular code, we denote by X_1 the permuted trinucleotide set $\mathcal{P}(X_0)$ and by X_2 the permuted trinucleotide set $\mathcal{P}^2(X_0)$.

Definition 2.7. A trinucleotide circular code X_0 is C^3 self-complementary if X_0 , $X_1 = \mathcal{P}(X_0)$ and $X_2 = \mathcal{P}^2(X_0)$ are circular codes satisfying the following properties: $X_0 = \mathcal{C}(X_0)$ (self-complementary), $\mathcal{C}(X_1) = X_2$ and $\mathcal{C}(X_2) = X_1$.

The concept of necklace was introduced by Pirillo [20] for circular codes in order to have an algorithmic characterization of circular codes. Let $l_1, l_2, \dots, l_{n-1}, l_n, \dots$ be letters in \mathcal{A}_4 , $d_1, d_2, \dots, d_{n-1}, d_n, \dots$ be diletters in \mathcal{A}_4^2 and $n \geq 2$ be an integer.

Definition 2.8. Letter Diletter Continued Necklaces (LDCN): We say that the ordered sequence $l_1, d_1, l_2, d_2, \dots, d_{n-1}, l_n, d_n, l_{n+1}$ is an $(n+1)$ LDCN for a subset $X \subset \mathcal{A}_4^3$ if $l_1d_1, l_2d_2, \dots, l_nd_n \in X$ and $d_1l_2, d_2l_3, \dots, d_{n-1}l_n, d_nl_{n+1} \in X$.

Proposition 2.9. [20]. Let X be a trinucleotide code. The following conditions are equivalent:
(i) X is a circular code.
(ii) X has no 5LDCN.

There are 528 self-complementary circular codes (Table 3 in [24] and Table 2(d) in [1]). There are 216 C^3 self-complementary circular codes (Tables 4a, 5a and 6a in [18] and Table 2(d) in [1]). Thus, there are $528 - 216 = 312$ circular codes which are self-complementary but not C^3 self-complementary. We denote them by $\overline{C^3}$. Using the three following propositions, we will prove that, for each $\overline{C^3}$ self-complementary circular code X_0 , the sets X_1 and X_2 have both a necklace 5LDCN, so nor X_1 neither X_2 are circular codes.

There are 28 self-complementary pairs of trinucleotides which are codified according to Table 1 (as in [24, 18]), giving to each pair the name of a letter of the english alphabet augmented by the two supplementary letters z' and z'' .

$a = \{AAC, GTT\}$	$b = \{AAG, CTT\}$	$c = \{AAT, ATT\}$	$d = \{ACA, TGT\}$
$e = \{ACC, GGT\}$	$f = \{ACG, CGT\}$	$g = \{ACT, AGT\}$	$h = \{AGA, TCT\}$
$i = \{AGC, GCT\}$	$j = \{AGG, CCT\}$	$k = \{ATC, GAT\}$	$l = \{ATG, CAT\}$
$m = \{CAA, TTG\}$	$n = \{CAC, GTG\}$	$o = \{CAG, CTG\}$	$p = \{CCA, TGG\}$
$q = \{CCG, CCG\}$	$r = \{CGA, TCG\}$	$s = \{CTA, TAG\}$	$t = \{CTC, GAG\}$
$u = \{GAA, TTC\}$	$v = \{GAC, GTC\}$	$w = \{GCA, TGC\}$	$x = \{GCC, GGC\}$
$y = \{GGA, TCC\}$	$z = \{GTA, TAC\}$	$z' = \{TAA, TTA\}$	$z'' = \{TCA, TGA\}$

Table 1. The 28 self-complementary pairs of trinucleotides.

3. Results

Proposition 3.1. *If a circular code X_0 contains one of the four doublets*

$$\alpha_1 = \{a, p\}, \alpha_2 = \{b, y\}, \alpha_3 = \{e, m\}, \alpha_4 = \{j, u\}, \quad (3.1)$$

then neither its permuted set $X_1 = \mathcal{P}(X_0)$ nor its permuted set $X_2 = \mathcal{P}^2(X_0)$ are circular codes.

