

Special Feature—Roundtable Discussion

Fish Models for Studying Adaptive Evolution and Speciation

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The following represents an email discussion in September 2005 on the topic of fish model systems for the study of evolution. The participants included scientists working on a range of fish model systems, including cavefish, Danios, sticklebacks, cichlids, and trout. Editing has been kept to a minimum, to maintain the character of the on-line discussion.

Question #1:

What makes a species a “model”? Is a genome sequence for the organism necessary/sufficient? What are the minimal requirements for a species to become the focus of research by a community of scientists? Do we like the term “non-model” for species outside the mainstream of biomedical research?

Bill Jeffery:

My definition of a model species has several parts. First, the species must obviously exhibit the phenomenon to be studied in a form as generally applicable as possible. Second, the species must have many favorable intrinsic attributes (e.g., abundance, laboratory culture, favorable embryonic qualities, accessibility to experimental manipulation, mutagenesis, and genetics) and be tractable to numerous manip-

ulative tools and approaches (transgenesis, gene inhibition, etc.) as possible in order to clearly answer a question about the phenomenon.

Tom Kocher:

Is it possible to know if a species exhibits a general phenomenon, until we have evaluated generality by studies of several species?

I think it must be possible to do classical genetic analysis in a model species—so the fish must have reasonable brood sizes, and it must be possible to complete the life cycle in the lab in a reasonable time (1 year?). But Gary is a more patient man than I, and has been successful in quantitative trait loci (QTL) mapping life history traits in salmonids with longer generation times.

What do you mean by favorable embryonic qualities? Lots of fish have clear embryos. Do

your criteria eliminate livebearers such as guppies, where embryonic development happens internally? Surely we can still use such species to study adult traits, such as life history and behavior?

Transgenesis currently requires quite a lot of technology development for each new species. Is this an absolute requirement? Do we think this barrier will be lowered with new transgenic techniques currently under development?

Todd Streebman:

I think a more interesting question may be what technology can (has/will) do to the concept of the “model” organism. Anderson and Ingham (2003) conclude with the following:

“Is it now acceptable to work on apparently arcane aspects of biology in model organisms without making direct connections to human health? It must be, because the best investigators recognize interesting questions that don’t fit into a predefined paradigm and follow the biology for its own sake. These curiosity-driven experiments are the ones that lead to truly surprising discoveries. We can expect that studies of seemingly exotic developmental events will continue to provide new perspectives on evolution and human biology.”

I like this passage, especially if you remove the word “model” from the first sentence. As technologies such as genome sequencing, gene knock-down, and microarrays become more affordable and tractable, I can see a new assistant professor using the first year of start-up funds to have a few genomes sequenced. In the future, questions and not the organism will drive the science. The distinction between model and non-model organisms will disappear. All organisms can be models, if the science is right.

Katie Peichel:

I think that the definition of a model organism completely depends upon the questions that one is asking. Any organism that one uses to address a question becomes a model to understand a given biological process. For some questions, having a genome sequence is not important, for others it is extremely important.

However, for those questions in which genomic and genetic tools are necessary, I agree with the comments that technology is no longer limiting. We can ask questions, then choose the model to fit the questions, rather than choosing the questions to fit the model. The days of being limited to working in traditional model systems are over.

Dave Parichy:

I generally also try to be careful in defining the term “model” and like to preface it when possible; for example we have generally recognized biomedical model organisms like zebrafish, drosophila, etc., but also equally valid and recognized behavioral model organisms like guppies, naked mole rats, etc. It seems to me the “model” designation has more to do with a concentration of effort and knowledge than any real technological attributes. I agree with Katie that advanced technologies can now be applied to more and more nontraditional, nonbiomedical model organisms, though of course this raises the issue of how to apportion the limited funds that such technologies demand.

There will always be concentrations of people working on particular organisms, whether we call them model organisms or not. Whatever term is used for designating these groups, it is bound to be exclusionary to some degree and rather politically motivated in its application: it’s nice to call one’s own group a model for something as it seemingly elevates the group to a more prominent position relative to other groups. The more people involved, the easier to feel legitimate in calling the group or species a model.

