Meiosis in *Paris*. II. Spontaneous breakage and fusion of chromosomes

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Received October 20, 1952

Introduction

Bridge formation and fragmentation of meiotic chromosomes were first described more than thirty years ago (Geerts 1911, cf. Haga 1946). McClintock (1931, 1933), by means of correlated genetic and cytological evidence, showed that in *Zea mays* heterozygosity for an inverted chromosomal segment gave rise to a bridge accompanying a fragment at first anaphase. Müntzing (1934), in the F1 hybrid between *Crepis divaricata* and *C. dioscoridis*, inferred from the observation of an anaphase bridge that this hybrid was heterozygous for an inversion. At about the same time, several genetical analyses and cytological studies of salivary gland chromosomes showed that inversions are a very frequent type of structural rearrangement in *Drosophila* (Dobzhansky 1939). Consequently, cytogeneticists have generally inferred from the presence of an anaphase bridge that structural hybridity for an inversion is present. In this publication, such an inference is designated as the inversion-bridge hypothesis.

Diagrams published by many authors (Darlington 1936, 1937b, Richardson 1936, Upcott 1937a, Frankel 1937, McClintock 1938b) have shown clearly that crossing over within an inverted segment results in bridge formation. There is, however, no reason for believing that all bridge-fragment configurations result from inversions and crossing over, and many previous investigators have overlooked evidence against this interpretation. The purpose of the present paper is to present evidence from the writer’s own observations which contradicts this hypothesis, but which favors the hypothesis that bridges may be formed which have no relation to crossing over within inversions.

Material and methods

Pollen mother-cells of *Paris verticillata* MB., constituting a clone with karyotype 2n-III, were studied. This karyotype, as described previously (Haga 1942), consists of the following chromosomes (fig. 1): two pairs of relatively large chromosomes, one with median (designated as A) and one with slightly submedian kinetochores (designated as B); two somewhat smaller pairs (C and E) with submedian to subterminal
kinetochores, the short arm of C being shorter than that of E; one pair with subterminal kinetochores (D), this pair being heterozygous for the presence vs. the absence of a satellite. In addition, a single case of bridge formation within a univalent chromosome is described from a plant of the hybrid *Trillium Hagae* Miyabe et Tatewaki. Belling's iron aceto-carmine was used exclusively as stain and fixative. For further details on technique see the first paper of this series (Haga 1944).

**Fig. 1.** Chromosomes at mitotic metaphase in pollen grains of *Paris verticillata*, illustrating the karyotype 2n-III. a. Chromosome D bearing satellite. b. Chromosome D without satellite. ×1600.

**Observations and interpretations**

In the present section, the types of metaphase and anaphase configurations which yield evidence for the writer's hypothesis will be described and interpreted. The following principles have served as a basis for the interpretations.

1. Chromatid fusion usually takes place only between two broken ends. This fact has been well established by studies of x-ray breakage (Sax 1938, 1940, Sax and Mather 1939, etc.), by mechanical breakage of meiotic and somatic bridges (McClintock 1938a, b) and also by observation of spontaneous breakages of unknown origin (Giles 1940). Nevertheless, Matsuura and Haga (1950) recently found that fusion may occur between a broken and an unaffected end. Both of these types of fusion are assumed to be taking place in the origin of the configurations described below.

2. In the present material, the kinetochores of the homologous chromosomes usually remain synapsed and closely adjacent to each other until the commencement of the first anaphase. In some instances they may be more or less widely separated, as in bivalent A of figure 2, bivalents A, B, and E of figure 5, and bivalent D of figure 10. This condition was found in 8 out of 65 bivalents examined in 13 metaphases showing aberrations, or 12.3 per cent.

1. **Configurations observed at I metaphase.** One type of configuration observed consisted of an akinetic chromatid fragment and a dikinetid chromatid, which were held together within a bivalent (bivalent B, fig. 2). This configuration could be explained on the basis of the inversion-bridge hypothesis, but could also arise from simple breakage.
and fusion of two chromatids within a bivalent (Matsuura and Haga 1950).

