

CONTRIBUTIONS TO GENETIC ALGEBRAS

by H. GONSHOR

(Received 20th September 1969)

1. Introduction

Etherington introduced certain algebraic methods into the study of population genetics (6). It was noted that algebras arising in genetic systems tend to have certain abstract properties and that these can be used to give elegant proofs of some classical stability theorems in population genetics (4, 5, 9, 10).

The aim of this paper is to both modernize the derivation of existing results and obtain new results. Among the former, we indicate how the theory of duplication (7) can be developed in a basis free manner, and how the technique of (10) can be improved. Among the latter we extend the work in (10) to include mutations. Finally, we shall emphasize genetic algebras rather than special train algebras.

Although, unfortunately, there has not been much work in this area the subject has been kept alive by the interesting work by Holgate in (11-15) and by the appearance of some results in book form in (2).

We recently noticed an interesting coincidence connected with the remark after Theorem 5.3 in (10) referring to the proof of Lemma 6.3 in (9). The same self-reciprocal transformation arising in the theory of polyploidy is used in the study of Hausdorff methods in summability theory in (17).

2. Genetic algebras

For convenience we shall deal with algebras over the complex numbers. At any rate, we are not interested at this time in searching for the most general field of coefficients for which a given theorem is valid. In fact, as in (9) and (10) the coefficient field will play a background role only.

We define a genetic algebra to be a commutative algebra for which there exists a basis a_0, a_1, \dots, a_n with a multiplication table of the following kind:

$$a_i a_j = \sum \lambda_{ijk} a_k \text{ where } \lambda_{000} = 1; \quad (1)$$

$$\text{for } k < j, \lambda_{0jk} = 0; \quad (2)$$

$$\text{and for } i, j > 0 \text{ and } k \leq \max(i, j), \lambda_{ijk} = 0. \quad (3)$$

Remark. Although we aim in most cases for basis free definitions, this particular definition is expressed most succinctly with the help of a basis.

The reader is reminded that a baric algebra is an algebra for which there exists a non-trivial homomorphism w , called the weight, into the coefficient

field. w exists and is unique for any genetic algebra. In fact, necessarily $w(a_0) = 1$ and $w(a_i) = 0$ for $i > 0$.

A special train algebra is a genetic algebra in which in addition all powers of the ideal $I = \{a_1, a_2, \dots, a_n\}$ are ideals. We note first that all theorems in (9) stated for special train algebras are valid for genetic algebras. This is clear since the special condition on the ideal $\{a_1, a_2, \dots, a_n\}$ is never used in a proof.

Schafer (20) has also defined the concept of a genetic algebra. The use of the same term is justified by the next theorem.

Theorem 2.1. *An algebra is genetic in our sense if and only if it is genetic in the sense of Schafer.*

Proof. We first state Schafer's definition. Let \bar{a} represent multiplication by a . Then an algebra is genetic if and only if it is baric and the characteristic polynomial of the determinant of the transformation $\lambda I + f(\bar{b}_1, \dots, \bar{b}_n)$ where λ is a scalar and f is a polynomial, depends only on the weights of the elements b_1, \dots, b_n and not on these elements themselves.

Schafer has essentially shown in (20) that a genetic algebra in our sense is a genetic algebra in his sense. Although he stated the result for special train algebras, the extra property satisfied by these algebras is not used in the proof.

The proof of the converse uses some results in linear algebra. Unfortunately, we know of no source for the next result from an elementary linear algebra text but require a text on Lie algebras ((16), p. 34) which has it in a more general form than is desired.

A set S of nilpotent matrices closed under multiplication can be simultaneously brought into triangular form. (The stated result refers to closure under a more general type operation but this does not concern us here. Note that this is trivially equivalent to the statement that there exists an m such that any product consisting of m elements of S is zero.)

Let G be a genetic algebra in the sense of Schafer. Let a_0, a_1, \dots, a_n be a basis such that the weight w satisfies $w(a_0) = 1$ and $w(a_i) = 0$ for $i \geq 1$. Let A_i denote multiplication by a_i . Note, for example, that the characteristic polynomial of the determinant of A_i for $i \geq 1$ is the same as the characteristic polynomial corresponding to multiplication by zero since the algebra is genetic, hence is λ^{n+1} . Thus A_i is nilpotent for $i \geq 1$.

