What is metamorphosis?

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Synopsis Metamorphosis (Gr. *meta-* "change" + *morphe* "form") as a biological process is generally attributed to a subset of animals: most famously insects and amphibians, but some fish and many marine invertebrates as well. We held a symposium at the 2006 Society for Integrative and Comparative Biology (SICB) annual meeting in Orlando, FL (USA) to discuss metamorphosis in a comparative context. Specifically, we considered the possibility that the term "metamorphosis" could be rightly applied to non-animals as well, including fungi, flowering plants, and some marine algae. Clearly, the answer depends upon how metamorphosis is defined. As we participants differed (sometimes quite substantially) in how we defined the term, we decided to present each of our conceptions of metamorphosis in 1 place, rather than attempting to agree on a single consensus definition. Herein we have gathered together our various definitions of metamorphosis, and offer an analysis that highlights some of the main similarities and differences among them. We present this article not only as an introduction to this symposium volume, but also as a reference tool that can be used by others interested in metamorphosis. Ultimately, we hope that this article—and the volume as a whole—will represent a springboard for further investigations into the surprisingly deep mechanistic similarities among independently evolved life cycle transitions across kingdoms.

Introduction

Metamorphosis is an inherently integrative concept, with relevance to developmental biology, ecology, life history evolution, physiology, cell biology, and even conservation biology. Although most people are in agreement about a general conception that metamorphosis represents a transformation of some sort (think caterpillar to butterfly), there is little agreement on the specifics. In early January 2006, we gathered in Orlando, FL (USA) to discuss metamorphosis in a comparative context. Our goal was to address—through platform talks, contributed articles, posters, and organized and informal discussions, as well as a Web site forum—the following questions: What is metamorphosis? Is it specific to animals, or can the term be rightly applied to life-cycle transitions in non-animal groups? When comparing independently evolved metamorphic (or metamorphic-like) transitions across taxa, do we see any superficial and/or deep parallels in the underlying signaling systems that regulate these disparate life-cycle transitions? Why has metamorphosis apparently evolved repeatedly in the history of multicellular life? The various articles in this volume represent an attempt to frame answers to these questions, if not to address them specifically. Still, it is clear that the diversity of views of metamorphosis is arguably comparable in scope to the diversity of organisms that undergo such life-cycle transitions. Therefore, we did not intend, nor did we produce, consensus answers to the questions we posed above. It has been suggested (see Michael Hadfield's definition, below) that the meaning of the term "metamorphosis" should be defined before proceeding to use it. In that spirit, we here present our various views on metamorphosis, in many cases influenced in

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Table 1 Summary of the various conceptions of metamorphosis presented here

Author	Habitat shift	Major morphological change	Change in adaptive landscape	Rapid	Change in feeding mode	Pre metamorphic stage is post-embryonic	Usually pre-reproductive to reproductive stage transition	Transition is generally hormone-regulated	Is plant flowering metamorphic?
Cory Bishop			X			X	X		Yes
Deniz Erezyilmaz		X	[1]			X	X	X	Yes
Thomas Flatt	X	X	X		X	X	X		No
Christos Georgiou		X	X					X	Yes
Michael Hadfield	X	X	X		X	X			No
Andreas Heyland	X	X	X		X	X	X	X	No
Jason Hodin	X	X	X		X	X	X	X	Yes
Molly Jacobs	X	X	X	X[a]	X[a]	X[a]			No
Svetlana Maslakova	X	X	X		X	X			No
Tony Pires		X	X[3]			X	X		No
Adam Reitzel	X		X		X	X	X		No
Scott Santagata	X	X[4]	X			X			No
Kohtaro Tanaka	X	X	X			X			Yes[5]
John Youson	X	X	X		X	X	X	X	No[6]

"X" indicates that the author considers the feature in question (see column headings) to be a key element of (that is, a proposition that is generally true about) metamorphosis. Blanks indicate that those features are not considered by the author to be integral to metamorphosis. As a way of addressing the applicability of metamorphosis across kingdoms, each author responded to the following question: "Is the vegetative to flower transition in angiosperms an example of metamorphosis?" (last column).

[1]Deniz Erezyilmaz supports the idea that metamorphosis represents a shift from an adaptive peak to another, without involving a change in the adaptive landscape itself.

