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ON THE NUMBER OF PERMUTATIONS ARISING FROM A PROBLEM IN CELL-BIOLOGY

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Abstract: Arrangements of chromosomes according to Bennett's model can be characterized by a certain type of permutations of n objects. The number of these permutations is determined for arbitrary even n and upper and lower bounds are given for any odd n . As a consequence it is proved that in both cases the relative frequency of the considered permutations converges to zero with n increasing to infinity (which is of interest especially from the biological point of view).

In cytogenetics the question is important whether there exists an ordered arrangement of the n chromosomes of a haploid genome during

metaphase (a certain stage of cell division). The best known theory in favour of an ordered disposition of the chromosomes is Bennett's model (cf [1], [4], [5]). In terms of permutations the problem of the existence of an ordered arrangement according to Bennett's model can be formulated as follows (cf [2]):

Given $\pi \in S_n$, does there always exist $h, \rho \in S_n$ such that

$$(1) \quad |h(2k) - h(2k + 1)| = 1 \quad \text{for } k = 1, 2, \dots, \lfloor \frac{n}{2} \rfloor$$

$$(2) \quad |\rho(2k - 1) - \rho(2k)| = 1 \quad \text{for } k = 1, 2, \dots, \lfloor \frac{n}{2} \rfloor$$

and $\pi = h\rho^{-1}$?

Here S_n denotes the symmetric group on n letters, $\lfloor r \rfloor$ indicates the greatest integer that does not exceed r , $h(n+1)$ stands for $h(1)$ and $h\rho^{-1}$ is meant to indicate that first the inverse of ρ has to be performed and then h . If $\pi \in S_n$ admits a representation in the form $\pi = h\rho^{-1}$ with h and ρ satisfying (1) and (2), π is called *admissible*.

The essential question now is: How many admissible permutations exist in S_n ?

Let AP_n be the set of admissible permutations of S_n and $A(n) = |AP_n|$. For n odd and $n \leq 11$ the numbers $A(n)$ were computed in [3]; in particular, for $n \leq 5$ $AP_n = S_n$ and for $5 < n \leq 11$ the number $A(n)$ does not much deviate from $|S_n|$. The question arises whether this is also true for an arbitrary odd n . (Some theoretical background on finding $A(n)$ for odd n can be found in [2].) On the other hand for even n computations show that $A(n)$ deviates very fast from $n!$ with increasing n .

In the following we will determine the exact value of $A(n)$ for all even n as well as lower and upper bounds for any odd n . As a consequence, we prove that in both cases the relative frequency of admissible permutations converges to zero.

As it was pointed out in [2] (for odd n but is analogously true for even n), an ordered arrangement of chromosomes according to Bennett's model can also be considered as an unorientated graph $G = \langle V, E \rangle$ with vertex set $V = \{1, 2, \dots, n\}$ and edge set E which is the product of two 1-factors F_1 and F_2 , i.e. $G = F_1 \times F_2$. We assign two colours to the edges of G , namely colour 1 to the edges of F_1 and colour 2 to the edges of F_2 . Now, if π is an admissible permutation to which the ordered arrangement represented by G belongs, and $\pi = h\rho^{-1}$ with

h, ρ satisfying (1) and (2), then according to [2]

$$(3) \quad \begin{aligned} F_1 &= \langle V, \{[1, 2], [3, 4], \dots, [n-1, n]\} \rangle \\ F_2 &= \langle V, \{[\pi 1, \pi 2], [\pi 3, \pi 4], \dots, [\pi(n-1), \pi n]\} \rangle \end{aligned}$$

for even n and

$$(4) \quad \begin{aligned} F_1 &= \langle V, \{[1, 2], \dots, [p-2, p-1], [p+1, p+2], \dots, [n-1, n]\} \rangle \\ F_2 &= \langle V, \{[\pi 1, \pi 2], \dots, [\pi(q-2), \pi(q-1)], \\ &\quad [\pi(q+1), \pi(q+2)], \dots, [\pi(n-1), \pi n]\} \rangle \end{aligned}$$

for odd n with $p, q \in \{1, 3, 5, \dots, n\}$.