Let $C_0 = (A_0 - \lambda_1) \dots (A_0 - \lambda_r)$ where $\lambda_1, \lambda_2, \dots, \lambda_r$ are the characteristic roots of A_0 . Then C_0 is nilpotent. Consider the semigroup S generated by $\{A_0^m C_0, A_0^m A_i\}$ where $m \geq 0$ and $1 \leq i \leq n$. Every element in the semigroup is either a product which contains an A_i as a factor for some $i \geq 1$ or a polynomial in A_0 which is a multiple of C_0 . In the former case, since the algebra is genetic, we can obtain the characteristic polynomial by replacing a_i by 0 (i.e. A_i by 0). In the latter case the element is clearly nilpotent. By the above result quoted from (16) the semigroup is nilpotent. (In the sense that any

product consisting of $n + 1$ elements of S is zero. The distinction between this and nilpotency of individual elements is crucial.)

The space V generated by $\{a_i\}$, $i \geq 1$, (i.e. the ideal of elements of weight 0) is invariant with respect to S . *A fortiori* S is nilpotent on V . Let $W = SV \subset V$. V is invariant with respect to A_0 and the eigenvalues of A_0 restricted to V are included in $(\lambda_1, \lambda_2, \dots, \lambda_r)$. Since V is spanned by elements x satisfying $(A_0 - \lambda_i)^t x = 0$ for some i and t , any basis of W can be extended to a basis of V by means of such elements.

If x satisfies $(A_0 - \lambda_i)^t x = 0$ then by a standard argument

$$x \in (A_0 - \lambda_1)(A_0 - \lambda_2) \dots \widehat{(A_0 - \lambda_i)} \dots (A_0 - \lambda_n)V.$$

Therefore $(A_0 - \lambda_i)x \in C_0V \subset SV = W$. Of course, for $i \geq 1$, $A_i x \in SV = W$. W is, of course, invariant with respect to A_i for $i \geq 1$. Since S is closed with respect to premultiplication by A_0 , W is also invariant with respect to A_0 .

The whole argument can now be repeated with W replacing V and continued by induction. We finally obtain a basis b_1, b_2, \dots, b_n of V such that if

$$A_i b_j = \sum \mu_{ijk} b_k$$

then $\mu_{ijk} = 0$ if $k < j$ and $\mu_{ijk} = 0$ if $i \geq 1$ and $k \leq j$.

Finally we show that with respect to the basis $a_0, b_1, b_2, \dots, b_n$ the algebra is genetic in our sense. Since $w(a_0) = 1$ and $w(b_i) = 0$ for $i \geq 1$ it follows that $\lambda_{000} = 1$. Since $a_0 b_i = A_0 b_i$ then $\lambda_{0jk} = 0$ for $k < j$. Consider $b_i b_j$ where $i \geq 1$ and $j \geq 1$. b_i has the form $\sum_{h \geq 1} v_h a_h$. Hence $b_i b_j = \sum_{h \geq 1} v_h a_h b_j = \sum_{h \geq 1} v_h A_h b_j$. Hence $\lambda_{ijk} = 0$ for $k \leq j$. By commutativity $\lambda_{ijk} = 0$ for $k \leq i$. This completes the proof.

By a careful examination of the proof it can be seen that a weakened form of Schafer's condition suffices. We shall not pursue this point; in fact, the rest of this paper is independent of Theorem 2.1.

3. General remarks

In our definition of a genetic algebra, it is enough to have a finite partially ordered set with zero of indices for the basis elements with the following conditions on the multiplication table.

$$\lambda_{000} = 1 \tag{1}$$

$$\lambda_{0jk} \neq 0 \Rightarrow k \geq j \tag{2}$$

$$\lambda_{ijk} \neq 0 \Rightarrow k > j \text{ and } k > i. \tag{3}$$

Although this is trivial, it is worth mentioning, since in many important systems arising in genetics a partial ordering is naturally obtained with the required properties. This remark makes it unnecessary to explicitly choose a linearly ordered extension in each individual case. Polyploidy with multiple alleles (10) is a good example. We can define

$$D_1^{i_1}(D_1 - D_2)^{i_2} \dots (D_1 - D_n)^{i_n} \geq D_1^{j_1}(D_1 - D_2)^{j_2} \dots (D_1 - D_n)^{j_n}$$

if and only if for all $t \geq 2$, $i_t \geq j_t$.

