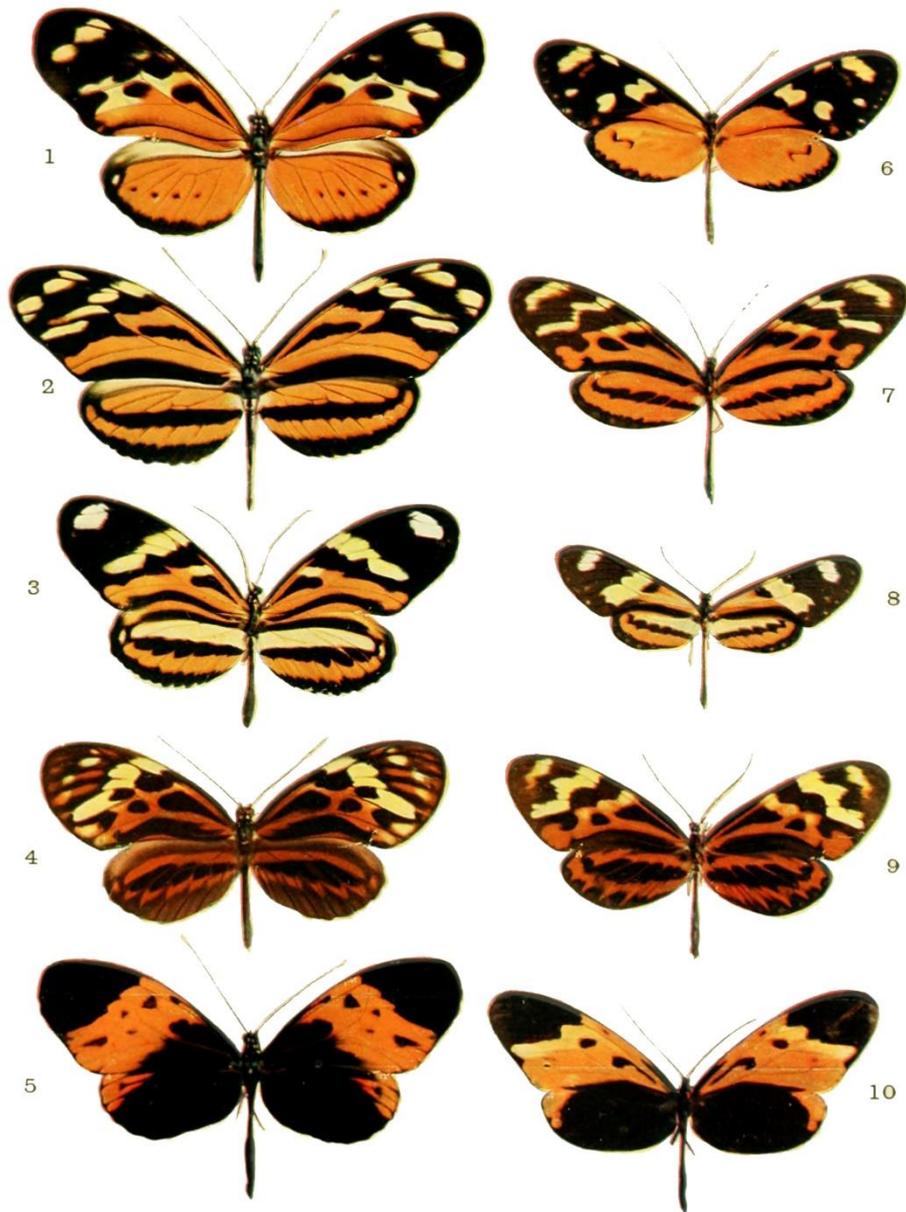


Mimicry in butterflies



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Abstract

Mimicry is found in a lot of organisms including butterflies. This essay focusses on two specific genusgenera, namely: *Heliconius* and *Papilio*. The species of the *Heliconius* genus possess Mullerian mimicry. And on the other hand the species of the *Papilio* genus possess Batesian mimicry. With Mullerian mimicry two poisonous species use the same wing pattern. With Batesian mimicry a harmless species mimics a poisonous species. Both species use wing pattern as a warning colour for predators. The main question of this essay is: Does mimicry develop in different ways in *Heliconius* and *Papilio*? The genetic basis for mimicry of 6 *Heliconius* species is compared in this essay. In *Heliconius numata* supergene P control the wing pattern. In most *Heliconius* species the optix transcription factor prefigures the variety of red wing elements. Cortex controls the white/yellow pattern. Small differences are found between the species of the *Heliconius* genus. In *Heliconius hecale* and *Heliconius ismenius* a multilocus architecture controls wing patterning. In the *Papilio* genus, mimicry is only seen in females, causing non-mimetic males. In *Papilio dardanus* the phenotypic variation is mostly due to a single Mendelian locus, named *H. H* co-segregated with transcription factor invected and its paralogue engrailed. In *Papilio polytes*, a single locus called *doublesex* determines the wing pattern. The selection pressures are different for both genera, due to the Mullerian/Batesian aspects of the mimicry: in *Heliconius* there is a strong selection on mimicry, while in *Papilio* the selection depends on the abundance of the model species. For the *Heliconius* species, it is better when there are more mimics present, while it is better for the *Papilio* species when less mimics are around. Polymorphic mimicry is found within both genera. But the genes controlling the wing-pattern differ between the *Heliconius* genus and the *Papilio* genus. Neither there is found one locus or gene that influences wing-pattern within one of the genera. Concluding mimicry in different species diverges from each other and the data suggests mimicry has evolved multiple times in different genes in different species.

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Introduction

Warning colouration is seen a lot in nature. Warning colours are bright and conspicuous patterns. For a lot of animals it is used as a mechanism of protection against predators. The bright colours or the pattern gives predators a signal, that an organism is poisonous. The predator will learn to recognize those patterns and therefore avoid these preys. For example, all people know that bees and wasps can sting, so the most humans try to avoid them. Humans recognize the yellow and black colour pattern and therefore know it is a bee or wasp. In butterflies the warning colouration is seen in wing pattern and bright colours. The ecological role of wing pattern is well studied, as well as the selection that causes the variation (Huber et al., 2015)