Proof. We prove the first case, the other cases being similar. If $\alpha_1 = \{a, p\} = \{AAC, GTT, CCA, TGG\} \subset X_0$ then $\mathcal{P}(\alpha_1) = \{ACA, TTG, CAC, GGT\} \subset X_1$. So, $A, CA, C, AC, A, CA, C, AC, A$ is a 5LDCN for $\mathcal{P}(\alpha_1)$, hence also for X_1 which, consequently, is not a circular code. Furthermore, $\mathcal{P}^2(\alpha_1) = \{CAA, TGT, ACC, GTG\} \subset X_2$ and $T, GT, G, TG, T, GT, G, TG, T$ is a 5LDCN for $\mathcal{P}^2(\alpha_1)$, hence also for X_2 which, consequently, is not a circular code. ■

Proposition 3.2. *If a circular code X_0 contains one of the 24 triplets*

$$\beta_1 = \{a, r, w\}, \beta_2 = \{a, s, z''\}, \beta_3 = \{b, r, w\}, \beta_4 = \{b, z, z''\}, \beta_5 = \{c, s, z''\}, \beta_6 = \{c, z, z''\}, \quad (3.2)$$

$$\begin{aligned} \beta_7 &= \{e, l, s\}, \beta_8 = \{e, o, r\}, \beta_9 = \{f, i, m\}, \beta_{10} = \{f, i, u\}, \beta_{11} = \{f, o, x\}, \beta_{12} = \{f, o, y\}, \\ \beta_{13} &= \{g, k, m\}, \beta_{14} = \{g, k, z'\}, \beta_{15} = \{g, l, u\}, \beta_{16} = \{g, l, z'\}, \beta_{17} = \{i, p, v\}, \beta_{18} = \{i, q, v\}, \\ \beta_{19} &= \{j, k, z\}, \beta_{20} = \{j, v, w\}, \beta_{21} = \{k, p, z\}, \beta_{22} = \{l, s, y\}, \beta_{23} = \{o, r, x\}, \beta_{24} = \{q, v, w\}, \end{aligned}$$

then neither its permuted set $X_1 = \mathcal{P}(X_0)$ nor its permuted set $X_2 = \mathcal{P}^2(X_0)$ are circular codes.

Proof. We prove the first case, the other cases being similar. If $\beta_1 = \{a, r, w\} = \{AAC, GTT, CGA, TCG, GCA, TGC\} \subset X_0$ then $\mathcal{P}(\beta_1) = \{ACA, TTG, GAC, CGT, CAG, GCT\} \subset X_1$. So $A, CA, G, AC, A, CA, G, AC, A$ is a 5LDCN for $\mathcal{P}(\beta_1)$, hence also for X_1 which, consequently, is not a circular code. Furthermore, $\mathcal{P}^2(\beta_1) = \{CAA, TGT, ACG, GTC, AGC, CTG\} \subset X_2$ and $T, GT, C, TG, T, GT, C, TG, T$ is a 5LDCN for $\mathcal{P}^2(\beta_1)$, hence also for X_2 which, consequently, is not a circular code. ■

