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THE ROLE OF SEXUAL SELECTION AS AN ISOLATING MECHANISM IN THREE SPECIES OF POECILIID FISHES

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The role of sexual isolating mechanisms in maintaining the integrity of ecologically coincident yet specifically distinct populations of sympatric species does not seem to have been very fully investigated. In part, this may be due to the actual rarity of such complete ecological coincidence among species mixtures under natural conditions. It is well known that, among a very considerable proportion of sympatric terrestrial species, ecological differentiation, if only in response to minor features of the common environment, is sufficiently marked so that its importance as an isolating mechanism in speciation cannot be neglected. In part, the paucity of observations of this kind is undoubtedly due to the relatively small number of species mixtures of terrestrial organisms which are sufficiently well understood to make possible any certain conclusion as to the presence or absence of such ecological isolating mechanisms, or any estimate of their relative importance.

Observations upon mixtures of sympatric species the members of which were known to be essentially identical in food habits and environmental preferences would obviously be of great value in a study of the role of physiological and sexual isolating mechanisms in the absence of ecological factors. On the whole, populations of aquatic organisms seem to present more promising material for investigations of this sort than do terrestrial ones. Such truly mixed populations are perhaps most evident among freshwater organisms which inhabit streams and restricted lake environments. It seems likely, for instance, that certain members of the so-called "species swarms" of Cichlidae found in some African lakes, such as those studied by Bertram, Borley, and Trewavas (1942) and others, may properly fall within this category. In other cases, although the ecological coincidence is less perfect, there is still a large and important environmental area in which intimate species mixtures occur without any loss of distinctness on the part of either population. The geographical overlap of the viviparous Poeciliid fishes *Xiphophorus hellerii* and *Platypoecilus maculatus* in Mexican streams is well known and has been extensively studied by Gordon and his coworkers (1947).

The present report is concerned with a single aspect of a study now in progress of the ecological relations within a mixture of three sympatric species of Poeciliid fishes which show an extraordinary degree of habitat coincidence in certain of the fresh waters of Trinidad. These three species are *Lebistes reticulatus* Peters, *Micropoecilia parae* Eigenmann, and *Poecilia vivipara* Bloch and Schneider. All three are closely related taxonomically, being included by Hubbs (1926) in a single tribe, the Poeciliini of the subfamily Poeciliinae. Mixed schools of these three species of fish are found in many Trinidad waters, and they exhibit almost identical feeding habits and prefer closely similar stream environments. Such populations appear to offer unusually good opportunities for a study of the operation of sexual and physiological isolating mechanisms in speciation quite apart from the influence of ecological isolation.

THE EXPERIMENTAL MATERIAL

Poecilia vivipara, Micropoecilia parae, and *Lebistes reticulatus* are all relatively

small, largely surface-feeding viviparous top-minnows native to parts of the West Indies and northeastern South America. In Trinidad, the two first-named species are normally fish of quiet coastal streams and brackish lagoons, being especially abundant in swamps and the irrigation ditches of cocoanut plantations. *Lebistes reticulatus* occupies a wider range of habitat. It is common in relatively swift upland streams, but penetrates throughout their courses and coexists in great numbers with the other two species in lower waters. Evidence is accumulating to indicate that the populations of lagoons and lower river courses may represent a physiologically somewhat distinct race from those in swifter and fresher water, but this is by no means certain.

The food habits of the three species are closely similar. All are essentially omnivorous, picking insects and other food from the water surface and foraging at the bottom for algae, insects, and crustacea. *Lebistes* and *Micropoecilia* characteristically swim at the surface, often in intimately mixed schools. *Poecilia* sometimes appears with them, especially younger specimens, but mature individuals tend to remain at lower levels, as is true to a degree of larger females of the other two species. Since the waters in which the studies are being conducted are only about eight to twelve inches in depth, and since the smaller specimens of all three species make constant foraging trips from the surface to the bottom and back, even this habitat preference is probably of little significance.

Reproductive isolation between the three species appears to be essentially complete in nature. No intergrades have so far been found in any of the mixed populations studied. Hybrids between *Poecilia vivipara* and *Lebistes reticulatus* have been obtained in the laboratory. Phenotypically they resemble *P. vivipara* and are relatively large, well developed, and extremely hardy, but it is probable that they are sterile. It is clear, therefore, that physiological isolating mechanisms are of importance in maintaining the species structure of the population. These may involve such physical factors as differences in gonopodial structure between the species (which are considerable), factors of partial sterility involving sperm competition, or differential viability of hybrid and non-hybrid embryos. The question is being investigated further.