Further $G = F_1 \times F_2$ is a Hamiltonian circle in the even case and a Hamiltonian path in the odd case, with edges of alternating colours in both cases (shortly: alternating H -circle and H -path resp.). Moreover the sequence of vertices within the alternating H -circle and H -path resp. is given by $h1, h2, \dots, hn$, and the notation is chosen in such a way that the first edge $[h1, h2]$ always belongs to F_2 . Hence, if n is odd, $h1 = p$ and $hn = \pi q$. The same graph G may be induced by different admissible permutations π . On the other hand, G is determined uniquely by π if n is even, but not for odd n .

The graph $G = F_1 \times F_2$ can be defined by (3) or (4) for an arbitrary $\pi \in S_n$. But then in general G consists of several alternating H -circles in the even case, of an H -path and one or more circles in the odd case. Actually, for n even, π is admissible if and only if G is an alternating H -circle. For an odd n , this is the case if p, q can be chosen appropriately so that an alternating H -path results.

Now, for any n , let $\alpha_n = \frac{A(n)}{n!}$. This is the relative frequency of admissible permutations. For odd n we define further:

$$\begin{aligned} K_n &= 2^{n-1} \left(\frac{n-1}{2}!\right)^2 = (n-1)^2 (n-3)^2 \dots 2^2, \\ k_n &= \frac{K_n}{n!} = \frac{(n-1)(n-3)\dots 2}{n(n-2)\dots 3 \cdot 1} \end{aligned}$$

Remark 1. $\lim_{n \rightarrow \infty} k_n = 0$, since

$$\begin{aligned} \frac{1}{k_n} &= \left(1 + \frac{1}{n-1}\right) \left(1 + \frac{1}{n-3}\right) \dots \left(1 + \frac{1}{2}\right) = \\ &= 1 + \left(\frac{1}{2} + \frac{1}{4} + \dots + \frac{1}{n-1}\right) + \dots \rightarrow \infty. \end{aligned}$$

Theorem 1. For any even n , $\alpha_n = k_{n-1}$, hence $\lim_{n \rightarrow \infty} \alpha_n = 0$.

Proof. The number of possible alternating H -circles is $2^{\frac{n}{2}-1} \left(\frac{n}{2} - 1!\right)$. To see this, we assume one edge of colour 1, say $[1, 2]$, in a fixed position,

provide the edge with an orientation, which we keep also fixed, then we count the number of permutations of the remaining edges of the same colour and consider that each edge may be orientated in two ways. Thus there are $2^{\frac{n}{2}} \cdot \frac{n}{2}!$ permutations π which induce the same set of edges $\{[\pi 1, \pi 2], \dots, [\pi(n-1), \pi n]\}$, i.e. the same alternating H -circle. This gives $A(n) = 2^{n-1} \left(\frac{n}{2} - 1\right)! \frac{n}{2}! = n(n-2)^2(n-4)^2 \dots \cdot 2^2 = nK_{n-1}$, therefore $\alpha_n = \frac{nK_{n-1}}{n!} = k_{n-1}$. \diamond

In the odd case, the difficulty arises that an admissible permutation π may induce different alternating H -paths through different choices of p and q in (4). We recall that the corresponding H -path is given by the sequence $h1, h2, \dots, hn$, where $h = h\rho$, h, ρ satisfy (1) and (2), $h1 = p$, and $\rho n = q$. First we compute the number of admissible permutations for fixed p, q , then for a fixed p with arbitrary q .

Lemma 1. *Let n be an odd number and $A_n(p, q)$ be the set of permutations $\pi = h\rho^{-1} \in AP_n$ with $h1 = p$ and $\rho n = q$. Then $|A_n(p, q)| = K_n$ for any $p, q \in \{1, 3, \dots, n\}$.*

Proof. There are $\frac{n-1}{2}!$ possibilities to choose the order of the edges of F_1 (or F_2) in the alternating H -path and for each edge there are two possible orientations to fit them in. Then, each H -path is induced by $2^{\frac{n-1}{2}} \cdot \frac{n-1}{2}!$ permutations in $A_n(p, q)$ which gives the total number of $2^{n-1} \left(\frac{n-1}{2}\right)!^2 = K_n$. \diamond

