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Re-semblance and re-evolution: Paramorphism and semiotic co-option may explain the re-evolution of similar phenotypes

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Abstract. The independent emergence of similar features in phylogenetically non-allied groups of organisms has usually been explained as the result of similar selection pressures particular to specific environments. This explanation has been more or less helpful in elucidating convergent resemblances among organisms since the times of Darwin. Nevertheless, intensive research has brought new knowledge on the emergence of structural similarity among organisms, especially during the last two decades. We now have manifold evidence of the phenomena of evolutionary re-entries or re-evolution, which happens when a particular character present in one organic taxon also appears in another taxon which does not share an immediate ancestry. This is not the re-appearance of the same character, but rather of a similar one. Here I propose a model of threefold origin of similar phenotypic features in unrelated organisms stemming from intrinsic, extrinsic and semiosic causation. It is suggested that neither externalist nor internalist explanations *per se*, nor any combination thereof, are sufficient to cover all the manifold instances of character re-evolution. There is also a special group of resemblances that consists of what is originated, shaped, and retained in evolution due to meaning attributed to them by particular organic subjects. These cases cannot be fully understood without inviting a biosemiotic approach. Integrating Uexküll's theory of meaning with the recent evolutionary developmental perspective could complete our understanding of phenotypic re-evolution.

Introduction

This paper focuses on the emergence of biological similarities within the context of recent knowledge on the re-evolution of similar phenotypes: a phenomenon frequently reported from diverse investigations in different fields of biology (for example, Wake 1991, 1996, 1999; Meyer 1999; Whiting *et al.* 2003). In the last hundred years, different concepts treating the emergence of similar phenotypes have appeared: for example, homomorphy (Nowikoff 1935), homologous series in variation (Vavilov 1922), homoiology (Plate 1922; Hennig 1950, 1966), latent homology (de Beer 1971), underlying synapomorphy (Saether 1979), and evolutionary convergence (Conway Morris 2003, 2010). These concepts convergently emerged from different biological fields such as morphology, development, taxonomy, variation study, paleontology etc. All these concepts, regardless of their exact definitions, point towards the fact that even when working in different paradigmatic attitudes and periods, biologists have sought the concealed, but common basis of superficial similarity (Kleisner 2008a).

The independent emergence of similar features in phylogenetically non-related groups has usually been explained either as a result of sharing the same evolutionary constraints in different evolutionary lineages or by a similarity of selection pressures particular to certain environments. This traditional explanation has been used more or less successfully for the last 150 years. Nevertheless, intensive research has brought new knowledge on the emergence of structural similarity among organisms especially during the last two decades. There is manifold evidence of a phenomenon called *evolutionary re-entries* or *re-evolution.* The word re-entry does not mean the return of an initial state; rather we are dealing with the re-evolution (or re-entry) of something similar but certainly not the same. However, some results also show the possibility of re-evolution of whole organs that appear almost identical to ancestral ones, such as the loss and re-appearance of wings in *Phasmatodea* (Whiting *et al.* 2003).

Here I argue that some cases of superficial similarity may easily re-evolve because they are only seemingly superficial, and stem from common genetic and/or organizational underpinnings. These may be latent in the genomes of an organism, together with the “know how” to re-call them into service. The sharing of these evolutionarily latent elements should increase the probability that similar phenotypic features will repeatedly pop up in the course of evolution. In a further step, the externalized phenotypic traits of an organism may acquire a meaningful role for other organisms, and thus come to be shaped by evolution according to the parameters of their Umwelten. Features that show some genuine degree of similarity will more likely be classified as having a similar meaning, and will also be much easier to co-opt for a particular biological role. Similarities of traits that carry a particular meaning imply similarities in the Umwelten of the organisms to which the sign has been addressed.