The role of sexual selection as an isolating mechanism is suggested by several conspicuous features in the biology of all three species. In all of them, sexual dimorphism is most pronounced, and includes important features of structure, coloration, and behavior. In *Micropoecilia* and *Lebistes* the mature male averages somewhat less than half the size of the fully grown female. In all three species, the mature male is highly colored and shows some secondary modification of fin morphology in addition to the specialized development of the gonopodium characteristic of all Poeciliid fishes. In *Poecilia* this modification of color and fins is relatively slight. At maturity an intense salmon-red coloration replaces the normal gray of the female and immature forms, but the basic reticulate melanin pattern remains unchanged. In *Micropoecilia* the mature male takes on a conspicuous coloration which is very different from that of the female and involves elaborate patterning of the dorsal and caudal fins with areas of melanin and carotinoid pigments and some characteristic coloration of the body. In *Lebistes* the mature male shows the great variety of highly polymorphic patterns of fin and body coloration which have made the guppy a favorite aquarium fish, as distinct from the coloration of the adult female as is the case with *Micropoecilia parae.*

The mature males of all three species thus differ strikingly in appearance both from the females of their own species and from each other. They are even more distinctive with respect to their courtship patterns. Elaborate and characteristic courtship patterns dominate the activities of the males and are a usual, though not

an invariable, prelude to mating. A description of these patterns would be unduly lengthy here. Suffice it to say that they are an unmistakable and, in their total complex, an invariantly distinguishing species characteristic.

In contrast to the males, the females of *P. vivipara, M. parae,* and *L. reticulatus* resemble one another to a marked degree, and this further emphasizes the interest attaching to an investigation of the role of sexual selection in isolation. The females of *Micropoecilia* and *Lebistes* are closely similar in size, conformation, coloration, and behavior. Both are of an inconspicuous gray color with fins of the generalized type common to the tribe, clear and without obvious patterning, save that some females of *M. parae* in Trinidad carry a small black spot near the upper margin of the base of the caudal fin. The females of *Lebistes* carry no pattern of body coloration save for the characteristic reticulation. The females of *Micropoecilia* show a somewhat less conspicuous reticulation and are of a slightly more golden color, with a few irregular black dots caused by local aggregations of micromelanophores. There is also a small but more or less conspicuous black lateral spot, located near the distal margin of the pectoral fin when at rest against the body and surrounded by a few gold scales. This spot tends to disappear in many old specimens. The fully mature female of *P. vivipara* averages somewhat larger in size than those of the other two species. It is also of a plain gray coloration with less evident reticulation, but with a black lateral spot, surrounded with golden scales as in the case of *M. parae* and located in a similar relative position. The fins are clear and with a more or less distinctive patterning of minute black spots. The dorsal fin is located somewhat more anteriorly than in *Micropoecilia* and the caudal fin is more sharply angulated.

In mating pattern, as in appearance, the females of the three species show no such distinctive differences as do the males. In all three cases, the female is a relatively passive agent in the mating process, responding little in any obvious way to the courtship patterns of the male. The females of *P. vivipara* and *M. parae* respond to actual gonopodial contact of the male to the extent of halting momentarily in swimming and rotating the body slightly toward the side from which the male has approached, thus facilitating such contact. This behavior pattern is common to the members of several related genera of Poeciliine fishes, such as *Mollienisia* and *Limia.* In *Lebistes,* on the other hand, the female remains throughout an apparently entirely passive agent in the whole act of fertilization. There is normally no marked halting in swimming, and no evidence of cooperation in any active way, except possibly in the case of females which have been reared in isolation in the laboratory.