In addition to chromatid fragments, akinetic chromosome fragments were also observed. These may be connected to the original bivalent by means of a chiasma or matrical connection, as in bivalent A of

![Figure 3, bivalent C of figure 8 and bivalent A of figure 10. In other instances they are completely free, as in figures 5-9 and 11-13. The presence of such free fragments cannot be explained by the inversion-bridge hypothesis, since according to this hypothesis fragments should remain connected to the mother configuration until first anaphase.
Figs. 6a,b—14a,b. Breakage-fusion alterations observed at first metaphase. In the following descriptions, subscript 1 and s annexed to the chromosome symbol denote long and short arm respectively. In bivalent A subscript 1/2 indicates an arm of it.
In some instances, exceptional configurations were formed by the fusion of two broken chromosome arms, or by union of a broken end to an unbroken end of a chromosome. In one instance (fig. 5), the two short arms of bivalent C were broken off at a position close to the kinetochore, and the resulting two fragments were united into a single fragment. In figure 11, one or both of two arms of bivalent B have become broken and the proximal ends fused to form a loop. Figure 12 shows fusion of arms belonging to two separate bivalents, C and E, after one or both of them had been broken. In bivalent A of figure 13, two arms were broken near the synapsed kinetochores. Since these arms were held together at the distal end by a terminal chiasma, fusion of the broken proximal ends gave rise to an akinetic fragment in the form of a ring. This akinetic fragment is interlocked with the kinetic fragment, which in turn forms a closed ring with synapsed kinetochore and an interstitial chiasma. Union of a broken and an unbroken end is shown in figure 14, in which an entire short arm of chromosome C has become translocated to the homologous short arm of the same bivalent.

It is evident from these metaphase aberrations that chromosome breakage happens accidentally during prophase, and that the broken ends are able to fuse with either a broken or an unbroken normal end. Breakage-fusion alterations in chromosome arms furnish evidence for the assumption that meiotic bridges may be formed without any relation to crossing over in inversions.

One instance worthy of mention in detail is that of interchange between the chromatids of bivalents A and C (fig. 4). In this alteration a chromatid of bivalent A was broken at a median position along the arm, and the kinetic segment was attached to an akinetic chromatid fragment belonging to the short arm of bivalent C. The kinetic chromatid of the short arm of bivalent C has been united to the akinetic fragment belonging to bivalent A. All of these alterations are still held in the relationship which existed during prophase. This configuration

Akinetic fragment is indicated by a small letter of the symbol of the mother chromosome. ×870. 6a,b. Intercalary break, A1. 7a,b. Proximal break, Ds of satellited chromosome D. 8a,b. Proximal break, C1. 9a,b. Proximal break, C1. 10a,b. Proximal break, akinetic fragment being connected to the kinetic one by a fine matrical thread, A1. 11a,b. Intercalary break and fusion, B1. It is not certain whether the fragment b originated in fusion of two fragments or simple detachment from an arm. 12a,b. Break and fusion between C1 and E1, releasing fragment f. It is not clear whether the fragment f is composed of single fragment from an arm or of two fragments from both arms C1 and E1. 13a,b. Proximal break and fusion within bivalent A. Broken ends of fragments are fused, forming a ring with a terminal chiasma at the unaffected ends. This ring interlocks with the mother configuration which in turn forms a ring by synapsed kinetochores and an interstitial chiasma. 14a,b. Translocation of an entire C1 to the homologous arm.
might be interpreted as the results of crossing over in a small intercalary translocation, but such an explanation seems highly improbable to the writer.

2. Configuration observed at I anaphase. The nature of these configurations depends chiefly on the way in which the chromatids or chromosomes broke and became reunited, and on the position of the break with reference to the kinetochore. By far the largest number

Figs. 15a,b–20a,b. 15a,b. Simple detachment of a fragment from a chromatid, $D_1$.
16a,b. Intercalary bridge and fragment, $B_1$.
17a,b. Ordinary loop and fragment, $B_2$.
18a,b. Two ordinary loops passing to the opposite poles and two akinetic fragments left behind at equatorial zone, $B_3$. 19a,b. Two proximal bridges and two fragments, $C_3$ and $D_3$.
20a,b. Proximal loop and fragment, $E_3$. $\times760$. 
of breaks involved two adjacent chromatids. Fusion following such breaks gives rise to a dikinetic chromatid and an akinetic fragment. The dikinetic chromatid will appear as either a bridge or a loop at I anaphase, depending upon whether the kinetochores which it connects pass to opposite poles or to the same pole (figs. 15-20). The various possibilities in this connection are mentioned in the discussion section.