Gary Thorgaard:

I suppose that one could argue that an organism needs to either have at least one superlative attribute or a set of cumulative positive features to become a successful focus of research. For example, *Fugu* seems to have the advantage of a small genome size, even though it is problematic from some other standpoints. The zebrafish has a set of cumulative positive features related to its ease of breeding, visualization of development. Trout have an extensive body of life history and culture knowledge, as

well as ample body size for a number of biochemical and immunological studies.

Bill:

I don't think having a sequenced genome is absolutely necessary to answer every important question in biology using a model species. I admit that it helps, but often a large collection of expressed sequence tags (ESTs) is satisfactory, or even better.

Tom:

Hmm. I'm having a hard time imagining how a large collection of ESTs trumps a genome sequence. Maybe if the comparison was between a very low-coverage genomic shotgun (1x) and an EST project.

Gary:

It seems like having a sequenced genome is highly desirable and as the analytical tools become better it may even be necessary. At this point it seems like a lot of features can lead to an organism being a successful model. I suppose that in some senses one could argue that in the case of *fugu* a sequenced genome, driven by its small genome size, has been sufficient for it to become a model species.

Bill:

Of course both a genome project and large EST project are desirable but the ESTs (backed up by in situ hybridization data) allow one to focus on particular transcribed mRNAs in a specific tissue or cell without the worry of alternative transcripts expressed at different places and time, etc. An example is the recent work on the hemichordate body plan by Lowe et al. (2003) in which considerable information was obtained using an EST database in the absence of a genome project. In the end, however, it depends on the question one is addressing.

I don't like the term non-model species. The "non-model" species may not be useful for answering any of the particular questions addressed by biologists at the present time. As we know more, we hope ask new questions, which in turn may convert a "non-model" into a "model" species.

Of course, model species cannot answer every important question in biology. A prime example

is the generation of evolutionary novelty, which cannot be addressed using only one species.

Tom:

My impression is that the term non-model species has been used for species that have not had their genome sequenced, or are not in the mainstream of biomedical research. So, some would say the only "model" fish species are zebrafish and medaka. "Non-model" sounds derogatory, so I've tried to get people to use "alternative model" to describe all the other species we work on.

Gary:

I don't personally like the term "non-model." It seems like what one would use if the goal were to discount the value of work on a particular species.

Katie:

I don't like the term "non-model" either, and I agree that it sounds derogatory. Alternative model does not seem to fit the bill either. I personally like the term "non-traditional" model organism. Of course, I particularly like the recent description of sticklebacks as a "super-model," but I am biased.

Tom:

But I wonder, is *Fugu* a model organism? Or just an unfinished genome sequence? Doesn't the term "model" implicitly mean "experimental model"? There has been some recent work to develop *Fugu* and its relatives as experimental models (Crnogorac-Jurcevic et al. 1997; Kai et al. 2005), but if ever the term "non-model" was appropriate, it would seem to apply to *Fugu*?

Question #2:

Have studies of extralaboratory models changed our view about the genetic basis of adaptation, in terms of the number of genes, the kinds of genes/mutations underlying adaptive evolution?

Katie:

Studies on alternative model systems have contributed greatly to our understanding of the genetic basis of adaptation. These types of studies just can't be done in traditional model systems because there is very little phenotypic variation in inbred laboratory strains. Variation

between inbred strains exists, but it is the result of strong artificial selection, which may or may not be a good model for natural selection.

Recent work in sticklebacks, cichlids, and cavefish has shown that genes of major effect (sometimes nearly Mendelian) can underlie adaptive phenotypic differences in natural populations. So, contrary to the prevailing theories following the evolutionary synthesis of the last century, adaptation in the wild can happen via mutations of large phenotypic effect. In addition to major genes, work in sticklebacks has also shown that there are other loci of smaller effect that contribute to adaptive phenotypes, and that these loci have a combined additive effect on phenotype. In sticklebacks, the genes underlying two traits have been identified. Surprisingly, both are genes known from previous work in developmental genetics: the *Pitx1* gene is responsible for loss of pelvic structures, and the *Ectodysplasin* gene (*Eda*) is responsible for loss of lateral plates. Both of these appear to be due to regulatory, rather than coding changes, lending support to the hypothesis that evolutionary change will proceed via changes in regulatory elements, to avoid the negative pleiotropic effects that a coding change might have on viability in the wild.