The process of fertilization in *M. parae, P. vivipara,* and *L. reticulatus* is internal, as in all the Poeciliidae. Encapsulated spermatophores are probably transferred along the male gonopodium to the genital pore of the female in one or more contacts. The contact may be a relatively lengthy one, as typically in the case of *P. vivipara, M. parae, Mollienisia* and *Limia,* and notably in the cases of the Xiphophorine fishes studied by Clark, Aronson and Gordon (1948). It may, on the other hand, be swift and of momentary duration, as is commonly if not always true in *Lebistes.* This difference of mating procedure between *L. reticulatus* on the one hand and *M. parae* and *P. vivipara* on the other may be of importance to the present investigation, and will be referred to further.

Experimental Objectives and Procedure

The pronounced sexual dimorphism of coloration, form, and behavior in the males of these three species on the one hand and the conservatism and similarity of the females on the other suggests *a priori* that the selection of appropriate mates in intimately mixed populations may be largely a matter of female discrimination of and

TABLE 1. *Gonopodial contacts of fourteen males of* Lebistes reticulatus *with any of three available females immediately and after one week*

Experiment I. Four males, from Maracas River, Trinidad

	Immediately	After one week
Contacts with *Lebistes* female	56	98
Contacts with *Micropoecilia* female	34	2
Contacts with *Poecilia* female	10	0
	100	100

Experiment II. Five males, from Santa Cruz River, Trinidad

Contacts with *Lebistes* female	16	(1–100)	93
Contacts with *Micropoecilia* female	79		7
Contacts with *Poecilia* female	5		0
	100		100
	39		Not made
	59	(101–200)	
	2		
	100		

Experiment III. Five males, from St. Joseph River, Trinidad

Contacts with *Lebistes* female	28	Not made
Contacts with *Micropoecilia* female	65	(♀ *Micropoecilia* died)
Contacts with *Poecilia* female	7	

Totals:

	Initial exposure	After one week
Contact with *Lebistes* female	139 (34.7%)	191 (95.5%)
Contact with *Micropoecilia* female	237 (59.3%)	9 (4.5%)
Contact with *Poecilia* female	24 (6.0%)	0 (0.0%)

The same three females, from wild stock, were used throughout these experiments. They were selected as nearly as possible of equivalent size. Their respective measurements were:

	Lebistes	*Micropoecilia*	*Poecilia*
Weight (mg.)	402	531	612
Length (snout to base of caudal fin, mm.)	26.0	28.0	28.5
Greatest depth (mm.)	7.0	8.0	8.5

The difference in percentage of incorrect and correct choices between the first contacts and those after one week of exposure is statistically significant.

reaction to the highly distinctive stimuli of color, form, and behavior offered by the males of the proper species, and rejection of the inappropriate stimuli involved in the advances of other males. If this were true, the situation would be closely similar to that so well known and relatively so well understood among many birds. In such an event, the evolution of specialized patterns among the males could be considered as a readily understandable corollary of sexual selection in the conventional Darwinian sense, and the role of sexual selection as an isolating mechanism in this sympatric species population would be relatively straightforward. The experiments reported were designed, therefore, to test the question of whether the reaction of females of the three species to the stimuli presented by the males was specific, and of importance in assuring that only the appropriate matings should occur, as has been well demonstrated by Tinbergen and Van Iersel (1947) for the

case of the stickleback. The results have been unexpected and surprising and are currently presented with no attempt at a full explanation.

The experiments were simple in design and execution. An aquarium of fifteen gallons capacity was arranged to simulate as closely as possible a section of the lagoon environment. This arrangement was made with considerable care since it was deemed important to maintain the ecological situation as nearly intact as possible. Into this tank were introduced simultaneously three females, one of each of the three species concerned, and several males of one. The females selected were all already pregnant (the normal condition in the wild state) and wherever possible were taken directly from mass cultures of their own species. The males used were all actually wild fish taken from Trinidad waters or were first-generation descendants of such individuals. They were all taken directly from mass cultures of their own species immediately before the experiments were begun.

The males were introduced to the tank containing the three females and observations were begun within an hour. The behavior of the males was closely noted, and all gonopodial contacts with females of each species were recorded. When 100 or 200 such recordings were made, the observations were discontinued for a period of six days and the fish left undisturbed *in situ*. On the sixth day another set of 100 observations of gonopodial contacts was made. The males were then removed, the females being left in place alone for twenty-four hours. A new group of males was then introduced and the observations were repeated.

Owing to the much greater sexual activity of *Lebistes* males than of males of the other two species it proved experimentally most convenient to work with them. All records presented in this series, therefore, refer to the behavior of *Lebistes* males in the presence of females of the other species.