Two types of breaks are recognized on the basis of position. *Proximal* breaks are at or near the kinetochore; *intercalary* breaks are some distance away from it. Proximal breaks form bridges which consist of

![Figs. 21–26. 21. Proximal bridge, B₁. Two long arms are cast off as two non-fused fragments. Fragments are slightly out of focus. 22. Proximal bridge, C₁. Two long arms are fused in a fragment. 23. Proximal bridge, D₁. Two long arms from the satellited chromosome D are cast off as a fused fragment. Two satellited short arms are seen suspended on the middle of the bridge. Spindle-shaped swellings at the base of the short arms contain no spiral chromonema, indicating that they represent kinetochores themselves imbedded in matrix. 24. Proximal bridge, E₁. Two short arms are cast off as a fused fragment. 25. A bridge formed between satellited chromosome D and non-satellited D-, going upper and lower pole respectively, the fusion being incomplete. Note a fine thread at the middle of the bridge. 26. Detachment of a fused chromatid from a proximal bridge configuration. ×1460.](image)

a fine thread stretched between two kinetochores, as in figures 21-26. The anaphase loops formed by proximal breaks are so small that they are hardly visible (figs. 20, 32, 36, 38). On the other hand, intercalary breaks produce relatively long, thick bridge (figs. 16, 28, 30) or clearly visible loops (figs. 17, 18, 31).

The relative frequency of proximal vs. intercalary breaks was estimated at both I metaphase and I anaphase. The metaphase observations were 8 proximal and 12 intercalary breaks, but these data are too few to be significant. At I anaphase, 97 breaks were observed and classified both as to the chromosome arm in which they occurred and to their
position within the arm. The results, given in table 1, show that proximal and intercalary breaks occur with about an equal frequency.

Table 1. Position of breaks analyzed at first anaphase

<table>
<thead>
<tr>
<th>Chromosome arm</th>
<th>A₂</th>
<th>B₁</th>
<th>B₂</th>
<th>C₁</th>
<th>C₂</th>
<th>D₁</th>
<th>D₂</th>
<th>E₁</th>
<th>E₂</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercalary</td>
<td>14</td>
<td>21</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td>Proximal</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td>6</td>
<td>9</td>
<td>1</td>
<td>8</td>
<td>2</td>
<td>7</td>
<td>47</td>
</tr>
</tbody>
</table>

This shows that the proximal regions adjoining the kinetochore are particularly likely to undergo the breakage-fusion alteration. Similar data were obtained for the European *Paris quadrifolia* L. by Geitler (1938);

Figs. 27—41. 27. Proximal bridge, A₂. 28. Intercalary bridge, A₂. 29. Proximal bridge, B₂. 30. Intercalary bridge, B₁. 31. Intercalary loop, B₁. 32. Proximal loop, C₁. 33. Proximal bridge, C₂. 34. Proximal bridge formed by satellited chromosome D and non-satellited D−, unaffected satellited chromatid passing to the upper pole, D₂. One of the two satellited short arms is cast off as a fused fragment. 35. The same alteration as the preceding one, but satellited chromatid is passing to the lower pole, D₂. 36. Proximal loop formed within a satellited chromosome D, the loop passing to the lower pole, D₂. 37. Proximal bridge, E₁. 38. Proximal loop, E₂. 39. Proximal bridge, releasing two non-fused fragments, E₁. 40. Failure of fusion of broken ends between two chromatids passing to the opposite poles, D₁. 41. Failure of fusion between broken ends of the kinetic fragments passing to the opposite poles, D₁. Note the marked difference in length of the two affected chromatids. ×870.
namely, 798 proximal: 633 intercalary breaks. His different interpretation of these configurations is discussed below. Observations made on three different plants showed that proximal as well as intercalary breaks may occur on either arm of any of the five chromosomes.