Lemma 2. *Let n be odd and $\overline{A_n}(p)$ the set of all $\pi = h\rho^{-1} \in AP_n$ with $h1 = p$. Then $|\overline{A_n}(p)| = 2\left(1 - \left(\frac{1}{2}\right)^{\frac{n+1}{2}}\right)K_n$ for any $p \in \{1, 3, \dots, n\}$.*

Proof. We now write $F(p), F_\pi(q)$ instead of F_1, F_2 in (4), in order to express their dependence on p, q and π . Let $\pi = h\rho^{-1} \in A_n(p, q)$ with $q \geq 3$, thus $F(p) \times F_\pi(q)$ is an alternating H -path. Then π belongs to $A_n(p, q-2)$ if and only if $F(p) \times F_\pi(q-2)$ is an alternating H -path, too, i.e. if and only if the substitution of the edge $[\pi(q-2), \pi(q-1)]$ by $[\pi(q-1), \pi q]$ produces another Hamiltonian path. This is the case if $\pi(q-1) = hi$, $\pi(q-2) = h(i+1)$ for some i (then $i = \rho^{-1}(q-1)$ is odd and $i+1 = \rho^{-1}(q-2)$ is even). If, on the contrary, $\rho^{-1}(q-1)$ is even, i.e. $\pi(q-2) = hi$, $\pi(q-1) = h(i+1)$ for some i , then deleting the edge $[\pi(q-2), \pi(q-1)]$ and linking $\pi(q-1)$ to πq splits the path into a path (possibly a single vertex) and a circle.

For any $\pi \in A_n(p, q)$ let $\pi' = \pi\tau_{q-1, q-2}$ where $\tau_{q-1, q-2}$ is the transposition interchanging $q-1$ with $q-2$. Then π' also is in $A_n(p, q)$, but $\pi' \in A_n(p, q-2)$ if and only if $\pi \notin A_n(p, q-2)$. Thus, to any $\pi \in A_n(p, q) \cap A_n(p, q-2)$ there corresponds a $\pi' \in A_n(p, q) - A_n(p, q-2)$ and

vice-versa. Since $|A_n(p, q)| = |A_n(p, q - 2)|$ by Lemma 1, exactly half of the elements of one set belong to the intersection of the two. Taking into account that π and π' as above either both belong to $A_n(p, r)$ for some $r > q$ or neither of them does, we infer that an analogous argument is valid for the sets $A_n(p, q) - \bigcup_{r>q} A_n(p, r)$ and $A_n(p, q - 2) - \bigcup_{r>q} A_n(p, r)$.

Now let $B_q = A_n(p, q) - \bigcup_{r>q} A_n(p, r)$ for any odd $q \leq n$, then $B_n = A_n(p, n)$, $B_{n-2} = A_n(p, n - 2) - A_n(p, n)$, etc. Further $\overline{A_n}(p) = B_n \cup B_{n-2} \cup \dots \cup B_1$, where these sets are pairwise disjoint, and $|B_{q-2}| = |(A_n(p, q - 2) - \bigcup_{r>q} A_n(p, r)) - (A_n(p, q) - \bigcup_{r>q} A_n(p, r))| = \frac{1}{2}|A_n(p, q) - \bigcup_{r>q} A_n(p, r)| = \frac{1}{2}|B_q|$. Consequently, $|\overline{A_n}(p)| = |B_n| + |B_{n-2}| + \dots + |B_1| = |A_n(p, n)|(1 + \frac{1}{2} + \dots + \frac{1}{2^{\frac{n-1}{2}}}) = K_n(2 - (\frac{1}{2})^{\frac{n-1}{2}}) = 2(1 - (\frac{1}{2})^{\frac{n+1}{2}})K_n$. \diamond

As an immediate consequence we get the following lower bound for the relative frequency of admissible permutations.

Theorem 2. For any odd n , $\alpha_n \geq 2(1 - (\frac{1}{2})^{\frac{n+1}{2}})k_n$. \diamond

Finally we deduce an upper bound of α_n by a similar method.

Theorem 3. For any odd n , $\alpha_n \leq 2(1 - (\frac{1}{2})^{\frac{n+1}{2}})^2 k_n$. Therefore, $\lim_{n \rightarrow \infty} \alpha_n = 0$.