It is well known that males of *Lebistes*, when exposed to several females of their own species, tend to pay most attention to the largest individuals, and the size differential among them need not be great. Especial care was used, therefore, to select females of closely similar size. Rec-

TABLE 2. *Gonopodial contacts of single male of* Lebistes reticulatus *with any of six females of three species over a period of nineteen days*

Single male, from the Arima River, Trinidad
Two females each of *Lebistes reticulatus* (Arima River), *Micropoecilia parae*, and *Poecilia vivipara*

Date	Contacts with *Lebistes*	Contacts with *Micropoecilia*	Contacts with *Poecilia*
10/22/47	15 (30.0%)	34 (68.0%)	One approach, no contacts (2.0%)
10/23/47	34 (68.0%)	16 (32.0%)	0 (0.0%)
10/27/47	58 (100.0%)	0 (0.0%)	0 (0.0%)
10/28/47	98 (98.0%)	1 (1.0%)	1 (1.0%)
10/31/47	68 (98.6%)	0 (0.0%)	1 (1.4%)
11/2/47	93 (98.9%)	0 (0.0%)	1 (1.1%)
	(Male *M. parae* introduced)		
11/4/47	53 (98.1%)	1 (1.9%)	0 (0.0%)
	(One female of *P. vivipara* died. Replacement introduced. This created no excitement.)		
11/8/47	86 (100.0%)	0 (0.0%)	0 (0.0%)
11/10/47	38 (97.4%)	1 (2.6%)	0 (0.0%)

Errors were high on the first two days, as in the initial exposures recorded in table I. By the third day, discrimination had become remarkably good, and remained so to the end.

ords are given of the weights of each female, the length from snout to base of caudal fin, and the greatest body depth. Since the same females were used throughout, their states of pregnancy varied with the experiment. Parturition was observed in none of them during the work. The males used were from stock taken from three distinct Trinidad locations. The female *Lebistes* were taken from one of these. Fourteen males were involved, and observations were made of 600 gonopodial contacts. The data are summarized in table 1.

As a check upon these experiments, a more detailed and complete series of observations was made involving a single male and two females of each of the three species, so matched for size that a larger and a smaller individual of each species was present. As in the previous situation, records of 600 gonopodial contacts were made, and courting behavior was carefully noted. Observations were made for a period of approximately ten hours, distributed over a period of twenty days. The data are summarized in table 2.

Discussion

The experiments described included observations on the behavior of fifteen wild *Lebistes* males from four environments in Trinidad when exposed to wild females of their own and the other two sympatric species. In all, 1200 gonopodial contacts were recorded. In two experiments the *Lebistes* females were taken from the same actual body of water as the males. In two cases they were from adjacent and similar, but not identical, locations. This made no observable difference.

The results are on the whole uniform in character. In every case the males showed an initial preponderant choice of the females of *Micropoecilia parae* with which to make gonopodial contact. In every case this initial error of choice was striking. It was clearly aided by the behavior of the females of *parae,* which reacted to the *Lebistes* males in exactly the fashion characteristic of their reaction to males of their own species, halting in swimming and rotating the body, thus cooperating in the formation of contact—a procedure never seen in *Lebistes* females from mass culture as already indicated. A number of erroneous contacts were also made with *Poecilia vivipara.* These were in all cases less numerous, although the reaction of the *vivipara* female was likewise typical of its reaction to males of its own species, and therefore slightly positive. Throughout the experiments the reactions of the females of *parae* and *vivipara* to males of *Lebistes* differed in no detectable way from those normal to their own species. No evidence of female discrimination has been found so far.

After a relatively short time, the errors in gonopodial contact were sharply reduced, as will be seen, and in every case observed finally reached a very low level. In all the observations, there was every indication that this rectification followed from a learning process on the part of the *male alone.* Females of the other species continued to react positively to the relatively few gonopodial contacts which were achieved. After prolonged exposure, males regularly continued to approach the females of *Micropoecilia parae* as they had earlier, poised or executed typical courtship patterns, but then turned away sharply without contact.