Externalist and internalist explanations of the independent emergence of similarity

An often proposed explanation for the evolutionary re-appearance of similar phenotypes is the existence of latent developmental programs that are only occasionally re-activated. Such a re-activation of latently preserved developmental cues in distantly related groups may be responsible for patterns of similarities that are not derived from commonality of descent. Nowadays, this internalist way of reasoning is popular among adherents of Evo-Devo (*Evolutionary Developmental Biology*). A quite opposite situation — that is, various externalist explanations — is pervasive amongst paleontologists. According to this view, the re-evolution of similar traits in phylogenetically non-related groups is effectively controlled by climatic and environmental circumstances (Martin, Meehan 2005). Accordingly, non- or distantly related organisms that show striking similarity in phenotype are termed *ecomorphs* (*ecological morphotypes, sensu* Williams 1972).

Ecomorphs usually evolve under similar ecological and/or different climatic conditions in different geological periods (for example, the re-evolution of saber-tooth forms among non-allied groups of Cenozoic mammals). Ecomorphs from different geological layers usually belong to distantly related groups; however some phylogenetic relationship remains, and this puts the question of whether their phenotypic resemblances should be considered *convergences* or *parallelisms*. Moreover, one may ask whether a strict distinction is meaningful in such cases. *Parallelism* presumes the existence of some remote common ancestor. This population gives rise to different evolutionary lineages, which then further split, only to have some similar phenotypic features emerge in descendant groups due to the persistence of homologous genetic/developmental mechanisms. In principle, *convergence* does not presuppose the existence of any common ancestor: structures are generated *de novo* in non-related organisms. However, if we consider the monophyletic origin of all life on our planet, the distinction between parallelism and convergence is just a matter of convention because some common ancestor is simply always there, however remote (see Willmer 2003).

Nowadays, the term *convergence* or *convergent evolution* refers to similarities in phenotype that have evolved in response to similar selection pressures acting in particular environments, for example, hydrodynamic body shapes of dolphins, sharks, and ichthyosaurs. Convergence in body architecture is explained as an adaptation for life in an aquatic environment. Although this is a textbook-like example of convergence, we may ask whether the hydrodynamic adaptation emerged in all groups as a response to environmental selection. One may alternatively suppose that not only external forces but also internal cues may have played an important role in the evolution of this adaptation; consider, for instance, the hypothetical re-activation of genetic complexes inherited from a common aquatic ancestor of the mentioned groups and latently preserved during the course of evolution. The notion of “genetic and developmental latency” is nothing uncommon in contemporary biological thought (see, for example, Stone, Hall 2004; Sanetra *et al.* 2005; Willmer 2003).

Although the re-evolution of phenotypes, that is, the independent evolutionary emergence of similar phenotypic features in unrelated life forms, is a frequently reported phenomenon, its understanding is still insufficient. This situation is probably caused by the dominance of externalist approaches stemming from the ecological perspective wherein the phenotypic features of organisms are understood as a result of selective pressures in particular environmental conditions. In contrast, I maintain the conviction that parallel re-appearance of similar phenotypic features during evolution should not be explained only as the actions of extra-organismal causes, but also from the perspective of internal causation particular to every organism.

Paramorphism meets convergence

The principle of paramorphism represents a very promising internalist explanation for how parallel similarities come into existence. This is mainly because it connects genetic and morphological processes under a common conceptual frame. The hypotheses of axis paramorphism suggests that the re-expression of the duplicated genes from the main body axis into lateral body outgrowths may cause a certain similarity in the arrangement of the body and its appendages, as well as similarities amongst the appendages of distantly related animal species (Minelli 2000, 2002; Oakley 2003). Thanks to the modular nature of organic beings, not only genes but also the cassettes of genes, developmental pathways, and finally all semi-individualized modules at every level of organization might be wholly or partially duplicated, co-opted, exapted, or modified in various degrees. The engagement of all these processes in evolution may lead to the possibility of re-using, or of the using of similar (partially changed), developmental modules to produce a similarity of form. The perceived similarities of organisms may provide some information about the degree of modification of processes and modules that re-constitute the organisms.

In the same way in which two copies of duplicated genes, that is, paralogs, can be recruited for different roles, we may assume similar processes at the level of body parts (paramorphs). Minelli's hypothesis of "axis paramorphism" thus considers body appendages such as arthropod or vertebrate limbs and chordate tails, as evolutionary divergent duplicates of the main body axis. As such, these lateral and caudal outgrowths may have convergently evolved from ancestors having no patterned appendages.