Proof. For $\pi \in \overline{A_n}(p)$, $\pi' = \tau_{p-1, p-2}\pi$ also belongs to $\overline{A_n}(p)$. It suffices to interchange the vertices $p - 1$ and $p - 2$ in a corresponding H -path. Now let $\pi \in \overline{A_n}(n)$, so $\pi \in A_n(n, q)$ for some $q \in 1, 2, \dots, n$. As in the proof of Lemma 2, $\pi \in A_n(n - 2, q)$ holds if and only if $[n - 2, n - 1]$ can be substituted by $[n - 1, n]$ so that another alternating H -path results. This is the case if and only if $h^{-1}(p - 2)$ is even and $h^{-1}(p - 1)$ is odd (then $p - 2 = hi, p - 1 = h(i + 1)$ for some i). Otherwise, $\pi \notin A_n(n - 2, q)$ but still $\pi \in A_n(n - 2, q')$ is possible for some $q' \neq q$ (it is easy to find examples). Since $\pi \notin A_n(n - 2, q)$ implies $\pi' \in A_n(n - 2, q) \subseteq \overline{A_n}(n - 2)$, at least half of the elements of $\overline{A_n}(n)$ belong also to $\overline{A_n}(n - 2)$. Therefore, since $|\overline{A_n}(n) - \overline{A_n}(n - 2)| \leq \frac{1}{2}|\overline{A_n}(n)|$ by Lemma 2, $|\overline{A_n}(n) - \overline{A_n}(n - 2)| \leq \frac{1}{2}|\overline{A_n}(n)|$. In the same way, with $C_p = \overline{A_n}(p) - \bigcup_{s>p} \overline{A_n}(s)$, we infer $|C_{p-2}| \leq \frac{1}{2}|C_p|$. Since $AP_n = C_n \cup C_{n-2} \cup \dots \cup C_1$ with $C_n = \overline{A_n}(n)$ we obtain $A(n) = |AP_n| \leq |\overline{A_n}(n)|(1 + \frac{1}{2} + \dots + \frac{1}{2^{\frac{n-1}{2}}}) = 4(1 - (\frac{1}{2})^{\frac{n+1}{2}})^2 K_n$. To complete the proof, we need only

divide by $n!$. \diamond

Remark 2. The upper bound of Theorem 3 is not strict (for small n , we obtain values greater than 1), but it is sufficient to prove that the relative frequency of admissible permutations converges to zero. Compare the table below where we indicate the upper and lower bounds of α_n according to Theorem 2 and 3 for some biologically relevant values of n .

n	lower bound	upper bound
5	0.9333334	1.633334
7	0.8571429	1.607143
9	0.7873017	1.525397
11	0.7272728	1.431818
13	0.6766568	1.342741
15	0.6340328	1.263112
17	0.5979067	1.193478
21	0.5402465	1.079985
25	0.4962781	0.992435
29	0.4614604	0.9228927
33	0.433052	0.8660973
39	0.3988169	0.7976331
45	0.3715961	0.743192

References

- [1] BENNETT, M.D.: Nucleotypic basis of the spatial ordering of chromosomes in eucariotes and the implications of the order for genome and phenotypic variation. In: G.A. Dover and R.B. Flavell (eds.): *Genome evolution*, Academic Press, London and New York (1982), 239 - 261.
- [2] DORNINGER, D.: On permutations of chromosomes. In: *Contributions to General Algebra 5*, Verlag Hölder-Pichler-Tempsky, Wien, and Teubner-Verlag, Stuttgart (1987), 95 - 103.
- [3] DORNINGER, D. and TIMISCHL, W.: Geometrical constraints on Bennett's predictions of chromosome order, *Heredity* **58** (1987), 321 - 235.
- [4] HESLOP-HARRISON, J.S. and BENNETT, M.D.: Prediction and analysis of spatial order in haploid chromosome complements, *Proc. R. Soc. Lond.*, B(1983), 211 - 223.
- [5] HESLOP-HARRISON, J.S. and BENNETT, M.D.: The spatial order of chromosomes in root-tip metaphases of *Aegilops umbellulata*, *Proc. R. Soc. Lond.*, B(1983), 225 - 239.