Mimicry is also a well-known phenomenon in nature. The definition of mimicry for biology is: “the resemblance of one organism to another or to an object in its surroundings for concealment and protection from predators” (freedictionary.nl). It is seen in a wide range of organisms, especially in insects and plants. It is a complex adaptive trait, and therefore it is an interesting subject for research. The aim of evolutionary biology is to understand how some traits evolved and which genetic changes cause adaptation. The study of mimicry contributes to the knowledge of evolution and adaptation. There are 3 types known of mimicry with colouration. Namely Batesian mimicry, Mullerian mimicry and Mertensian mimicry. When there is Batesian mimicry a dangerous species, with a certain warning system, is mimicked by a harmless species (Bates, 1862). An example of Batesian mimicry are hoverflies (*Syrphidae*). These organism look like bees (*Anthophila*) and wasps (*Apocrita*) but hoverflies are harmless while bees and wasps can sting other organisms. The hoverflies copy the yellow and black pattern, which functions as the warning sytem, of the bees and wasp for protection against predators. With Mullerian mimicry two or more unrelated species that are poisonous use the same warning systems, such as the same pattern or bright colours. The predator has to learn which species to avoid. If both have the same warning system, the preys share the costs of creating a warning system and educating the predators. This is seen in butterflies of the genus *Heliconius*, as two species that live closely to each other look very similar. Mertensian mimicry is less known and less common. When there is Mertensian mimicry a harmless species is mimicked by a deadly species. It is beneficial for a deadly species to mimic a harmless of a less toxic species, in order to have a bigger chance of survival of an individual. If a species is deadly the predator cannot learn, because the predator dies. So it is beneficial for an individual to mimic harmless species, so there are more individuals with the same pattern and with a bigger group the change of being predated reduces. An example of Mertensian mimicry are coral snakes. Scarlet king snakes (*Lampropeltis elapsoides*) a non-venomous species is mimicked by the Eastern coral snake (*Micrurus fulvius*).

Mimicry in warning colours is seen in many butterfly species. Butterflies are used as model organisms for studying the genetics of mimicry and speciation. Therefore there is a lot known about the way mimicry is possessed in those species. Two specific genus are mostly used for these studies, namely the *Heliconius* species and the *Papilio* species. On that account this essay will focus on these two species. The *Heliconius* butterflies possess Mullerian mimicry and the *Papilio* butterflies possess Batesian mimicry.