Three impressions are very strongly given by these observations. First, discrimination of the correct females by wild males of *Lebistes* in mixed populations of the three sympatric species can be carried out with a high degree of accuracy if the populations have been in equilibrium for a period of twenty days or more. Sexual selection, therefore, favors the transfer of more gametes to the correct than to the incorrect females. This is in accord with the general principle of the "conservation of gametes" originally stated by Dobzhansky and recently further elucidated by Mayr (1948). An estimation of the importance of sexual selection as an isolating mechanism in this situation must await a

more complete estimate of the extent of physiological isolation which is involved.

The second and more striking impression, which has been consistent under varying conditions, is that this discrimination is made on the part of the male alone, the female being an essentially passive agent in the process. This is the reverse of what might be expected in view of the similarity of the females of the three species and the marked differentiation of the males, but is consistent with the hypothesis advanced by Noble and Curtis (1935) that the selection basis of male coloration in *Lebistes* is that of warning between males rather than stimulation of females.

Third, and perhaps most striking, the evidence seems very good that the discrimination of *Lebistes* males which have been kept for long periods in mass cultures of their own species alone is at first exceedingly imperfect, and that a high order of perfection is achieved gradually, the reaction being apparently a learned one.

There are three questions which are important in analyzing these conclusions and in applying them to a study of natural populations of these sympatric species. First, what is the meaning of the "gonopodial contact" in genetic terms? Does each gonopodial contact represent an actual transfer of sperm, or are the great majority of these contacts without specific genetic meaning? Second, cannot the initially large percentage of errors of the *Lebistes* males be explained merely as a high and therefore uncritical threshold which was gradually lowered by "saturation" of contacts until only stimuli from the correct females was sufficient to evoke the contact reaction? If this were true, there would be no indication of any learned reaction, but only of a lowered generalized reaction threshold. Third, is it really clear that reactions on the part of the female, too small to be noticed by the observer, were not actually responsible in part for the discrimination observed? Is it clear, in other words, that there is not in fact here a series of "reaction chains" between male and female, differing from the similar situation recorded for many other organisms only in that it is more difficult to detect? These questions require some further discussion.

1. *The Genetic Meaning of the "Gonopodial Contact" in* Lebistes

Clark, Aronson and Gordon (1948) have made rather extensive observations on the process of fertilization in *Xiphophorus hellerii* and *Platypoecilus maculatus,* among themselves, in crosses, and among the F_1 hybrids. They have reported the existence of two rather distinct types of gonopodial contact, the first, which is more frequent, being momentary and somewhat of the *Lebistes* type, the second less frequent and more prolonged. It has been shown by the method of smears that the transfer of sperm takes place only in the second type of contact.

It is necessary to know, therefore, that in *Lebistes* the observed type of contact results, at least in many cases, in the actual transfer of sperm. There is some evidence that this is true. In many thousands of observations of *Lebistes,* no type of gonopodial contact other than that observed in these experiments has been distinguished, and no observations of other types of contact have been recorded, so far as the authors are aware. The question, however, is being further investigated experimentally.

Thus evidence seems indicative that sperm transfer is actually effected from *Lebistes* males to *Lebistes* females by gonopodial contacts of the type recorded. It does not, of course, indicate the percentage of cases in which such transfer is effected. Experiments are currently in progress to determine this by exposing virgin females to single and to counted multiple contacts and thereafter sectioning them to determine the percentage of ova that are fertile in each case. The results of this work are not yet available. The evidence also does not indicate that sperm transfer from *Lebistes* males occurs successfully in the case of a similar percentage of er-

roneous contacts, although the fact that it can be successfully accomplished in the case of *P. vivipara* is proved by the laboratory hybrids which have been produced. This question is an important one, but belongs in the study of physiological isolating mechanisms now in progress.