[2]Molly Jacobs notes that 3 of the features selected—rapid transition, change in feeding mode, and that the pre-metamorphic stage is post-embryonic—are often but not always true of metamorphoses across taxa.

[3]Tony Pires notes that the change in adaptive landscape is more accurately described as the selective pressure driving the evolution of metamorphosis rather than a feature of metamorphosis *sensu stricto*.

[4]Scott Santagata notes that major morphological changes can also occur gradually in a series of smaller steps from the "larval" stage to the juvenile form. This can still be considered a type of metamorphosis and not direct development as long as there is a change in adaptive landscape between stages.

[5]Kohtaro Tanaka notes that plant flowering should be considered metamorphic (or metamorphic-like), even though it does not involve habitat shifts, and morphological changes occur only in parts of individual plants. Given their lack of mobility and the way they develop, this is the only way plants can carry out the type of change analogous to metamorphosis in animals.

[6]John Youson notes that flowering in angiosperms does share some similarities with animal metamorphosis.

their specifics by our attendance at the 2006 symposium. By way of summary, we present a table (Table 1) indicating the common and unique aspects of these various definitions. Our hope is that this collection of thoughts, in combination with the other symposium articles in this volume, will not only provide useful tools for other researchers with similar interests, but also point the way to a detailed research program, integrative both disciplinarily and taxonomically, to investigate the importance of key transitions in organismal life cycles.

Definitions

Cory Bishop

Metamorphosis, loosely conceived, is a component of organismal ontogeny. In considering this symposium, I think it is appropriate to transcend arbitrary or exclusive definitions of metamorphosis based on: (1) the extent of specific and overt changes in morphology or ecological parameters and (2) larval type. Thus, I define metamorphosis, in the broadest sense, as a transition between vegetative and sexually reproductive multicellular stages of a life history. This definition serves to describe a process by which post-embryonic life cycle phases that are not sexually reproductive, but whose existence is selected to increase reproductive success, make a transition into a form or stage that is reproductive, within a single life cycle. While this broader definition may "dilute" conceptions of metamorphosis involving more substantive transformations (see Andreas Heyland's definition, below), it facilitates our ability to compare the regulation of life-history transitions across wide phylogenetic distances. For example, in recent years, the physiological mechanisms that control life-history transition among incredibly disparate organisms such as fungi, slime molds, plants, and animals share some similarities. These similarities caused me to wonder whether it is valid to conceive of these life-history transitions as a metamorphosis because of this shared feature. Doing so allows us to formally compare control of similar biological processes at the physiological level. Thus, I consider the vegetative to flowering transition of the mustard plant Arabidopsis thaliana to be analogous to metamorphosis. Isopod crustaceans and hemimetabolous insects are examples of organisms that fall into this broad conception of metamorphosis, but are not normally considered to have metamorphosis. In contrast, I would not include the life histories of mammals and holoplanktonic rotifers in this definition.

Deniz Erezyilmaz

Metamorphosis is often described as the trick of making a genome produce 2 different forms. However, how different the 2 forms should be to constitute a metamorphosis seems to be a matter of degree. Insects, for instance, utilize one of 3 different life history strategies. Holometabolous insects such as flies and moths have complete metamorphosis, while hemimetabolous insects, such as crickets and grasshoppers merely gain functional wings and genitalia at the final molt. This latter group also includes more "radical" hemimetabolous insects such as the dragonflies; although their larval forms are aquatic, their overall development more closely resembles that of other hemimetabolous insects. Ametabolous insects such as the firebrat, are truly direct developers, with the adult distinguished only by size and genitalia. Similar to most entomologists, I consider insects of the monophyletic Holometabola to be truly metamorphic. However, the field of insect physiology has shown that the same machinery that is used during complete metamorphosis of flies and moths is also used to produce the polymorphisms and heteromorphoses of hemimetabolous insects. Therefore, on a fundamental level, the difference between these broad groups of insects is the extent to which this "metamorphosis machinery" is deployed. In my opinion, we can make more meaningful descriptions of metamorphosis by comparing the activity of this shared machinery between the 2 groups.