Proposition 3.3. *If a circular code X_0 contains one of the 23 quadruplets*

$$\begin{aligned} \gamma_1 &= \{a, h, j, r\}, \gamma_2 = \{a, h, n, w\}, \gamma_3 = \{a, h, n, z'\}, \gamma_4 = \{a, l, n, y\}, \\ \gamma_5 &= \{b, d, e, w\}, \gamma_6 = \{b, d, r, t\}, \gamma_7 = \{b, d, t, z'\}, \gamma_8 = \{b, k, p, t\}, \\ \gamma_9 &= \{c, d, t, u\}, \gamma_{10} = \{c, h, m, n\}, \gamma_{11} = \{d, e, l, t\}, \gamma_{12} = \{d, e, q, t\}, \\ \gamma_{13} &= \{d, f, p, u\}, \gamma_{14} = \{d, i, t, u\}, \gamma_{15} = \{d, p, t, x\}, \gamma_{16} = \{d, p, t, z\}, \\ \gamma_{17} &= \{e, s, t, u\}, \gamma_{18} = \{f, h, m, n\}, \gamma_{19} = \{h, j, k, n\}, \gamma_{20} = \{h, j, n, x\}, \\ \gamma_{21} &= \{h, i, m, y\}, \gamma_{22} = \{h, n, q, y\}, \gamma_{23} = \{h, n, s, y\}, \end{aligned} \quad (3.3)$$

then neither its permuted set $X_1 = \mathcal{P}(X_0)$ nor its permuted set $X_2 = \mathcal{P}^2(X_0)$ are circular codes.

Proof. We prove the first case, the other cases being similar. If $\gamma_1 = \{a, h, j, r\} = \{AAC, GTT, AGA, TCT, AGG, CCT, CGA, TCG\} \subset X_0$ then $\mathcal{P}(\gamma_1) = \{ACA, TTG, GAA, CTT, GGA, CTC, GAC, CGT\} \subset X_1$. So, $C, TT, G, GA, C, TT, G, GA, C$ is a 5LDCN for $\mathcal{P}(\gamma_1)$, hence also for X_1 which, consequently, is not a circular code. Furthermore, $\mathcal{P}^2(\gamma_1) = \{CAA, TGT, AAG, TTC, GAG, TCC, ACG, GTC\} \subset X_2$. Then $G, TC, C, AA, G, TC, C, AA, G$ is a 5LDCN for $\mathcal{P}^2(\gamma_1)$, hence also for X_2 which, consequently, is not a circular code. ■

Table 2 reports the complete combinatorial study of the 312 $\overline{C^3}$ circular codes (self-complementary circular codes but not C^3). They are listed using the same order of Tables 4b, 5b and 6b in [18].