Generally, natural conventions, that is, sets of rules among organismic constituents established in an evolutionary past, may be reinvented for the actual need of present or future situations. As Simon Conway Morris remind us "[…] it is sometimes forgotten that the main principle of evolution, beyond selection and adaptation, is not the drawing of new plans but relying on the tried and trusted building blocks of organic architecture" (Conway Morris 2003: 8). In the organism-centered perspective, axis paramorphism may be re-interpreted in such a way that an organism re-used the existent patterning "know-how" of the main body axis to introduce a similar order to its lateral outgrowth. This has consequences for our understanding of superficial similarity of organisms. For example, it explains why the zebra has its stripes oriented transversally to the main body axis whilst its legs have stripes that are oriented crosswise to the main body pattern but again transversally to the proximo-distal axis of the appendage. Again, the coloration simply follows the same order as the segmental patterning of main body axis and appendages; both of which are transverse on the longitudinal axis. At the same time it explains why the legs in both zebra and okapi, for instance, are patterned crosswise to the longitudinal axis of the leg (see Fig. 1). Eventually, it provides the only reasonable explanation why the stripes (if present) of tails and legs in the vast majority of mammals, tend to be oriented orthogonally to the proximo-distal axis of these bodily extremities. This is simply because the tails and legs are axis paramorphs of the main body axis.

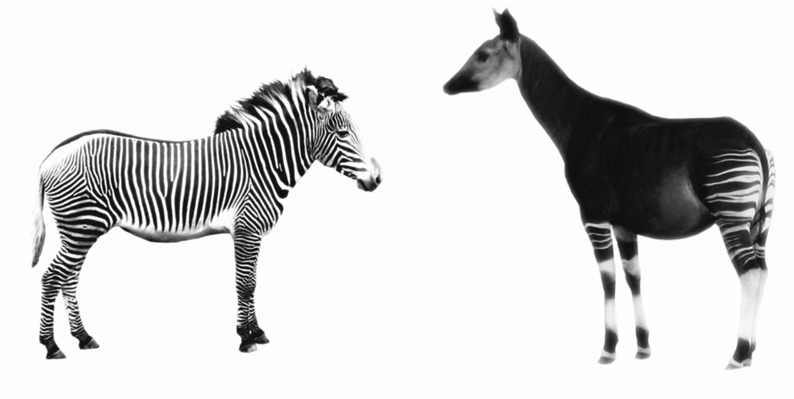

Figure 1. Left: Grévy's Zebra (*Equus grevyi*); *Right:* Okapi (*Okapia johnstoni*). The relationships in coloration between the legs and trunk most likely reflects the organizational set up established very early in animal evolution.

Hornet's stripes and fungus' hyphes

Various stripes transversal to the longitudinal axis of an animal will presumably represent a very simple surface color pattern. We find such coloration along the various, often distantly related, arthropod clades. This universality of occurrence may imply that such a basic pattern is for some practical reason readily established during ontogenesis. In the case of abdominal coloration (that is, the main body axis), a black and yellow pigment pattern is established according to the compartmental boundary set by an early expression of the segmentation genes. Interestingly, this compartmental boundary may bear a meaningful signal not only for the developing insect embryo *per se*, but also for an alien organism such as a fungus.

An interesting example of the binding collaboration between the fungus and wasps is well described by Ishay and Shmuelson (1994). The Oriental hornet (*Vespa orientalis*) has a conspicuous abdominal pattern consisting of brown and yellow stripes oriented transversally to the main body axis. The cuticle of the yellow stripes differs structurally from the cuticle of the brown stripes. As a result of this difference, the yellow stripes contain fungal spores interwoven by fungal hyphes that contain a yellow pigment and are thus responsible for the yellow color. The mutualism between the fungus and the wasp brings advantage to both sides. Hornets likely provide nutrients from haemolymph, protection against direct insolation, optimal temperature and high humidity in the nests; whilst the fungus gives its metabolits (toxins, antibiotics). The fungus also provides pigment that on one hand works as a conspicuous signal in warning coloration, and on other hand, acts as an electric element picking up light and heat energy (thermoluminiscence; Ishay, Shmuelson 1994).