Thomas Flatt

Metamorphosis in the strict sense describes a particular life history transition in multicellular organisms, from a larval to a juvenile (or adult) stage, accompanied by dramatic morphological, physiological, and ecological changes. Such changes typically include a major restructuring of morphology, and often involve a transition from a non-reproductive to a reproductive state, dispersal and settlement to a new habitat, and a shift in nutrition and feeding behavior. Organisms that do exhibit metamorphosis under the definition given above include holometabolous insects such as butterflies (a classical example) and *Drosophila*; amphibians (some frogs such as *Rana temporaria* being a classical example); some fish such as jawless fish; and echinoderms such as sea urchins. Organisms that do not fit the strict definition include the hemimetabolous insects such as grasshoppers; nematodes such as *Caenorhabditis elegans*; many fish; reptiles, birds, and mammals; plants, etc. Yet, while the above definition applies to metamorphosis in the strict sense, it might be useful for the purpose of the symposium to consider metamorphosis as but a particular example of the more general concept of life-history transitions: a life-history transition is a transition between different stages and modes of life occurring during the life cycle of an organism, for example, larval-to-pupal, larval-to-juvenile, juvenile-to-adult, non-reproductive-to-reproductive, feeding-to-non-feeding, non-diapause-to-diapause, non-dispersing-to-dispersing, and reproductive-to-post-reproductive.

Christos D. Georgiou

The basic shape, form, and structure of an organism (whether animal, plant, or fungus) emerges as a result of a sequence of developmental adjustments. Each of these is usually irreversible within its morphogenetic sequence, although often reversible by some gross disturbance (for example, regeneration after injury). The whole process whereby the final organization and pattern of the organism is established in terms of metamorphosis (a synonym of morphogenesis) applies to all eukaryotic organisms. Each adjustment is made by cells already specified by earlier adjustments to belong to a particular developmental pathway. Consequently, developmental adjustments are made from among progressively smaller numbers of alternatives, until the particular structure to which the cell will contribute is finally determined. Within the developing tissues, cells follow particular routes of differentiation in response to their intrinsic genetic program, to external physical signals (light, temperature, gravity, humidity), or to chemical signals from other regions of the developing structure. These chemicals (termed inducers or morphogens) seem to inhibit or stimulate entry to particular states of determination. Chemical signals may contribute to a metamorphic activity around a structure (cell or organ), which permits continued development of that structure, but inhibits formation of another structure of the same type. All these phenomena contribute to the pattern formation that depends on positional information, which prompts or allows the cell to differentiate in a way appropriate to its position in the structure. Positional information may be conveyed by concentration gradients of 1 or more morphogens (for example oxidants, antioxidants, hormones), emitted from 1 or more spatially distinct sources. The responding cell senses the concentration of the morphogen and initiates a differentiation program appropriate to the physical position at which that morphogen concentration is normally found. In essence, the cell adjusts its morphogenetic response in accord with its position relative to the controlling incoming signals. Populations of cells, which respond in a similar way, are said to show regional specification. The basic rules of pattern formation seem to be that regional specification (directed by organisms producing morphogens) occurs first, regulating gene activity in ways specifically geared to metamorphosis so that particular cells are first specified (a state which is still flexible) and then determined (a state which is inflexible) to their differentiated fates. These major events contribute to eukaryotic metamorphosis.

Michael Hadfield

Similar to many others, I have pondered this question for decades. I have finally concluded that there is not, nor ever will be, a single definition for metamorphosis, and that no longer worries me. The important thing is that the person using the word defines what he or she means by metamorphosis in the context within which he or she is writing. That said, I have always restricted my use of metamorphosis to refer to the transitions of an animal from a larva to a juvenile. This definition thus requires 3 more definitions: transitions, larva, and juvenile. By transitions, I mean the morphological, physiological, and behavioral modifications that proceed while a larva transforms to a juvenile. By larva, I mean a post-hatching, free-living developmental stage that differs in morphology, physiology, and often habitat from the adult. By juvenile, I mean a stage with most of the morphological, physiological, and ecological traits of an adult, but typically not reproductive. It must grow and develop gonads to become an adult. I am convinced that metamorphosis, as defined above, is polyphyletic, and thus is not homologous across all animals. That is, insect metamorphosis is not evolutionarily homologous with molluscan metamorphosis, even if some of the same transcriptional/translational events are utilized. Given the lack of homology, there can be no absolute definition for metamorphosis. This definition begs explanation for what to call larva-like stages that remain encapsulated and transform—usually gradually—into the juvenile form prior to hatching. Because these stages lack the ecological and behavioral characteristics of larvae, I prefer to call them something else, for example, veliger-stage embryos. But they are part of direct development, which is a pattern without larvae. And that—above—is a LOT more to say about definitions of metamorphosis than I ever planned to do again.