2. *Erroneous Contacts and Male Threshold versus "Learned" Reactions*

The processes of sex recognition and courting in *Lebistes* have been extensively studied by Breder and Coates (1935) and by Noble and Curtis (1935). The former authors observed that sexually active males will attempt to fertilize a variety of objects more or less indiscriminately. The specimens with which they worked reacted positively to anaesthetized females of their own species and to specimens of *Cyprinodon variegatus, Fundulus heteroclitus,* and *Barbus conchonius,* as well as to the shadows of living fish projected on the sides of the aquarium. These observations would seem to indicate that the "threshold" in *Lebistes* males is extremely low, and that, in the present experiments, the increasing perfection of discrimination did in fact represent a progressive raising of that threshold through "saturation." It is to be noticed, however, that the *Lebistes* males used by Breder and Coates had been isolated from all females for one week before experiments were begun. In contrast, males used in the present experiments were taken directly from cultures in which many female *Lebistes* were present, and should therefore have been as "saturated" at the beginning of the experiment as at the end. Noble and Curtis, on the contrary, used males which had had free and continuous access to females of their own species, and reported greater success and higher discrimination on the part of old and "experienced" males, while young males reared alone attempted at first to mate with males, but gradually came to correctly discriminate males from females—results which tend to substantiate the hypothesis of a "learned" reaction in the present case.

3. *Role of the Lebistes Female in Determining Correct Contacts*

It is extremely important theoretically to determine whether mate selection in *Lebistes* is in fact a function of male discrimination only, or whether a "chain" of reactions exists between male and female, resulting in the accumulation of stimuli which eventually culminate in fertilization, as has been demonstrated for many other organisms. As already mentioned, no visual evidence of this situation has been found, although it has been very carefully looked for.

To test the matter further, a rather extensive series of observations are in progress which will be reported elsewhere. Though not yet completed, enough evidence has accumulated to be significant. Experiments have been set up identical to those reported here, except that the *Lebistes* have been given a choice, not of females of three species, but of females of three genetically homogeneous strains of *Lebistes* differing among themselves in only a single autosomal gene. In every case so far studied, wild-type males have been used, taken from mass cultures of genetically homogeneous wild-type strains, and the choice given has been between wild-type females of the same strain and two classes of females of the same strain but carrying a recessive allele for xanthic body coloration.[1] These females are otherwise completely normal and are fully interfertile with the wild strain. In these experiments also, initial "errors" were high, but after several days of association, the percentage of discrimination of wild-type females by these wild-type males was as good as at the close of the experiments here reported. It seems extremely unlikely that in all these cases the single autosomal gene difference of the mutant fe-

[1] These body-color alleles to wild-type are "golden" and "blond" described by Goodrich (1944), Winge (1947), Haskins and Druzba (1938), and Haskins and Haskins (1948).

males would markedly influence their sexual behavior so as to break the chain of mutual stimulation if it existed. Discrimination on the part of the male alone seems much the simpler explanation.

The evolutionary significance of this situation requires further analysis, but it is suggestive that the function of male sex coloration, at least in *Lebistes,* is wholly a repellant one between males, and plays little part in sexual isolation, while male discrimination, on the other hand, is important in this connection.

Summary and Conclusions

Preliminary studies are described designed to explore the mechanism of sexual selection and its role as an isolating mechanism among populations of three sympatric species of Poeciliid fishes which normally coexist in the coastal waters of Trinidad and which exhibit an extremely low degree of ecological isolation. The studies have involved the reactions of fifteen males of *Lebistes reticulatus,* taken from four separated locations in Trinidad, to wild females of *Lebistes,* of *Micropoecilia parae,* and of *Poecilia vivipara.* The study is still in progress, but three tentative conclusions seem justified on the basis of the data reported and of certain auxiliary experiments which are described. These conclusions are:

1. Measuring the reaction of the male *Lebistes* to females of its own and the other species by the relative frequency of gonopodial contacts, a rather good discrimination of *Lebistes* for *Lebistes* exists in mixed populations which are at equilibrium.

2. This discrimination is based essentially upon the behavior of the male, despite the fact that in all three species pronounced sexual dimorphism exists on the part of the male in form, coloration, and courtship patterns, while the females have remained markedly conservative on all three scores. It has not been possible to obtain any evidence of a "chain" of stimulation reactions between male and female, and some fairly convincing evidence has been obtained against it.

3. Discrimination among males which have been kept with females only of their own species is at first very poor, but improves rapidly in a matter of days until a high efficiency is attained. Females of alien species, on the other hand, continue to tolerate erroneous contacts with the same degree of readiness at the end as at the beginning of the experiments, showing no detectable change of behavior. The change of behavior on the part of the males gives some evidence of being a "learned" reaction.

Work is in progress to investigate this situation by other methods, as well as to determine more completely the degree of physiological isolation between these species, which appears to be considerable.

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