This evokes a suspicion that the coloration of wasps was genuinely in the service of thermoregulation and only later co-opted for a semantic warning function due to the natural conspicuousness caused by the contrast of alternating stripes with cuticular dark pigment (melanin) and fungal yellow pigment.

Interpretational polymodality of animal color patterns

It would probably be a gross simplification to understand animal coloration as always having a single function. More likely, the various animal color patterns acquire two or more, often contrasting, roles. The number of which will depend upon the context in which the signal is situated and the diversity of receivers. Considering the number of receivers two possibilities are imaginable: a particular surface pattern addresses only one kind of receiver with identical or similar perceptional abilities, for example, a potential mating partner or a particular predator species. Or, alternatively, the surface appearance is addressed to several receivers with different sensorial perception, each of them appreciating different aspects of the surface pattern as a signal. In other words, the surface appearance of an animal might, in the most extreme cases, be perceived within the single Umwelt of a particular species, or its different aspects can be regarded as meaningful within each of several different Umwelten of the representatives of different clades. Dependent upon the actual context, the single surface pattern may stand for absolutely opposing signals with no regard to whether they are being perceived within either a specific Umwelt of an animal or different Umwelten of unrelated lifeforms.

The first experimental evidence of the existence of polymodality of animal pattern coloration comes from Tullberg *et al.* (2005): the authors supported the hypothesis that some color pattern may combine *warning coloration* at a close range with *crypsis* at a longer range. In this study, the images of larva of the swallowtail butterfly (*Papilio machaon*) were manipulated from their natural state to be more cryptic and more conspicuous in order to measure and compare detection time by human observers. In comparing the detection time of three types of images taken at different distances, Tullberg and colleagues concluded that the natural coloration is *not* maximally conspicuous at longer distances as well as maximally cryptic at short distance.

In spite of the fact that these experiments were carefully performed, and "conspicuousness" was understood as a term relative to different human subjects, the 'readers' were always human subjects with their human experience. Perception and interpretation within the Umwelt of one species may be qualitatively different from that of the other. Sometimes, differences in reactivity to the same stimuli in different species of organisms are caused by differences of sensorial physiology; the one is not, however, limited to the other. The main reason for this suggestion is that there may be serious differences in pattern recognition and thus different “concepts” for what is cryptic or conspicuous. Very simply, very different living beings show very distinct experiencing of the world. These experienced worldly relationships, historically established during the course of evolution, are what eventually determine the sensorial equipment (and setup) of organisms, not vice versa.

However vague it may sound, being aware of all this should prevent us from making premature conclusions such as, for instance, that two species of organisms have the same experiencing of the same visual event because the same photoreceptors of their retina are excited at the same time during experimental exposition. The reactivity of receptors and the experiencing of an organism are different things.

Conclusions

Traditionally, parallelism presupposes the existence of shared developmental underpinnings and parallel phenotypes thus result from intrinsic causation. In contrast, convergence refers to absolutely different developmental and ancestral precursors evolving similar characters, and presumes that environmental forces or extrinsic causation does the job. Nevertheless, a sharp distinction between similarities externally caused (convergence) and those internally caused (parallelism, homology) seems to be rather unwarranted under the light of current biological knowledge. It is also often difficult to differentiate between these two categories in a practical phylogenetic context (Diogo 2005). Phenomena such as axis paramorphism and latent homology may represent a prospective cause of the appearance of similar features in distantly related species or even unrelated phyla. Furthermore, the gap between the externalist and internalist perspectives could be bridged by recent knowledge that particular environmental cues were evolutionarily co-opted as developmental signals and fully integrated into the ontogenesis of particular lineages. Hormones represent such a proxy between development and environment. Some hormones were originally molecules present in the environment that were repeatedly adopted for signaling within organisms. For instance, the thyroid hormone was most likely recruited independently for the control of metamorphosis in different animal taxa, for example, echinoderms and sea squirts (Heyland *et al.* 2004, 2005). Perhaps this may also explain other unexpected similarities among phylogenetically distant taxa.