Andreas Heyland

Metamorphosis is a life-history transition that involves radical changes in habitat, morphology, and physiology. The pre-metamorphic phase is characterized by a distinct larval stage that is often not reproductive and lives in a different habitat than does the adult. Metamorphosis is tightly regulated within an animal's life cycle by hormones and a variety of environmental signals. Competence, the developmental capacity to undergo metamorphosis, can last from days to months in marine invertebrate larvae. It is ended when the larva finds a highly specific settlement cue. Examples that fit my definition are: Lampreys (jawless fish), *Xenopus laevis* (frog), *Drosophila melanogaster* (fruit fly), *Aplysia californica* (sea hare), and *Strongylocentrotus purpuratus* (sea urchin). Examples that do not fit my definition: most fish except those, like flounders, that undergo a change in habitat and radical changes in morphology, and those, like salmon, that change habitat and physiology; flowering in plants; the transition to the adult in the roundworm *C. elegans*; the formation of the juvenile in the direct-developing slime star *Pteraster tesselatus*. For my definition of larva see Heyland and Moroz (this volume).

Jason Hodin

Metamorphosis is a more or less substantial morphological transformation between 2 multicellular phases in an organism's life cycle, often marking the transition from a pre-reproductive to a reproductive life stage. It usually involves major physiological changes and a shift in habitat, feeding mode, etc., and can generally be subdivided into an extended phase that involves transcriptional regulation, and a shorter phase (such as settlement in marine invertebrates, adult eclosion in insects) that does not. Depending on the metamorphic taxon, the extended phase can precede, follow, or be coincident with the shorter phase. I agree with Svetlana Maslakova (below) that the degree of morphological change required to justify a transition as metamorphic is something "more distinct than simply growth and morphogenesis." In other words, typical isometric/allometric growth during ontogeny is not metamorphic change. Examples of metamorphosis that fit my definition (but are not often considered metamorphic) include the aquatic-to-terrestrial transition at adult eclosion in dragonflies, and the mycelium-to-fruiting body transition in mushrooms. Examples that do not fit my definition include any life-history transition involving an intervening single cell/zygote stage (that is a reproductive transition, not metamorphosis). Grasshoppers and free-living nematodes, for example, are also non-metamorphic, as they only undergo a subtle transition at the adult molt.

Molly Jacobs

Metamorphosis is an ecological and a morphological transition that an organism undergoes as a normal part of ontogeny. Multicellular organisms which reproduce sexually face the challenge of growing from a very small and morphologically simple thing (a zygote) to a larger and more morphologically complex thing with differentiated tissues that must perform all sorts of complicated tasks, such as getting energy and reproducing. Natural selection can act very differently on an organism over time as it passes through different size ranges and starts to perform different tasks. Many organisms add mass and complexity very gradually as they grow, for example nematodes and marine algae. However, other organisms display abrupt transitions (metamorphoses) in morphology and habitat over ontogeny. There is a gray area regarding how abrupt the transition needs to be in order to be called a metamorphosis. I am inclined to call any ontogenetic morphological change (even a minor change) that is associated with a large change in ecological role a metamorphosis. Examples range from the classic larval/juvenile transition in benthic invertebrates such as ascidians, to epitoky in some polychaetes. By the same token, a radical morphological change that is associated with only a small shift in ecological role could also be a metamorphosis. Embryos that pass their larval stages in capsules (for example many gastropods) are an interesting variation on this theme: they undergo a meaningful developmental transition that is obviously homologous to the metamorphoses of related free-living larvae, but in an ecological sense they are direct-developers.