We outline a basis free approach to duplication. Let A be an arbitrary commutative algebra and let $A \otimes A$ be the usual tensor product as a vector space. Let W be the vector space generated by vectors of the form $a \otimes b - b \otimes a$. Let $A \times A = A \otimes A / W$. By the third isomorphism theorem $A \times A$ may be regarded as the group G freely generated by (a, b) where $a, b \in A$, divided by the ideal I generated by all elements of the form $(a, b+c) - (a, b) - (a, c)$, $(\lambda a, b) - (\lambda a, b)$, and $(a, b) - (b, a)$. We denote the class containing (a, b) by $a \times b$. Define scalar multiplication by $\lambda(a \times b) = \lambda a \times b$. It is easy to verify that this is well-defined and that with this operation $A \times A$ is a vector space.

Let $\{a_i\}$ be a basis of A . We claim that $\{a_i \times a_j\}$, where $i \leq j$, is a basis of $A \times A$. It is obvious that this is a spanning set. The only problem, as usual, is the danger of "unwanted" cancellation. Let Q be a vector space with basis $\{d_{ij}\}$ where $i \leq j$. If $b = \sum \lambda_i a_i$ and $c = \sum \mu_i a_i$ let

$$f(b, c) = \sum \lambda_i \mu_i d_{ii} + \sum_{i \neq j} (\lambda_i \mu_j + \lambda_j \mu_i) d_{ij}.$$

Then f extends to a map of G into Q . It is easy to verify that $f(I) = 0$, hence f induces a map of $A \times A$ into Q . $f(a_i \times a_j) = d_{ij}$. There is a map g of Q into $A \times A$ such that $g(d_{ij}) = a_i \times a_j$. Clearly $gf = fg = 1$. In particular the set $\{a_i \times a_j\}$ is independent.

We now define multiplication in $A \times A$. Let $(a, b)(c, d) = (ab, cd)$. Extend this to make it bilinear on G . If either factor is in I the product is in I . Hence this induces a multiplication on $A \times A$: $(a \times b)(c \times d) = ab \times cd$, which makes $A \times A$ a commutative algebra. This is the duplication algebra. By choosing a basis it is clear that this is equivalent to the definition in (7).

The usual properties can easily be proved in this context. For example, if $ab = 0$ then $(a \times b)(c \times d) = ab \times cd = 0 \times cd = 0$. Also, define a map T of G into A such that $T(a, b) = ab$. Then T induces a map of $A \times A$ into A such that $T(a \times b) = ab$. T is linear. Furthermore,

$$T[(a \times b)(c \times d)] = T[ab \times cd] = (ab)(cd) = T(a \times b)T(c \times d).$$

Hence T is a homomorphism. In addition, if A is baric with weight w then $A \times A$ is baric with weight wT .

It is easy to see that if A is genetic then $A \times A$ is genetic. Although this follows from Theorem 2.1 and (20) we outline a simple direct proof.

Let A be genetic with basis a_0, a_1, \dots, a_n . Define an ordering on the basis $\{a_i \times a_j: i \leq j\}$ by $a_k \times a_l \geq a_i \times a_j$ if $l > j$ or $l = j$ and $k \geq i$.

It is routine to verify that $A \times A$ is genetic with respect to this basis with the above ordering. In fact, without loss of generality assume $a_k \times a_l \geq a_i \times a_j$. Then consider

$$(a_k \times a_l)(a_i \times a_j) = a_k a_l \times a_i a_j = \sum_{m,n} \lambda_{klm} \lambda_{ijn} (a_m \times a_n).$$

The coefficient of $a_m \times a_n$ is necessarily 0 for $a_m \times a_n \leq a_k \times a_l$ unless possibly if $k = 0$. In that case $a_k \times a_l$ can have a non-zero coefficient in the product

only if $i = j = 0$, and all smaller basis elements have zero coefficients. This completes the proof.