Despite these advances, more work is needed on multiple traits in multiple systems to determine if we can see any general patterns underlying the genetic basis of adaptation!

Gary:

Somewhat similar to what was just reported in Katie Peichel's informative answer on sticklebacks, we have been surprised in our work with rainbow trout at the frequency with which major QTLs have been found to associate with traits that are likely to be associated with adaptations. Examples include embryonic development rate, natural killer cell-like response, variations in numbers of meristic elements, and differences in resistance to a myxosporean parasite present in some river systems and not in others. We haven't been able to associate any of these QTLs with specific genes or specific types of mutations as yet in the trout model. However, it seems likely that this will be possible in the near future. By the way, the ap-

proach we are using involves rapid (two generation) production of homozygous lines for use in the QTL analyses. The homozygous lines we use thus are representative of the source natural populations from which they were derived.

Todd:

It's probably important to point out that Fisher's infinitesimal model was clarified on theoretical grounds in the late 1990s by Allen Orr and others who showed that the accumulation of fitness effects during adaptive evolution followed an exponential distribution (Orr 1998). This work demonstrated the likelihood that empiricists would uncover genes of major effect. It's also notable that many other systems (including some that may not even fit our "alternative model" definition) have contributed to this body of work, including fire ants, monkeyflowers, and butterflies.

Next, I wonder why the genes identified or suggested to be involved in adaptive evolution thus far (e.g., *Pitx*, *Eda*, *Pax*, *Bmp*) are well known from studies of developmental genetics. Is this because developmental geneticists know so much about so many genes, or does this suggest something more fundamental—that genes of major phenotypic effect turn out by necessity to be master regulatory genes? Does this suggest further that continued study of genes underlying adaptive evolution is likely to tell us more about the novel deployment of familiar genes, or does this approach offer up the chance to discover new functions for "unknown" loci?

Or alternatively, and as pointed out by Katie, are we getting a representative view of the genetics of adaptation by focusing on this small tail of the exponential distribution?

Dave:

It would be nice to have a better sense how luck and publication bias contribute to the picture so far. While it's certainly the case that results from sticklebacks and other systems have resulted in a paradigm shift towards fewer genes of large effect underlying adaptive evolution, I can't help wondering if there are other efforts that have not yielded such clear answers:

maybe because the critical region didn't harbor a well-known developmental gene and so it's taking a long time to narrow down a field of candidates, or because there really were many moderate effect QTL that hamper identification (to say nothing of small effects that escape detection because of small panels etc.). Do you more QTL-oriented folks have any sense of this? Are there unlucky stickleback postdocs who don't come up with a well-known developmental gene and so haven't yet got a clear story for us, or is every effort initiated sure to be a Nature paper?

Another issue is the degree to which some of these studies tell us about early steps in adaptation. While the few analyses that have actually gone from phenotype, to a major effect gene, to demonstrating selection on that gene (or a single causal nucleotide) are very informative, one has to be careful about inferring too much from major effect differences observed between populations or species. Just because one can detect such extant differences, which may be associated with well-known loci, doesn't necessarily mean the early steps in an adaptive process occurred by changes of similarly large effect or even at that locus. This is more of a concern for the candidate gene analyses in which folks have simply gone after the loci for which they already have probes in their freezer, but it is something to keep in mind. So I can't help wondering if the pendulum has swung a little far towards few, large effect loci and the reality lies somewhere in the middle.

Bill:

With regard to the question of whether "non-model" systems have contributed anything to our understanding of the role of genes in adaptive traits, I can add a few comments about the *Astyanax* (cavefish) system.

Recall that *Astyanax mexicanus* is a single species (based on the ability to form viable hybrids in nature and the lab) consisting of multiple forms: a pigmented and sighted surface form (surface fish) and many de-pigmented and blind forms. It has been known for a long time that a single Mendelian gene controls loss of melanin pigment in cavefish. Recently, Meredith Protas in Cliff Tabin's lab at Harvard

Medical School identified this gene (Protas et al. 2005) by QTL analysis (if it can be called that for a single trait). Different mutations have been documented in the same gene in two or three independently evolved cavefish, suggesting either a mutational hotspot around the gene or some advantage of mutating this gene. In addition, our lab has shown that although melanophores do not differentiate in cavefish, xanthophores may be present in about the same numbers as in surface fish. Both pigment cell types are derived from the same embryonic source (neural crest), so neutral theory would predict that they should both be missing, which is not the case. Instead, there may be a specific advantage to losing melanin pigmentation, which seems to be controlled by a single gene, which has repeatedly mutated during adaptation to the cave environment.