abcegiuvxy	α_2	abcegiuvxy ^z	α_2	acfgjhloqyz ^z	α_1	bcdgviuvxy ^z	α_2	cdfglopqtu	β_{15}	dgkpuvuvxy ^z	β_{14}
abcfjlopq	α_1	abcegiuvxy	α_2	acfgihlnoqy	β_{12}	bcdfgikptz	γ_8	cdflopqstu	γ_9	dhipvuvxyz ^z	β_{20}
abcflopqst	α_1	abcegiuvxy	α_2	acghijknuv	γ_{19}	bcdfopqstz	β_5	cdghijkpvz	β_{17}	djkpuvuvxyz ^z	α_4
abciknovxyz	α_2	abceivxyz ^z	α_2	acghijkpvz	α_1	bcdfgikptvz	β_{17}	cdghijkpvz	β_{17}	djppqrsuz ^z	α_4
abcknovxyz	α_2	abcekovxyz	α_2	acghijlmqv	β_{18}	bcefgijlmqv	α_3	cdgijkpvuv	α_4	djqpsuvxyz ^z	α_4
abclpqrst	α_1	abcfjijlpq	α_1	acghijlpqv	α_1	bcefgilmovt	α_3	cdgijkptvz	β_{17}	djpquvxyz ^z	α_4
acegijkuvx	α_4	abcfjijpqz ^z	α_1	acghijpvz ^z	α_1	bcefgilmovq	α_2	cefgghijkmvz	α_3	dkpuvuvxyz ^z	β_{21}
acfhijilpq	α_1	abcfjijopqz ^z	α_1	acgijknuvx	α_4	bcefgilmovs	α_3	cefgghikmvz	α_3	dpstuvuvxyz ^z	β_{24}
acfhijipqz ^z	α_1	abcfjilmovq	α_2	acgijkpuvx	α_1	bcefgilmovs	α_2	cefgghilmqy	α_3	dptuvuvxyz ^z	γ_{15}
achijknuvz	β_{19}	abcfjlopqt	α_1	acgikptuvx	α_1	acikptuvz	α_1	cefgghilmov	α_3	eghilmovxyz ^z	α_3
acijknuvz	α_4	abcfjlopqs	α_1	achijkpvz	α_1	bcfgilmovqy	α_2	cefgghilmovz	α_3	eghilmovxyz ^z	α_3
ahnrvxyz ^z	β_1	abcfjopqsz	α_1	achijvz ^z	β_6	bcefgilmovsy	α_2	cefgghilmovz	α_3	eghmvuvxyz ^z	α_3
ahprvxyz ^z	α_1	abcfjloqsz	α_2	achijpvz ^z	α_1	bcgijlmnqv	β_{18}	cefgghilmqu	α_3	egkmtuvvz ^z	α_3
akptuvuvz ^z	α_1	abcfopqstz	α_1	achinvz ^z	β_6	bdektuvz ^z	γ_5	cefgghilmqu	α_3	egkmuvuvz ^z	α_3
apuvuvxyz ^z	α_1	abcfjilpqv	α_1	acijkpvuvz	α_1	bdeqrstz ^z	β_8	cefgghilmqu	α_3	egmruvuvz ^z	α_3
bcdgfgikxy	α_2	abcfjilmovx	α_2	bcfgijlmnqv	β_9	bdeqrstvz ^z	α_2	cefgghilmotuvz	α_3	egmvuvuvz ^z	α_3
bcdgfgikyz ^z	α_2	abcfjilpqv	α_1	aehrxyz ^z	β_1	bdeqrstvz ^z	β_3	cefgghilmotuvz	α_3	ehlmoqrstyz ^z	α_3
bcdgfgloqst	β_7	abcfjlopqv	α_1	ahjloqrst ^z	γ_1	bdeqrstvz ^z	α_2	cefgghilmotuvz	α_3	ehmoqrstyz ^z	α_3