Alternation of generations (as in marine algae and some terrestrial plants) might also be worth a mention. I agree with Jason Hodin (see above) that if there is an intervening unicellular stage we should not call it metamorphosis. However, I think alternation of generations should be viewed as an interesting alternative strategy to metamorphosis in organisms whose rigid cell walls preclude changes in form driven by the movement of cells relative to each other. Many of the characteristics discussed by others here for metamorphosis of metazoans can also be found in organisms that alternate generations: a single genotype coding for 2 different developmental programs which often come a program followed by the other in a normal life cycle, and with the 2 different developmental programs associated with different habitats, morphologies, and reproductive capabilities.

Svetlana Maslakova

Metamorphosis is a characteristic event in an organism's life history, which involves a morphological transformation, more distinct than simply growth and morphogenesis. That is, there are organs and structures characteristic of pre-metamorphic stages, which are lost at metamorphosis and structures characteristic of post-metamorphic stages. This transformation marks a transition between distinct stages in life history (for example larva and juvenile), which often occupy and are adapted to different environments (for example have different means of locomotion and feeding). I think change in habitat—such as pelagic to benthic, freshwater to aerial, terrestrial to aerial or fresh water to salt water—is central to the definition of metamorphosis, as the accompanying morphological and physiological changes are strongly linked to it. If a larva and juvenile are morphologically very different, metamorphosis may be rapid and accompanied by a dramatic loss of characteristic larval structures and development of characteristic juvenile/adult structures. Examples of organisms that fit this definition include larvae of many marine invertebrates (for example, cnidarians, molluscs, polyclad flatworms, nemerteans, polychaete annelids, sipunculids, echiurids, echinoderms, ascidians, hemichordates, phoronids, bryozoans) as well as freshwater and terrestrial larvae of holometabolous insects, and those vertebrates that have a distinct larval stage (like tadpoles of indirect-developing frogs). Other examples may include transitions between different stages of life history in parasitic flatworms and other parasites. Examples of organisms that do not fit this definition are hemimetabolous insects, most vertebrates, and free-living nematodes.

Although there are similarities in how metamorphoses are regulated across the animal kingdom, it is clear that morphological changes involved in metamorphosis in different animals evolved many times independently and, therefore, are not homologous. It is possible, however, that some sort of life history transition was present in the most recent common ancestor of all metazoans (considering how common and diverse are life history transitions in protozoans) and that all animals share the regulatory machinery controlling these transitions.

Tony Pires

To me, metamorphosis is a qualitative discontinuity in development, which results in the generation of a juvenile (sexually immature adult) body plan. Many of the proximate morphogenetic mechanisms by which metamorphosis may be accomplished, such as differential growth, cell migration, neuromuscular and sub-cellular motor programs, apoptosis and histolysis, may not be unique to the process of metamorphosis. The same may be true for the underlying signal transduction systems and gene networks. So, what makes metamorphosis special and distinct from other greater or lesser developmental discontinuities (for example, gastrulation, or early instar ecdyses of nematodes and arthropods) is its place in life history. If life history is critical to the definition of metamorphosis, then it is an easy step to lay on additional requirements such as have been proposed in other definitions found herein; for example, that metamorphosis places the animal into a new adaptive zone. If adaptive shifts accompanying major morphological change are really what we mean by metamorphosis, then we might drop the requirement for generation of the adult body plan, and include the redia-to-cercaria transition in trematodes (Platyhelminthes). I think it is safe to say that many of us end up crafting definitions to suit the phenomena that we find most compelling.

As I work mostly on the proximate end of the proximate-ultimate spectrum, I would like to know the mechanisms by which signals from the environment get access to the control mechanisms of metamorphosis. The context here is the rapid metamorphoses of marine invertebrates, induced by chemosensory cues. If there is a common cross-phyletic "toolbox" of morphogenetic mechanisms, yet a diversity of sensory cues that initiate metamorphosis, how do the latter plug into the former? As a neuroscientist, I am especially keen to find out new ways in which activity in neurons can regulate development—not just of themselves, or of other neurons (a well-trodden area of inquiry), but of the entire animal.