There are also more complex traits that have evolved in *Astyanax* cavefish that seem to be controlled by a single gene. For example, cavefish show different feeding behavior with respect to surface fish, which seems to be controlled by a single gene (or one major gene and two modifiers) and is adaptive for finding food in the darkness.

So, as in sticklebacks, work with the "non-model" cavefish has changed the notion that many genes always control adaptive traits, each having a small independent effect on the phenotype.

Katie:

As Todd and Dave have pointed out, we really need more data to see how generally applicable these trends will be!

Certainly in the stickleback work so far, we have purposefully focused on the genes of large effect, but have mapped loci with smaller effect. And for some traits, we weren't able to map any loci. So unfortunately not every effort is sure to be a Nature paper, especially now that I have switched to looking at behavioral traits.

I do think with many of the systems discussed (stickleback, cavefish, cichlids) can tell us about the early steps in an adaptive process because

these populations have diverged as recently as the past ten thousand years. It may be that the early adaptive steps are large and the later steps are small (as Orr predicted).

Dave:

So I wonder if it makes sense to develop additional “extra-model” systems (or whatever we’re calling them) or to put most effort into the current ones. One of the great things about sticklebacks is certainly the behavioral and ecological work over so many years, and the same can be said of cichlids. But what about guppies, swordtails, etc., for which the timeframe and relevance to early stages could be similar. Are there serious efforts to bring those groups to the same level in terms of genomic resources, etc.? Should there be?

Tom:

I don’t have much to add, except to say that as we have argued for funding for developing genomic resources, we have tried to identify species that are good models for studying a variety of traits. No model system is the perfect balance of every criterion, and there is certainly room for a diversity of model species. But I’ve always thought it was hard to justify major investments in a species to answer just one question. We could probably make a list of additional species that should be developed, and certainly guppies come to mind. There has been some work towards a genetic map of this species, but I think other resources are lagging. It still takes a village to organize a new model species!

Question #3:

What are the most useful/powerful experimental approaches for characterizing the genetic basis of adaptive evolution? What are the special characteristics of fishes that make them particularly useful for such studies?

Bill:

I would say the special characteristics of fishes are the ability to respond to environmental challenges with adaptive changes in phenotypes without altering the ability to produce viable offspring between the different conspecific populations that have evolved as a conse-

quence. This attribute permits forward genetic approaches, genetic analysis of adaptive traits, and eventual gene(s) identification. However, this attribute is certainly not a special characteristic restricted to fishes, any good laboratory “model” with a manageable generation time would be suitable as long there are natural populations with different phenotypes. Perhaps I am missing something especially singular about fishes, however, so I will listen to what other fish investigators have to say about this.

Tom:

I think this is a key point. For whatever reason, it is often possible to hybridize populations/species that are phenotypically very different, and still recover viable and fertile F1s for genetic analysis. This has generally not been possible with mammals (perhaps because of a high rate of chromosomal evolution), or even with many *Drosophila*. And it is not possible with many fish. For example, it is not possible to do formal genetic analysis between zebrafish and other danios, although Dave has been making good use of some F1 danio hybrids (Quigley et al. 2004). This is what we find so exciting about the cichlid system. We are able to do formal genetic analysis among intergeneric (and even interlake) hybrids, making it possible to study a huge range of morphological and behavioral traits (Kocher 2004).

We can’t forget also the ease of access to the embryos, relatively large clutch size, and usually small size of adults. Fish are also right-sized for ecological studies—big enough to see in the field, but not unmanageable for studies in captivity.

What about the fish-specific genome duplication? Do we think this has positive or negative impacts on the utility of fishes as a model system for studying adaptive evolution?

Katie:

I think most of the reasons for why fish are so great for studying the genetic basis of adaptive evolution have been given!

In regards to whole genome duplication . . . some people have speculated that duplicated genes partition the original function of one

gene, and this may make it possible for one of the genes to acquire a new function, or to modify its function. There is some data to support this hypothesis, but overall I am not sure how general this will turn out to be.