The problem of resemblance and its evolution is not fully explicable from either an externalist or an internalist position. Even when combined, they may explain some instances but certainly not all. Therefore, I suggest that explanations of resemblances as they appear within living beings should be approached from at least three perspectives: internalist, externalist and biosemiotic (or interpretative) which takes Umwelt-specific interpretations into account as a force of causation (Uexküll 1921; Portmann 1960; Maran 2007, 2003; Kleisner 2008b). Any phenotypic structure could be semiotically co-opted, acquiring specific meaning in the Umwelt of a particular species of organisms, and then further selected and shaped within the constraints given by the properties of the receiver's Umwelt (see Maran, Kleisner 2010).[1]

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Сходство и ре-эволюция: параморфизм и семиотическая кооптация могут объяснить ре-эволюцию сходных фенотипов

Возникновение сходных признаков между филогенетически не связанными между собой группами организмов обычно объясняли сходными селекционными воздействиями на специфическую для каждой из этих групп среду обитания. Это объяснение, начиная с Дарвина, оказалось более или менее подходящим для обоснования конвергентных сходств между организмами. Тем не менее, более углубленные исследования — особенно последних двух десятилетий — привнесли новые знания о структурном сходстве между организмами. У нас теперь имеется множество доказательств ре-эволюции, которая происходит, если какой-нибудь конкретный признак, проявляющийся в одном органическом таксоне, возникает и в другом таксоне, который не имеет с первым непосредственных общих предшественников. Это означает не возрождение того же признака, а скорее возникновение сходного признака. В статье я предлагаю трехчастную модель происхождения сходных филогенетических признаков у не связанных между собой организмов, которое происходит по внутренним, внешним и «семиозисным» причинам. Мне представляется, что как экстерналистские, так и интерналистские объяснения *per se* и их комбинации не являются достаточными для объяснения разнообразных случаев ре-эволюции признаков. Существует еще и особая группа сходств, которая состоит из того, что в эволюции унаследовано, сформировано и сохранено вследствие значений, приданных им конкретными органическими субъектами. Эти случаи невозможно полностью понять, не применив биосемиотический подход. Соединение теории значения Юксюолля с современными эволюционными теориями развития могло бы дополнить наше понимание фенотипической ре-эволюции.

Sarnasus ja taasteke: paramorfism ja semiootiline kooptsioon võivad põhjendada sarnaste fenotüüpide taasteket

Sarnaste tunnuste tekkimist fülogeneetiliselt mitteseotud organismide gruppide vahel on tavaliselt põhjendatud spetsiifilistele keskkondadele iseloomulike sarnaste valikusurvetega. See seletus on Darwini käsitlusest peale osutunud enamvähem kohaseks organismidevaheliste konvergentsete sarnasuste põhjendamisel. Siiski, eriti paari viimase aastakümne jooksul tehtud tõhusad uurimused on toonud uusi teadmisi struktuuraalsete sarnasuste kohta organismide vahel. Meil on nüüd hulk tõendeid evolutsiooniliste taas-ilmumiste kohta, mis tekivad, kui mingi konkreetne tunnus, mis esineb ühes orgaanilises taksonis, tekib ka teises taksonis, mis ei oma esimesega vahetuid ühiseellasi. See ei tähenda mitte sama, vaid pigem sarnase tunnuse taasilmumist. Käesolevaga esitan ma omavahel mitteseotud organismidel esinevate sarnaste fülogeneetiliste tunnuste päritolu kolmeosalise mudeli, mis lähtub sisemistest, välistest ja semioosilistest põhjustest. Artiklis väidetakse, et ei eksternalistlikud ega internalistlikud seletused *per se* ega nende kombinatsioonid pole piisavad seletamaks tunnuse taastekke mitmekesiseid juhtumeid. Eksisteerib ka spetsiaalne rühm sarnasusi, mis koosneb sellest, mis on evolutsioonis päritud, vormitud ja säilitatud tähenduste tõttu, mida on neile konkreetsete orgaaniliste subjektide poolt omistatud. Neid juhtumeid pole võimalik täielikult mõista võtmata kasutusele biosemiootilist lähenemist. Uexkülli tähenduseteooria lõimimine viimase aja evolutsiooniliste arenguteooriatega võiks täiendada meie arusaamu fenotüübilisest taastekkest.