This essay focusses on the differences and the similarities of mimicry in both species, especially of the differences and similarities in the genetic architecture. This will be done in order to conclude if mimicry evolved in the same way in both genera. This might also reveal more about the arising of mimicry in general in Lepidoptera. So this essay can contribute to understand the processes that give rise to novel traits. Therefore, the warning colours, mimicry, genetic basics of wing pattern and mimicry and

speciation in both species will be discussed. This leads to the question: Does mimicry develop in different ways in *Heliconius* and *Papilio*?

1. *Heliconius* butterflies

1.1 Introducing the species

The *Heliconius* genus is part of the *Nymphalidae* family and is commonly known as the longwings. *Heliconius* butterflies live in tropical and sub-tropical areas (Merrill et al., 2015). Many species of this genus possess mimicry and that is why this species is well-studied. *Heliconius* butterflies are toxic for predators and the wing colour pattern gives notice of their toxicity (Huber et al., 2015). Species within the *Heliconius* genus frequently share the same wing patterns, and therefore have similar signals of toxicity and thus enjoy survival benefits (Huber et al., 2015). Most species of the genus are found within the Amazon (Merrill et al., 2015). The following paragraphs focus on some specific species from the genus, namely: *H. numata*, *H. hecale*, *H. ismenius*, *H. erato*, *H. melpone* and *H. mepomone*.

1.2 Warning colours

The bright colour patches of *Heliconius* wings serve as warnings to predators, showing of the unpalatable nature of the butterflies (Wilts et al., 2017). The warning colours of the *Heliconius* genus consist of a limited number of stereotypical patterns. A “tiger pattern” is found in multiple species like *H. numata*, *H. hecale* and *H. ismenius*. A tiger pattern is a specific pattern with black and orange stripes. In *Heliconius* warning signals influence wing-pattern elements (Brown, 1981), colour shade (Sweeney et al., 2002) and wing shape (Jones et al., 2013).

Wing colouration has multiple functions simultaneously. That causes a conflict between the expressions of the different ways of signalling. A possible way to overcome this problem is spatially or dynamically separation of the colour signals. The ventral wing side is involved in predator avoidance, because most butterflies fold their wings above their body, and then only the ventral sides are visible (Wilts et al., 2017).

Wing pattern is also used for mate recognition and therefore there is a conflict between mimicry and interspecific communication (Estrada and Jiggins, 2008). In order to reproduce, the butterflies must be able to distinguish between their own species and other species (Wilts et al., 2017). When a female mimics a species that looks totally different from her own species, males will not recognize her anymore and she will not be able to reproduce.

1.3 Mimicry

The mimicry that evolved in the *Heliconius* genus is mullerian mimicry. Divergent lineages have repeatedly evolved to the same bright wing patterns. The selection regimes are heavily influenced by the distribution and abundance of notable signals used by local prey groups. The most *Heliconius* species show different wing patterns at different geographic regions. The populations are mostly fixed for a certain warning pattern, but that does not occur in hybrid zones. As a response to directional selection the geographic races show one well-defended pattern in each locality (Brown, 1981). On the other hand in *H. numata*, a polymorphism is found, the populations mimic multiple tiger-patterned species. It is driven by variation in the abundance of alternative tiger-patterned mimicry rings, which causes a balance in selection at a regional level (Joron et al., 1999). The selection coefficients favouring mimicry are very high, showing there is an intense selection for mimicry in *Heliconius* (Merrill et al., 2015). *Heliconius* butterflies are often found in mimicry rings. One species is able to join multiple mimicry rings (Brown, 1979).

1.4 Genetics

The genetics play an important role in wing pattern and colouration. Therefore it is well studied to understand which genes cause the colouration.

Four of the twenty-one chromosomes contribute mostly to the diversification of the colour patterns in distinct *Heliconius* species, although there are several minor loci detected (Huber et al., 2015). Two genes of those have been identified. The first is *WntA* signalling ligand that is a putative morphogen that determines the size and position of melanic patterns in the forewing median region (Huber et al., 2015). The other gene is a transcription factor, *optix*, which prefigures the variety of red wing elements controlled by a cluster of loci. At two other loci, the genes for the white/yellow pattern are found called *cortex*. *K* controls the white/yellow switch in *H. mepomone* and *H. cydno*. In *H. erato* the *CR* locus in the same region controls similar pattern variation (Huber et al., 2015). More small differences are found between the species of the *Heliconius* genus. "For instance, the red/yellow forewing and switch is caused by variation in a single locus, *D*, in *H. erato*, but by the interaction of two unlinked loci, *B* and *N*, in *H. melpone*" (Sheppard et al., 1985).