bcefgijlmov	α_3	abcfjloqsz	α_2	ahjnoqrst ^z	β_2	bderuvxyz ^z	α_2	ceghijkmvz	α_3	ehmoqrstyz ^z	α_3
bcefgilmov	α_3	abcflopqst	α_1	ahjrvuvz ^z	β_1	ahlnovxyz ^z	β_{22}	ceghijkmvz	α_3	ehmoqrstyz ^z	α_3
bdpqrstuvz ^z	β_3	abcijknuvz	β_{19}	ahjrvuvz ^z	β_{20}	bdeuvuvxyz ^z	α_2	ceghijkmvz	α_3	ekmouuvyz ^z	α_3
bdpqrsvz ^z	α_2	abcikptvz	α_1	ahjrvuvz ^z	β_4	bdjpvuvz ^z	β_3	ceghijkmvz	α_3	ekmvuvuvz ^z	α_3
blmnoqrstyz ^z	α_2	abcinuvz ^z	α_2	ahjpvuvz ^z	α_1	bdjpvuvz ^z	β_{21}	ceghijkmvz	α_3	ekmvuvuvz ^z	α_3
bmopqrstyz ^z	α_2	abcfjlopqv	α_1	ahjpvuvz ^z	α_1	bdopqrstvz ^z	γ_6	ceghijkmvz	β_9	emoqrstvz ^z	α_3
cdgfgijkuv	α_4	abkptuvz ^z	α_1	ahjpvuvz ^z	α_1	bdopqrstvz ^z	α_2	ceghijkmvz	β_9	emotuvuvz ^z	α_3
cdgfgiktuv	β_{10}	ablnovxyz ^z	α_2	ahjpvuvz ^z	α_1	bdopqrstvz ^z	β_{24}	ceghijkmvz	γ_{10}	emotuvuvz ^z	α_3
cefgghijlmq	α_3	abnoqrstvz ^z	β_2	ahnoqrstvz ^z	β_2	bdpruvxyz ^z	α_2	ceghijkmvz	β_{12}	emotuvuvz ^z	α_3
cefgghijlmqv	β_9	abnoqrstvz ^z	α_2	ahnorxyz ^z	β_{23}	bdptuvuvz ^z	α_2	ceghijkmvz	α_4	emruuvuvz ^z	α_3
dggpqrsvz ^z	α_4	abnoqrstvz ^z	β_2	ahnrvuvz ^z	γ_2	bdpruvxyz ^z	α_2	ceghijkmvz	α_4	emruuvuvz ^z	α_3
djjpqrsvz ^z	α_4	abnoqrstvz ^z	α_2	ahnoqrstvz ^z	α_1	bdpruvxyz ^z	α_3	ceghijkmvz	β_{15}	emruuvuvz ^z	β_{16}
dkptuvuvz ^z	β_{21}	abnoqrstvz ^z	β_4	ahpqrsvz ^z	α_1	bdpruvxyz ^z	α_2	ceghijkmvz	β_{13}	ghilmovxyz ^z	β_{16}
dghmrvuvz ^z	α_3	abnoqrstvz ^z	α_2	ahpqrsvz ^z	α_1	bdpruvxyz ^z	α_3	ceghijkmvz	β_{18}	ghilmovxyz ^z	β_{16}
chmrvuvz ^z	α_3	abnrsvz ^z	α_2	ahpqrsvz ^z	α_1	bemoqrstvz ^z	α_2	ceghijkmvz	β_{13}	ghilmovxyz ^z	α_4
ekmotuvuvz ^z	α_3	abntuvuvz ^z	β_4	ajkmuvuvz ^z	α_4	blmopqrstvz ^z	α_2	ceghijkmvz	α_4	ghilmovxyz ^z	α_4
ekmtuvuvz ^z	α_3	abnrvuvz ^z	α_2	ajkpvuvz ^z	α_1	blmopqrstvz ^z	α_2	ceghijkmvz	α_4	ghilmovxyz ^z	α_4