The structure and behavior of the proximal bridge deserve special attention. Because of its very short length, it is seen at late anaphase as a fine thread stretching between sister kinetochores as well as between the free chromosome arms (figs. 21-26). The thread between the free arms of the bridge apparently originates from the stretching of a bridging portion of negligible length, or of the fused kinetochores themselves. The remaining thread between the sister kinetochores of a chromosome or half bivalent must have originated in the viscous matrix surrounding these kinetochores, which under ordinary conditions pass to the pole tightly held together. Sometimes, these threads between sister kinetochores break under the severe stress of anaphase chromosome movement, so that two chromatids united by the bridge are cast off and remain near the equatorial region (fig. 26). This configuration of chromatids united by a thread-like bridge resembles closely the so-called misdivision of the kinetochores (Koller 1938, Darlington 1939). In the present material, however, all of the first anaphases containing bivalents with proximal breakage and fusion show five half-bivalents invariably passing to opposite poles (figs. 19, 20). This indicates that the kinetochores are unaffected by the breakage, even though it happened very close to them.

Some of the observed configurations appear to have resulted from the failure of broken ends to fuse, or from their partial fusion. The simplest configuration of this type is the detachment of a fragment from a chromatid of a half-bivalent (fig. 15). Another type results from breakage of two adjacent chromatids, with fusion of the kinetic ends to form a bridge, but without fusion of the akinetic ends, so that a single bridge and two akinetic fragments are produced (figs. 21, 39). The reverse situation, namely fusion of akinetic fragments to give a single fragment, but failure of fusion of the kinetic fragments so that no bridge is produced, is shown in figures 40 and 41. These occurrences are, however, exceptional. A possible instance of incomplete fusion is illustrated in figure 25, in which two broken ends are connected with a fine thread, probably of matrical origin. Occasional constrictions seen at the position of fusion probably are temporary conditions caused by mechanical deformation (figs. 19, 20).

3. Univalent bridge. In Trillium Hagae (3x=15), an allotriploid derived from natural hybridization between diploid T. kamtschaticum (2x=10) and tetraploid T. Tschonoskii (4x=20) (Haga 1937 a), a univalent bridge was observed at first anaphase. The bridge was composed
of two sister chromatids of chromosome $C_k$ from *T. kamschaticum* (fig. 42). In the plant concerned, the chromosomes pair as $(0-5)_{II} + (5-0)_{II} + (5-0)_{I}$. The three C-type chromosomes form a trivalent in 10 per cent, a bivalent and a univalent in 87 per cent, and three univalents in 3 per cent of the sporocytes. The position of the three C chromosomes in the sporocyte illustrated in figure 42 suggests that they existed as three unpaired univalents throughout the previous history of the sporocyte. Walters (1950) has shown similar configurations in a *Bromus* hybrid, indicating that spontaneous breakage and fusion can happen regardless of whether or not chromosome pairing has taken place. Univalent bridges, therefore, are reliable indications that spontaneous breakage and fusion have occurred.

**Discussion**

1. *Alternative interpretations of the described configurations.* All of the configurations described in this paper have been observed by other workers in various species of plants and animals, and have been interpreted according to the inversion-bridge hypothesis. In the present writer's opinion, however, these interpretations are highly improbable, at least when applied to the present material. Geitler (1938) found in *Paris quadrifolia* a high frequency of anaphase configurations with very short bridges and long akinetic fragments, but attributed these to localization of chiasmata near the kinetochore, and to the existence of
small proximal inversions in this region. This explanation is doubtful for the following reasons. First, the so-called localized chiasmata probably represent synapsed kinetochores. Second, there is no conclusive evidence for the assumption that the cytological chiasmata do result from genetical crossing over (Matsuura and Haga 1942, Haga 1944). Finally, small inversions are likely to pair in a non-homologous fashion, nullifying or decreasing the chance for bridge and fragment formation.

An alternative explanation of the univalent bridge at first anaphase was given by Upcott (1937 a, b) on the basis of observations on Tulipa and Lathyrus. She assumed that the univalents concerned had previously been paired with homologous chromosomes, and had formed a combination of chiasmata which would ordinarily produce at first anaphase a fragment and a loop, the loop becoming a bridge at second anaphase. But the early separation of the chromosomes from their homologues, plus the precocious division of the kinetochore which often happens in univalents, caused the bridge to appear at first anaphase. This explanation cannot be applied to the univalent bridge described and illustrated by the present writer in Trillium Hagae, since the position of the C-chromosomes concerned indicates that they had never been paired previous to the appearance of this configuration.