4. Polyploidy

Although the technique in (10) is an improvement over that in (9), the methods of (10) can in turn be improved. Although it was emphasized in (10) that $\prod_{i=1}^r \left(\sum_{j=1}^n a_{ij} D_j \right)$ is not a product within the algebra, it may be regarded as a product after all. This is done by regarding Π as a symmetric multilinear map from the multiple allelic algebra C to the polyploidy algebra D . Define Π on the basis elements in the obvious way:

$$\Pi(D_{i_1}, D_{i_2}, \dots, D_{i_r}) = D_{i_1} D_{i_2} \dots D_{i_r}.$$

Π extends by linearity to C^n . The natural weight can be expressed in the form

$$w[\Pi(y_1, y_2, \dots, y_n)] = w(y_1)w(y_2)\dots w(y_n).$$

Theorem 5.1 in (10) can be easily proved using this viewpoint. Let y_1, y_2, \dots, y_{2r} be arbitrary elements of C . We must show that

$$\begin{aligned} & [\Pi(y_1, y_2, \dots, y_r)][\Pi(y_{r+1}, y_{r+2}, \dots, y_{2r})] \\ &= \binom{2n}{n}^{-1} \sum_{(k_1 \dots k_r)} \Pi(y_{k_1}, y_{k_2}, \dots, y_{k_r}) w(y_{l_1}) w(y_{l_2}) \dots w(y_{l_r}) \end{aligned}$$

where (k_1, \dots, k_r) runs through all subsets of $(1, 2, \dots, 2r)$ containing r elements and (l_1, \dots, l_r) is the complementary subset. (w is, of course, the standard weight, i.e. it satisfies $w(D_i) = 1$ for all i .) By definition, this is true if all the y 's are basis elements. Since both sides are multilinear it is true in general.

Maps have already been used in (9) to study mutations. In general, given an algebra A and a linear transformation T one can define an operation \circ by $a \circ b = T(ab)$ and obtain an algebra B . This is an isotope of the original algebra. If A is baric and T is weight preserving then B is baric with the same weight. Furthermore, if the algebra is genetic with basis a_0, a_1, \dots, a_n and

$$T(a_i) = \sum_{j \geq i} \lambda_{ij} a_j,$$

the new algebra is clearly genetic with the same basis.

We give an example to show that the above result fails for special train algebras.

Let the basis be a_0, a_1, \dots, a_{20} . Suppose that for all j , $a_0 a_j = a_j$; for all $j \neq 20$, $a_1 a_j = a_{1+j}$; $a_1 a_{20} = 0$ and $a_i a_j = 0$ if $i, j \geq 2$.

$$\{a_1, a_2, \dots, a_{20}\} = I,$$

the ideal of elements of zero weight with respect to the unique non-trivial weight. Since $I^n = \{a_n, a_{n+1}, \dots, a_{20}\}$ this is clearly a special train algebra. Now let $T(a_n) = a_{2n}$. (We use the convention that if a subscript greater than 20 is obtained, the element is 0.) In the new algebra $I = \{a_1, a_2, \dots, a_{20}\}$,

$I^2 = \{a_4, a_6, a_8, \dots, a_{20}\}$ and $I^3 = \{a_{10}, a_{14}, a_{18}\}$. Since $T(a_0a_{10}) = a_{20} \notin I^3$, I^3 is not an ideal.

Note that in the special case found in (9), where it is shown that this situation occurs in the diallelic case with polyploidy, a special train algebra is obtained. Incidentally, the work simplifies tremendously if the multilinear maps mentioned above are used. In fact, let S be a mutation map in the simple gametic algebra. In this case $SD = (1-r)D+rR$ and $SR = sD+(1-s)R$ for some r and s (mutation rates). Then $S(D-R) = (1-r-s)(D-R)$ and SD may be expressed as $D-r(D-R)$. The mutation map T in the polyploidy algebra can be expressed conveniently as $T[\Pi(D_{i_1}, D_{i_2}, \dots, D_{i_r})] = \Pi(SD_{i_1}, SD_{i_2}, \dots, SD_{i_r})$. This is clear by elementary reasoning in probability and is valid for multiple alleles. It follows from multilinearity that $T[\Pi(b_1, b_2, \dots, b_r)] = \Pi(Sb_1, Sb_2, \dots, Sb_r)$, where the b 's are arbitrary in C . The collecting of terms in (9) makes the work harder. As mentioned in (10), $c_w = D^{n-w}(D-R)^w$. Hence

$$Tc_w = T[D^{n-w}(D-R)^w] = (SD)^{n-w}[S(D-R)]^w = [D-r(D-R)]^{n-w}(1-r-s)^w(D-R)^w.$$

By expanding we obtain the formula for Tc_w found in page 51 just above Theorem 7.1 in (9).