emuvuvxyz ^z	α_3	abopqrstvz ^z	α_1	ajnuvuvz ^z	α_4	bmopqrstvz ^z	β_3	ceghijkmvz	β_{13}	ghilmovxyz ^z	α_4
hlmnoqrstyz ^z	β_{22}	abopqrstvz ^z	α_1	ajpvuvz ^z	α_1	bmopqrstvz ^z	α_2	ceghijkmvz	α_4	ghilmovxyz ^z	γ_{20}
jlmnoqrstuz ^z	α_4	abopqrstvz ^z	α_1	akpvuvz ^z	α_1	bmopqrstvz ^z	β_2	ceghijkmvz	β_{13}	ghilmovxyz ^z	β_{20}
jlmnoqsuvz ^z	α_4	abpqrsvz ^z	α_1	anoruvz ^z	β_{23}	bmopqrstvz ^z	β_{12}	ceghijkmvz	β_{15}	ghilmovxyz ^z	β_{22}
jmpqrsvz ^z	α_4	abpqrsvz ^z	α_1	anrvuvz ^z	β_1	cdgfgloqy	β_{12}	chijkmvz	β_{19}	hmnovxyz ^z	γ_{22}
abcfjloqz	β_{11}	abpqstuvz ^z	α_1	aprvuvz ^z	α_1	cdgfgloqy	β_{12}	chikmvz	γ_{10}	hmnovxyz ^z	β_{23}
abcfjilmqv	β_{18}	abpruvz ^z	α_1	aptuvuvz ^z	α_1	cdgfgijlqv	β_{10}	cijkmvz	α_4	hmnovxyz ^z	α_4
acehivxyz ^z	β_6	abptuvz ^z	α_1	bcdefgkox	β_{11}	cdgfgikuvy	α_4	deghovxyz ^z	β_8	jlmopqrstuz ^z	α_4
bcdfjopqsz ^z	β_5	abpuvuvz ^z	α_1	bcdefgkoxy	γ_{11}	cdgfgloqv	β_{11}	deghovxyz ^z	β_{14}	jlmopqrstuz ^z	α_4
degkuvuvz ^z	β_{14}	acefgijkuv	α_4	bcdefgloqt	α_2	cdgfgloqv	β_{15}	dehoqrstvz ^z	β_8	jlmopqrstuz ^z	α_4
ghilmopqrz ^z	β_{16}	acefgiktuv	β_{10}	bcdefgloqv	β_{12}	cdgfgloqv	β_7	dehoqrstvz ^z	β_8	jlmopqrstuz ^z	α_4
mnoqvuvz ^z	β_{23}	acefgkotuv	β_{11}	bcdefgloqv	β_7	cdgfgloqv	α_4	degrstuvz ^z	γ_{12}	jlmopqrstuz ^z	α_4
mpqstuvz ^z	β_{24}	acehijkuvz	β_{19}	bcdefjoqsz	β_5	cdgfgloqv	γ_9	dghjpvuvz ^z	β_{20}	jmpqrsvz ^z	α_4
abcfjloqz	α_2	acehijvz ^z	β_6	bcdefloqsy	α_2	cdgfgikpvz	α_4	dghjpvuvz ^z	α_4	jmpqrsvz ^z	α_4
abcfjloqz	α_2	aceijkuvz	α_4	bcdefoqsz	β_5	cdgfgilpqv	α_4	dghjpvuvz ^z	α_4	jmpqrsvz ^z	α_4
abcfjloqz	α_2	acfhilnqv	γ_4	bcdefoqsz	α_2	cdgfgikpvz	β_{10}	dghjpvuvz ^z	α_4	kmpuvuvz ^z	β_{21}
abcfjloqz	β_7	acfhilnqv	α_1	bcdegikvxy	α_2	cdgfgilpqv	α_4	dghjpvuvz ^z	β_{14}	lmnoqrstuz ^z	β_{22}