The downside of the duplication is that one always has to be careful when cloning candidate genes!

Gary:

I wanted to add some comments before we leave this question. I feel that QTL analysis is a very powerful approach for studying the genetic basis of adaptive evolution. As discussed, some very divergent types of fish can produce fertile hybrids and can be utilized in QTL analyses. The power of this approach as opposed to pure sequence studies or in vitro studies is that it allows at the organismal level to be related to specific loci and genes.

Although I recognize that not many labs are utilizing this technology, I believe that the tolerance of fishes to induced uniparental inheritance (gynogenesis and androgenesis) which allows development of clonal lines and the use of doubled haploid mating designs for genetic analysis is a special characteristic of fish that makes them useful for QTL studies (Thorgaard et al. 2002). Streisinger et al. (1981) recognized the potential utility of clonal fish lines for research but the full potential of that technology, which allows the inbred lines and recombinant inbred lines to be generated rapidly, has not yet been realized.

Question # 4:

What roles can laboratory models play in supporting research on extralaboratory models?

Todd:

Laboratory models are often at the vanguard of technical development. We all likely borrow, or are working to employ techniques (e.g., embryo injection, morpholino knockdown) initially developed in fish models like zebrafish and medaka.

In a more fundamental sense, laboratory models can sometimes be used as 'testing grounds' for hypotheses generated in other groups. For

example, Aparicio and colleagues (1995) tested enhancer activity of evolutionarily conserved and putatively regulatory DNA sequences from *Fugu* in transgenic mice. Another example comes from some of our own work with cichlids. We have genetic and gene expression evidence that *bmp4* is a candidate controlling lower jaw form and function. Craig Albertson recently demonstrated that *bmp4* is sufficient to elicit a similar morphological change in zebrafish by overexpression in embryos (Albertson et al. 2005). This experiment remains a difficult one to do in our animals.

Of course, we also owe much of our understanding of gene function, development, and genome organization to studies of laboratory models. These models serve as great reservoirs of new projects for study in other lineages.

Katie:

I agree with Todd's comments. Most of us make use of tools, techniques and knowledge generated by work in traditional model organisms. Our work simply would not be possible without the past 20–30 years of work in developmental genetics and genomics carried out in traditional model organisms. To be successful in identifying the genetic basis of adaptation, it will be necessary to move back and forth between traditional and nontraditional model organisms, as the example shows, or as Dave's work on pigmentation in zebrafish species nicely highlights.

Bill:

It can be extremely helpful when a "non-model" system is closely related to a "model" system. For example, zebrafish have played a significant part in candidate gene analysis of phenotypic changes in cavefish. Among the laboratory fish models, aside from goldfish, zebrafish and cavefish are most closely related. Some zebrafish RNA probes can detect expression of the correct gene in cavefish. If a gene is already cloned in zebrafish it is usually possible to quickly clone the same gene in cavefish using the published sequence. Despite their relatively close relationship, however, there are some precautions that one must consider in direct comparisons. For example, although trying

for a long time, we have not been able to detect duplicated *pax6* genes in cavefish, as there are in zebrafish.

Gary:

Clearly, laboratory models contribute both technical innovations and scientific hypotheses that at times can be most easily or appropriately tested in extralaboratory models. No one model has all of the features that we need to address every question so there should be a constant interchange of methods and hypotheses among the various model systems in order to achieve the most insight.

Question #5:

How will studies of fishes contribute to our understanding of adaptation/speciation in other taxonomic groups?

Bill:

Our understanding of the molecular or genetic basis for adaptation/speciation, especially through developmental processes, is rudimentary in all taxonomic groups. Therefore, any contribution from fishes will be helpful. However, because of the many attributes of fishes revealed in our replies to the first few questions in this roundtable discussion, it seems likely that fishes will continue to make a significant contribution to our understanding of adaptation/speciation.

Katie:

As discussed earlier, I think we need many examples of the types of genes and mutations that underlie adaptation before we can make generalizations. In this sense, it is important to include fish models. It may be that many of these questions are just more tractable in fish for reasons discussed earlier.

Already I think that we can start to compare across disparate taxa such as flies, mammals, birds and fish and come up with some interesting trends. For example, it seems like there may be certain classes of genes that can tolerate coding mutations, such as in mutations in pigmentation specific genes in birds, mam-

mals, and fish, whereas more general developmental control genes with pleiotropic effects are more likely to harbor regulatory mutations.