We now combine polyploidy, multiple alleles, and mutations.

Theorem 4.1. *Polyploidy multiple allelic algebras with mutation are genetic algebras.*

Proof. Let the gametic types be D_1, D_2, \dots, D_n and choose the basis D, a_2, \dots, a_n where $D = D_1$ and $a_i = D_1 - D_i$ for $i > 1$. Then $\{a_2, a_3, \dots, a_n\}$ is invariant with respect to the mutation map S . A basis $\{u_2, u_3, \dots, u_n\}$ exists such that $Su_i \in \{u_i, u_{i+1}, \dots, u_n\}$. Note that $\{\Pi(D^i, v_1, v_2, \dots, v_{r-i})\}$ is a basis of the algebra where $0 \leq i \leq r$ and the set v_1, v_2, \dots, v_{r-i} is a subset of the u 's with repetitions possible. The basic formula for T which we use is

$$T[\Pi(b_1, b_2, \dots, b_r)] = \Pi(Sb_1, Sb_2, \dots, Sb_r)$$

for arbitrary b_i in C . By combining the above formula for T in the polyploidy algebra with Theorem 5.2 in (10) we obtain

$$\begin{aligned} \Pi(D^i, v_1, v_2, \dots, v_{r-i})\circ\Pi(D^j, w_1, w_2, \dots, w_{r-j}) \\ = \lambda\Pi[(SD_1)^{i+j-r}, Sv_1, Sv_2, \dots, Sv_{r-i}, Sw_1, Sw_2, \dots, Sw_{r-j}] \end{aligned}$$

where the v 's and w 's are among the u 's and λ is a scalar. Of course, if $i+j < r$ by convention this is 0.

It is easy to see that the algebra is genetic by defining a partial order on the basis elements as follows.

Let $a = \Pi(D^i, v_1, v_2, \dots, v_{r-i})$ and $b = \Pi(D^j, w_1, w_2, \dots, w_{r-j})$ where the v 's and w 's are among the u 's and are arranged so that the subscripts are in non-decreasing order. Then $a \geq b$ if and only if $i < j$ or $i = j$ and $v_k \geq w_k$ for all k . (Precisely speaking the latter inequality refers, of course, to the subscripts

of the corresponding u 's.) It is an elementary cute exercise that if the above inequalities are satisfied for the v 's and w 's in some order then they are automatically satisfied if they are arranged in the above order. To complete the proof that the algebra is genetic, note that the choice of the basis is such that Su_i contains no terms involving u 's with a subscript less than i .

Note that unlike the diallelic case in the general case the basis may depend on S .

It is even true though harder to prove that the algebra is special train. We verify this for the sake of completeness. We first note that the scalar λ referred to above is always distinct from zero when $i+j \geq r$. The ideal I of weight 0 is generated by $\{\Pi(D^i, v_1, v_2, \dots, v_{r-i}): i < r\}$ where the v 's are among the u 's. Let $V = \{u_2, u_3, \dots, u_n\}$. Then $V \supset SV \supset S^2V \dots S^mV \supset S^{m+1}V \dots$. In the diallelic case, for example, V is one-dimensional and $SV = 0$ if and only if $r+s = 1$. As mentioned in (9) the table is especially simple in that case.

We claim that I^m where $2 \leq m \leq r$ is generated by the set

$$\{\Pi[(SD)^i, v_1, v_2, \dots, v_{r-i}]\}$$

where $i \leq r-m$, all the v 's are in SV and if $2 \leq p \leq m-1$ then at least $m-p+1$ v 's are in S^pV (of course, I^m is 0 for $m > r$). We verify this by induction.

For $m = 2$ the last condition is vacuous and the result is clear. Note that if an SD is replaced by S^2D then the new term remains in the space generated by the above set.

$$\begin{aligned} \Pi(S^2D, b_1, b_2, \dots, b_{r-1}) \\ = \Pi(SD, b_1, b_2, \dots, b_{r-1}) + \Pi(S^2D - SD, b_1, b_2, \dots, b_{r-1}). \end{aligned}$$

Now $S^2D - SD = S(SD - D) \in SV$. Hence both the first and second term are in the above set. By extending the above reasoning, several SD terms may be simultaneously replaced by S^2D . In a similar way it can be seen that if all the SD terms are replaced by S^2D then the original set is included in the space generated by the new set.