Table 2. Complete combinatorial study of the 312 $\overline{C^3}$ circular codes. Only one “forbidden configuration” with one doublet (3.1), triplet (3.2) or quadruplet (3.3) is given for each $\overline{C^3}$ circular code.

Using the results of [1, 18] and Table 2, the following proposition can be deduced.

Proposition 3.4. *If a set of 20 trinucleotides is a self-complementary circular code then either its two permuted sets are both circular codes or its two permuted sets are both non-circular codes.*

Proof. Let X_0 be a self-complementary circular code among the 528 ones. If X_0 is one of the 216 C^3 self-complementary circular codes then both its permuted sets X_1 and X_2 are circular codes [1, 18]. If X_0 is one of the 312 $\overline{C^3}$ self-complementary circular codes then a “forbidden configuration” (a 5LDCN necklace) is identified (Table 2). If this “forbidden configuration” is a doublet (triplet and quadruplet, respectively) then Proposition 2 (3 and 4, respectively) applies. All the 312 $\overline{C^3}$ circular codes X_0 have a “forbidden configuration” proving that their permuted sets X_1 and X_2 are all non-circular codes. ■

References

- [1] D.G. Arquès, C.J. Michel. A complementary circular code in the protein coding genes. *J. Theor. Biol.* **182**, 45-58 (1996).
- [2] D.G. Arquès and C.J. Michel. A circular code in the protein coding genes of mitochondria. *J. Theor. Biol.* **189**, 273-290 (1997).
- [3] F. Bassino. Generating function of circular codes. *Adv. Appl. Math.* **22**, 1-24 (1999).
- [4] M.-P. Béal, J. Senellart. On the bound of the synchronization delay of a local automaton. *Theoret. Comput. Sci.* **205**, 297-306 (1998).
- [5] J. Berstel, D. Perrin. *Theory of Codes*. Academic Press, London, UK, 1985.
- [6] F.H.C. Crick, J.S. Griffith, L.E. Orgel. Codes without commas. *Proc. Natl. Acad. Sci. USA* **43**, 416-421 (1957).
- [7] G. Frey, C.J. Michel. Circular codes in archaeal genomes. *J. Theor. Biol.* **223**, 413-431 (2003).
- [8] G. Frey, C.J. Michel. Identification of circular codes in bacterial genomes and their use in a factorization method for retrieving the reading frames of genes. *Comput. Biol. Chem.* **30**, 87-101 (2006).
- [9] S.W. Golomb, B. Gordon, L.R. Welch. Comma-free codes. *Canad. J. Math.* **10**, 202-209 (1958).
- [10] S.W. Golomb, L.R. Welch, M. Delbrück. Construction and properties of comma-free codes. *Biologiske Meddel Danske Vidensk Selsk* **23**, 1-34 (1958).
- [11] R. Jolivet, F. Rothen. Peculiar symmetry of DNA sequences and evidence suggesting its evolutionary origin in a primeval genetic code. In First European Workshop in Exo-/Astro-Biology. Eds. P. Ehrenfreund, O. Angerer, B. Battrick. pp. 173-176, Noordwijk, The Netherlands, (2001).
- [12] M.V. José, T. Govezensky, J.A. García, J.R. Bobadilla. On the evolution of the standard genetic code: vestiges of critical scale invariance from the RNA world in current prokaryote genomes. *PLoS One*, **4**, e4340 (2009).
- [13] A.J. Koch, J. Lehman. About a symmetry of the genetic code. *J. Theor. Biol.* **189**, 171-174 (1997).

- [14] J.-L. Lassez. Circular codes and synchronization. *Int. J. Comput. Inf. Sciences* **5**, 201-208 (1976).
- [15] J.-L. Lassez, R.A. Rossi, A.E. Bernal. Crick's hypothesis revisited: the existence of a universal coding frame. Proceedings of the 21st International Conference on Advanced Information Networking and Applications Workshops/Symposia (AINAW '07), vol. **2**, pp. 745-751, (2007).
- [16] E.E. May, M.A. Vouk, D.L. Bitzer, D.I. Rosnick. An error-correcting framework for genetic sequence analysis. *J. Franklin Inst.* **341**, 89-109 (2004).
- [17] C.J. Michel, G. Pirillo, M.A. Pirillo. Varieties of comma-free codes. *Comput. Math. Appl.* **55**, 989-996 (2008).
- [18] C.J. Michel, G. Pirillo, M.A. Pirillo. A relation between trinucleotide comma-free codes and trinucleotide circular codes. *Theoret. Comput. Sci.* **401**, 17-26 (2008).
- [19] C. Nikolaou, Y. Almirantis. Mutually symmetric and complementary triplets: difference in their use distinguish systematically between coding and non-coding genomic sequences. *J. Theor. Biol.* **223**, 477-487 (2003).
- [20] G. Pirillo. A characterization for a set of trinucleotides to be a circular code. In *Determinism, Holism, and Complexity*. Eds. C. Pellegrini, P. Cerrai, P. Freguglia, V. Benci, G. Israel, Kluwer, Boston, Mass, USA, 2003.
- [21] G. Pirillo. A hierarchy for circular codes. *Theor. Informatics Appl.* **42**, 717-728 (2008).
- [22] G. Pirillo. Some remarks on prefix and suffix codes. *Pure Math. Appl.* **19**, 53-59 (2008).
- [23] G. Pirillo. Non sharing border codes. *Adv. Appl. Math.* **3**, 215-223 (2010).
- [24] G. Pirillo, M.A. Pirillo. Growth function of self-complementary circular codes. *Biology Forum* **98**, 97-110 (2005).
- [25] N. Štambuk. On circular coding properties of gene and protein sequences. *Croatica Chemica Acta* **72**, 999-1008 (1999).