2. Relative frequency of first anaphase bridges and loops. As mentioned in the description section, the dikinetic chromatid formed by breakage and fusion will appear as either a bridge or a loop at first anaphase, depending on the mode of separation of the kinetochores. If the assumption is made that the breakage-fusion alteration involves any two of the four chromatids at random, with no difference between sister and non-sister strands, then an alteration involving two non-sister strands will occur twice as frequently as one involving sister strands. This fact is shown by the diagrams of figure 44. In the heteromorphic D chromosomes, it was possible to distinguish between sister and non-sister chromatids at anaphase. Out of 13 configurations observed of this bivalent, 8 resulted from breakage-fusion alterations involving non-sister chromatids, and 5 from such alterations involving sister chromatids. These data, while too few to be significant, tend to support the writer’s assumption.

More extensive data are available on the relative frequency of bridges vs. loops at first anaphase. In interpreting these data, however, the manner of separation of the kinetochores must be considered. But such consideration still gives the expectation of 2 bridges: 1 loop at first anaphase. If sister kinetochores always pass to the same pole at first anaphase, the ratio is expressed by the diagrams of figure 44. If kinetochores separate either equationally or reductionally with the frequency ratio 2 post- : 1 prereduction, as indicated by the neo-two-plane
theory of Matsuura (1938), the expected ratio is again 2 bridges: 1 loop. The writer recorded 78 bridges: 19 loops in his material, but these data are not reliable. At the time of recording, no attention was paid to this problem, and many loops probably were not recorded. The ratio in some of the data obtained by Upcott (1937a) in *Tulipa* seems to conform well with the present expectation (table 2). Among breakage-fusion configurations induced by x-rays in *Trillium kamtschaticum* (Matsuura and Haga 1950), the total of 53 observed at first anaphase gave a ratio of 34 bridges: 19 loops. These two ratios suggest that the mode of breakage-fusion is the same in spontaneous as in experimental alterations. This indicates that the majority of spontaneous bridge configurations arise with no relation to inversions or to crossing over.

3. *The significance of fragment size.* One of the difficulties of applying the inversion-bridge hypothesis to all examples of bridge-fragment configurations has been the great variation in the size of the fragment, even in different configurations involving the same chromosome arm in different sporocytes of the same plant. Swanson (1940, 1941) has interpreted this situation as resulting from the presence of numerous small inversions scattered along the chromosome arm. Sax (1937b), interpreting the same situation in *Paeonia suffruticosa*, considers the presence of many small inversions as one possibility, but suggests also that fragments of different sizes may have resulted from the same inversion, through the occurrence of “inverted crossovers” in non-homologously paired inverted segments. The present writer’s hypothesis, that breakage and fusion can happen at any point along the chromosome, explains these difference in fragment size more simply than do the hypotheses of either Swanson or Sax.

4. *Breakage and fusion without synapsis.* The writer has described above a number of examples of chromosome breakage which are un-
related to any earlier conditions of chromosome pairing. The simplest of these are detachment of chromatid fragments without the formation of a bridge or loop. This type alteration has been described by several previous workers (Belling 1925, Nishiyama 1934, Katayama 1935, Stebbins 1938, Sax 1937a, Darlington 1937a, Darlington and Gairdner 1937, Frankel 1937). In addition, there are many records in the literature of chromosome breakage in cells where synapsis does not take place, such as archeiosporial cells (Döpp 1932, Armstrong and Huskins 1934), pollen grains (Whitaker 1936, Sax 1937a, Upcott 1937c, Husted 1937, Barber 1938, Tanaka 1939, Giles 1940, 1941) and in somatic cells (Plotnikova 1932, Meinskai 1939a, b, Emsweller and Jones 1938, Morgan 1939, Kostoff 1940, Jacob 1940, Pathak 1940). These examples of breakage and fusion obviously have no relation to chromosome pairing, crossing over or inversion. Since meiotic nuclei are more susceptible to x-rays than are somatic nuclei (Sax 1938), we might expect that they would also be more susceptible to the agent or agents which cause the spontaneous breakage.