Adam Reitzel

I would define metamorphosis as a dramatic, coordinated transition in an individual's life history that occurs post-embryogenesis, frequently connecting an immature stage with a reproductive stage. Nevertheless, this definition does not *a priori* exclude vegetative-to-vegetative stage transitions or an asexually reproductive phase transition (such as strobilation in scyphozoans). Although I think metamorphosis can be most clearly defined in cases where stages have large morphological differences (for example symmetry change, appendage variation), independent shifts in habitat and/or physiology that do not involve radical changes in morphology could also be considered in demarcating metamorphic versus non-metamorphic life histories. These extensions may be especially useful in cases where either the taxa of interest are morphologically simple throughout their life history (for example sponges, cnidarians), or when the biological significance of specific morphological characteristics used to separate stages would be questionable (for example the apical tuft in marine invertebrate larvae). To this end, I think qualifiers for proposed metamorphic life histories, such as "habitat metamorphosis" or "physiological metamorphosis," may be useful. An example of the utility of these different types of metamorphosis may be in species that have evolved parasitic life histories. In some parasitic organisms, the morphological shift between stages is relatively small when compared with metamorphosis in other animal phyla. Generally speaking, parasitic stages are frequently morphologically simplified at the macro-scale despite the evolution of stage-specific characters at a more micro-scale. From an echinoderm/amphibian/holometabolous insect view of metamorphosis, I do not know if these would qualify as true metamorphoses, as the parasitic stage may have a morphology similar to an immature adult stage. However, from a habitat and physiological perspective, these are indeed dramatic shifts in life history. The individual changes habitat because the individual is living either freely in the environment or occupies a specific position(s) in a specific host, likely requiring changes in feeding mechanisms, physiological responses, and potentially defensive strategies.

Scott Santagata

The majority of animal phyla have complex life histories that often exhibit at least a single or several intermediate life stages before forming the final body plan of the adult. These intermediate life stages (larvae) are often designed to exploit some other habitat than that occupied by the adult form. Larval morphology is the result of an alternative genetic program, driven by different sets of developmental, ecological, and evolutionary pressures than that of the adult. As a result, a transitional period is required when this intermediate (larval) body plan is transformed into the juvenile anatomical pattern. Generally, any anatomical remodeling between opposing life-history periods can be considered a form of metamorphosis. These changes can be rapid and cataclysmic, or can proceed gradually, depending on the particular developmental basis for the juvenile body plan within the body of the larva. While much is known about the metamorphosis of insects and amphibians the majority of animal phyla are relatively understudied. Perhaps the most important direction of new research will focus on the complex life histories of marine invertebrates that will yield new model systems and insight into the study of metamorphosis.

Overall, the subject of metamorphosis of marine invertebrate larvae has typically focused on 4 main avenues of research: (1) describing naturally occurring stimuli that induce metamorphosis in competent larvae, (2) isolation of cell signaling molecules involved in the transduction of metamorphosis, (3) describing the cellular mechanisms of tissue remodeling at metamorphosis, and (4) comparing the previous data in a phylogenetic and ecological context.

Kohtaro Tanaka

Metamorphosis is a post-embryonic event in which a particular stage of an organism undergoes a radical morphological change, thereby accommodating the functional and ecological demands of the next stage. The morphology and physiology of each stage (pre-metamorphic and post-metamorphic) is highly adapted to the function and ecology of that stage. According to this view, transitional, post-embryonic developmental stages such as planulae, ctenophore larvae, some fish larvae and some crustacean larvae are not morphologically distinct enough from the subsequent stage to be considered metamorphic. On the other hand, larval stages of some hemimetabolous insects, such as dragonflies and mayflies, would fit this definition. In organisms with metamorphosis, morphological disparity between 2 stages is usually drastic, in that specialized structures developed for the preceding stage have to be discarded or completely remodeled, and neural wiring extensively modified to accommodate new structures and behaviors. The transition is not limited to a non-reproductive to a reproductive stage, as exemplified by hypermetamorphoses and heteromorphoses in insects.

John Youson

Metamorphosis is an abrupt change in the form or the structure of an organism during post-embryonic development. It occurs at the end of a larval growth phase. Another condition is that the larva and the postmetamorphic individuals do not look alike (as they do in direct development). The process is triggered by an external (environmental) and/or internal (hormonal) cue. It usually involves the expression of separate genotypes from those that control sexual maturation. Fish with a metamorphosis are lampreys, eels, and flatfishes (for example flounder and sole). From my point of view, the majority of fishes do not have a true metamorphosis. I do not consider parr-smolt transformation in salmonids as a metamorphosis. However, many non-metamorphic fish species have transitional structures, such as the external gills that lungfish larvae lose in their transition to the adult.

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