Question #6:

If the cost of genome sequencing drops ten-fold, what other species could/should become models, and for what questions?

Bill:

Obviously, I would favor sequencing the *Astyanax* cavefish and surface fish genomes because of the wealth of comparative molecular information this would provide on constructive and adaptive traits that have appeared in a relatively short period of time in cavefish based on a well-known environmental cue, perpetual darkness in the cave environment. But of course the possibilities do not only include fishes. I would focus on sister species or divergent populations of the same species in any group of organisms that show interesting changes in embryonic or adult features. Well-known examples of these occur in echinoderms and ascidians. The case of *Molgula* (ascidian) species with tailed and tailless larvae is most attractive because of the small genomes and the completed genome projects in other ascidians. I guess the bottom line is that we will need to know the genome sequences of at least two taxa or differentiated populations within a clade to make intelligent conclusions about the molecular basis of adaptation/speciation.

Tom:

I think this represents a major shift in thinking about how genome sequencing effort should be allocated. Lately it seems the emphasis has been on getting sequence from a single representative of each major lineage in animal evolution. But of course, with these distant comparisons, it is impossible to extract information about recent adaptive evolution.

We've been thinking about "meta-genomic" approaches, in which a group of closely related species are each shotgun sequenced to draft stage, and a meta-assembly produced, including reconstructions of the genomic sequences of the ancestors of the clade. The cluster of draft

sequences could be scrutinized for variation related to adaptive differences among the species. This will take some new informatic tools, but may be especially powerful and cost-effective with the new sequencing technologies coming on the market.

Todd:

I agree with Bill's comments about the importance of looking at closely related species/forms. It seems to me the recently released draft sequence of chimp (and subsequent comparisons to human) demonstrate why this is important (once again assuming one's goal is to know about adaptive evolution and speciation). The chimp analysis clarifies a few points but leaves many questions about the molecular underpinnings of human-chimp differences unanswered.

In the end, sequencing will not be enough. Some of the powerful analytical strategies of population genetics infer the molecular signature of selection by comparing fixed differences between species to polymorphism within. As we advocate the sequencing of closely related genomes, or the meta-genomic approach that Tom articulated, we should also ensure that appropriate population samples are available, and we should exploit new technologies for polymorphism detection.

For us, the ideal situation would be a "finished" tilapia sequence coupled with the meta-genomics scenario discussed earlier. This would allow more efficient assembly of draft genomes via comparison to tilapia, *in silico* mapping of SNPs, and nice cross-species comparisons of stuff like the expansion of haplochromine-specific mobile elements.

I would also love to see marine (large population) versus descendent freshwater (small population) stickleback genomes (might also be done with *Fugu* relatives) to test hypotheses of increasing genome degeneration/complexity with decreasing effective population size.

Katie:

I definitely like the suggestion of sequencing multiple closely related species with interest-

ing phenotypic differences. These genomic comparisons should generate many interesting hypothesis. However, I would argue strongly that the only species or groups of species worth sequencing are those in which hypothesis generated by the genomic analysis can actually be tested experimentally! Under this criteria, pufferfish would probably not have been sequenced, while cavefish, sticklebacks, and cichlids all would be!

Todd:

I'd like to add some thoughts about other fish species (and rationale) one might choose to work on with reference to genomic approaches to adaptation, if and when costs of genome sequencing are reduced. Some of these already possess decent molecular and genetic resources:

Guppies, mollies: color, lifespan, size, mate preference

Killifish: environmental response, toxicity, salt tolerance, lifespan

Notably, it is also possible to breed and hybridize marine fishes (driven by the pet trade), which have large brood sizes and often small genomes. Particularly tractable might be:

Anemonefishes: color, trophic morphology, mutualism

Gobies: color, trophic morphology, mutualism
Seahorses/pipefish: sex-role reversal, trophic morphology, vertebral number

David:

I think Todd has a really nice idea that would probably make for a nice table listing our favorite current and future models and the relative advantages they provide.

Katie:

Some other fish models in which some genomic tools have been developed that have interesting biology:

Antarctic notothenioid fish (icefish): cold adaptation

Whitefish: ecological divergence and reproductive isolation

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