Another type of fragmentation which is unrelated to synapsis is the disintegrative fragmentation which has been reported at the first meiotic division in several plant species (McClintock 1929, Kattermann 1933, Bergman 1935, Haga 1937b, Gentcheff and Gustafsson 1940). In these examples, innumerable fragments and bridges have been seen in a few exceptional cells, while the great majority of the cells divide in normal fashion.

5. Time of breakage. The presence of configurations like that in figure 4, which must have originated from interchange between chromatids of different bivalents, indicates that breakage-fusion alterations happen at a stage when the chromosomes are effectively split. Since the visible chromosome split does not appear until the pachytene stage, the alterations probably occur at late pachytene and diplotene. Emsweller and Jones (1938) found that in the F1 hybrid of Allium cepa × A. fistulosum fragments appear as early as at pachytene. Frequency in percentage of sporocytes involving a fragment or fragments is as follows: zygotene, 0.0; pachytene, 0.9; diplotene, 6.9; diakinesis, 6.6; first metaphase, 24.6; first anaphase, 33.8. These data suggest that most of the breakage-fusion alterations are initiated at or after the diplotene stage.

6. Position of breaks and reasons for breakage. The high proportion of proximal breaks (table 1) indicates that the region of the chromosomes immediately adjoining the kinetochore is highly susceptible to the agent or agents which cause the breakage-fusion alterations. The reasons for this are unknown. It should be noted, however, that both spontaneous and x-ray breaks are frequent in the proximal regions in material like the pollen grains (microspores) of Tradescantia (Sax 1938,
Sax and Mather 1939, Giles 1940). Furthermore, Peto (1935) found that the proximal regions of somatic chromosomes in * Hordeum vulgare* are highly susceptible to somatic breakage induced by heat treatment. These high susceptibilities may be ascribed to the mechanical strains associated with the nuclear division or to some specific quality of the proximal region. The present data on *Paris verticillata* might be explained in the same manner.

The present discussion may be concluded by considering why and how the chromosomes break spontaneously. Unfortunately, little is as yet known about this point. Giles (1940) showed that the amount of natural radiation is far too low to induce breakage-fusion alterations in such a high frequency as 0.07 per cent, which he observed in microspores of *Tradescantia*. These spontaneous alterations must, therefore, have been induced by some unknown agents other than natural irradiation. The only clue to the solution of the problem of the fundamental mechanism of this alteration is the fact that its frequency is influenced by both genetical and environmental conditions (cf. Haga 1946).

**Summary and conclusions**

Evidence has been presented favoring the belief that spontaneous breakage and fusion of chromosomes occur frequently in the microsporocytes of *Paris verticillata* and other plants, and that many of the configurations occurring at first meiotic metaphase and anaphase which other authors have attributed to crossing over in inverted segments, actually are the result of this spontaneous breakage and fusion. The principal lines of evidence are as follows.

1. The presence of free chromatid or chromosome fragments, unaccompanied by bridges.
2. The presence of types of fragments which can be interpreted only as the result of the fusion of two originally separate fragments.
3. A configuration which apparently resulted from breakage and fusion of chromatids belonging to different non-homologous bivalents.
4. A univalent bridge (seen in *Trillium Hagae*).
5. The relative frequency of bridges and loops at first anaphase is that which would be expected on the basis of the breakage-fusion hypothesis.
6. Great variation in fragment size in different bivalents involving the same pair of chromosomes.

Since about half of the anaphase configurations must have resulted from breaks in the immediate vicinity of the kinetochore, this region is assumed to be particularly susceptible to breakage. Since chromatid as well as chromosome breaks are recorded, the time of breakage is assumed
to be chiefly late pachytene and diplotene. The causes of the breakage are unknown.

Acknowledgements

The writer wishes to thank Professor H. Matsuura of Hokkaido University for his valuable suggestions and kind taking of photomicro- graphs. To Professor G. L. Stebbins Jr. of the University of California the writer is indebted as well for his kindness in thorough reading and revision of the manuscript. The writer's thanks are also due to Doctor M. Kodani of Nagasaki ABCC for his critical reading of the manuscript. Expense of the present study was partly defrayed by a Grant in Aid for Fundamental Scientific Research of the Ministry of Education.

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