We can now verify the above for $m = 3$. For convenience we replace all terms D by SD in a typical generator of I . We now examine the possible terms in $(I^2)I$. Consider the product of a typical generating element in I^2 and a generating element of I . By the above simplification this is a monomial. The guaranteed two terms in I^2 of the form Sv give rise to two terms of the form S^2v . Otherwise, there is complete freedom in the v 's except that they belong to SV . We thus obtain what we want except for S^2D terms instead of SD terms. However, by an above remark, this is fine.

The rest of the induction is simple. We use the same manoeuvring with SD and S^2D . Also note that all terms contained in S^pV in I^m become terms contained in $S^{p+1}V$ in I^{m+1} .

To show that the algebra is special train it suffices to check that $(SD)^r I^m \subset I^m$. This is clear from the above since multiplication by $(SD)^r$ does no more than change SD terms to S^2D terms, add one more S to the v 's and contribute a scalar.

5. Mixture of algebras

This concept was introduced by Holgate (11). Let A and B be two algebras on the same underlying vector space. Denote the multiplications on A and B by f and g respectively. Define $a \cdot b = \lambda f(a, b) + (1 - \lambda)g(a, b)$ for some fixed scalar λ . Then the new algebra is a mixture of the given algebras. In the cases of most interest λ is real and $0 \leq \lambda \leq 1$. Now assume that the algebras are genetic with respect to a common ordering of the basis. It is clear from the definition that the new algebra is genetic. This generalizes in an obvious way to more than two algebras on the same space.

This is not true for special train algebras. Again, the extra condition on the powers on the ideal I of elements of weight 0 causes awkwardness. For example, let the common basis of the two algebras be a_0, a_1, a_2, a_3 . Let

$$\begin{aligned} f(a_0, a_i) &= g(a_0, a_i) = a_i \text{ if } i \neq 2; & f(a_0, a_2) &= g(a_0, a_2) = a_3; \\ f(a_1, a_1) &= g(a_1, a_1) = a_2; & f(a_1, a_2) &= g(a_1, a_2) = a_3; \\ g(a_1, a_2) &= -a_3; & f(a_2, a_2) &= g(a_2, a_2) = 0. \end{aligned}$$

All other products are necessarily 0 by definition of genetic algebra. In both cases $I^2 = \{a_2, a_3\}$ and $I^3 = 0$. Hence both algebras are special train.

We consider the mixture using $\lambda = \frac{1}{2}$. In that case $I^2 = (a_2)$ which is not an ideal since $a_0 \cdot a_2 = a_3$, and so the mixture is not a special train algebra.

6. Conclusion

We have seen that in all cases it is more natural to work with genetic algebras rather than special train algebras. It is true that special train algebras have an easier basis free definition than genetic algebras. On the other hand, we have seen that the property of being genetic is preserved with respect to various operations on algebras whereas the property of being special train is often not preserved. The same basic difficulty appears in all cases. If a basis is used the definition of a genetic algebra essentially says that in the multiplication table certain coefficients in the products are necessarily 0. This is what makes the proofs in (9) for example possible. The further requirement satisfied by a special train algebra is on one hand not useful for proofs and on the other hand hard to verify in various situations. The existence of extra zero coefficients not required by the definition of a genetic algebra often causes these difficulties and is the underlying trick for getting counter-examples. For example, $I^k \subset \{a_k, a_{k+1}, \dots, a_n\}$ from the definition of a genetic algebra. If we had equality for all k the algebra would clearly be special train. Roughly speaking, the problem can be regarded in general as one of unwanted cancellation.

We have emphasized throughout the use of mappings. Although an explicit computation of the multiplication tables would be highly involved we have seen that at least theoretically the structures of the algebras can be visualized. If we were forced to use the original basis elements which correspond to genotypes the table would truly become messy. But this is essentially what happens in

classical population genetics. Thus we have seen examples how the technique of genetic algebras can handle problems which are difficult to handle by classical methods.

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NEW JERSEY
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