H. numata shows a different genetics architecture for wing pattern than the other species of the *Heliconius* genus. The *H. numata* butterflies have wings with a mosaic of black, orange and white/yellow elements, also called a "tiger pattern". The genetic basis causing in the variation in these pattern is different. A single locus, *P*, controls the wing pattern variation in this species, *P* is a supergene. A supergene is "a genetic architecture involving multiple linked functional genetic elements that allows switching between discrete, complex phenotypes maintained in a stable local polymorphism" (Thompson & Jiggins, 2014). The position of supergene *P* is homologous to the *N* locus of *H. melpone* (Joron et al., 2006).

A study of Huber et al. (2015) in the silvaniform clade on whether the genetic architecture of colour pattern variation is associated with the phenotypic variation itself or with the selection regime shaping it, found that *H. hecale* and *H. ismenius* have a multilocus architecture for the control of wing patterning. The results show that the multilocus architecture of wing pattern variation is spread out on multiple chromosomes. The study also confirms that most species of the genus have that feature. The architecture for wing colour is largely homologous in most *Heliconius* species, but the gene interactions differ between the species and their detection depends on individual allele effects.

The multilocus architecture of the silvaniform species differs from the single-locus architecture controlling the mimicry in *H. numata*. This gives the indication that that de supergene *P* uniquely evolved in the *H. numata* lineage from a multilocus architecture (Huber et al., 2015). Both *H. hecale* and *H. ismenius* have a "tiger pattern" looking very similar to the "tiger pattern" of *H. numata*, so a specific wing pattern is not associated with a single-locus architecture.

1.5 Speciation

Speciation in *Heliconius* butterflies is well-studied and therefore that will be the focus of this paragraph. Time-calibrated phylogeny point out that much of the diversity in *Heliconius* species occurred in the Pleistocene (Merrill et al., 2015). It is most likely that speciation happened in parapatry and after the species had diverged significantly, the process is completed in sympatry (Mallet et al., 1998). There is no clear definition of a species found, because there is no clear concept to distinguish

between species and lower taxonomic levels (Merrill et al., 2015). Many populations who only differ in wing-pattern are considered as one species, because in transition zones they form intermediate forms (Merrill et al., 2015). Gene flow plays an important role in speciation and that makes it hard to make an accurate phylogenetic tree. For example, *H. melpomene* is for 40% of its genome more related to *H. cydno*, which occurs in the same area, as it is with *H. melpomene* from French Guiana (Martin et al., 2013). The speciation happened according to the islands-of-divergence model, which means genomic divergence begins at a few narrow regions, containing key loci, under selection, and these islands of divergence grow when speciation continues. In the end the whole genomes may differ from each other (Merrill et al., 2015). In wing pattern variation only a few loci differ. This differentiation under strong selection is a form of reproductive isolation. Divergence in colour pattern plays a major role in *Heliconius* speciation, because selection may limit gene flow (Merrill et al., 2015). Hybrids between species have a lower survival rate.

The species from the melopmene-silvaniform clade often have polyphyletic mimetic patterns and might actually hybridize in the wild (Dasmahpatra, 2012). Therefore it is hard to distinguish between those species. Normally it is one species when they reproduce fertile offspring in the wild. But that definition is not enough to distinguish the species of the melopmene-silvaniform clade.

2. *Papilio* butterflies

2.1 Introducing species

The genus *Papilio* is part of the swallowtail butterfly family, also called *Papilionidae*. It is a species rich genus and therefore the species of the genus can be found all over the world. The butterflies live on every continent except for Antarctica, but the majority can be found in tropical areas. The butterflies are harmless for predators. Some species mimic poisonous species as a protection mechanism. The evolution of divergent mimetic morphs in the species of the genus are often used to study complex adaptive traits (Davis, 2009). The *Papilio polytes* holds a special place in the study of mimicry, since Alfred Russel Wallace discovered the female-limited mimetic polymorphism in *Papilio polytes*. The following paragraph focuses on some specific species of the genus, namely: *Papilio dardanus*, *Papilio polytes*, *Papilio memnon* and *Papilio glaucus*.

2.2 Warning colours

Warning colours occur in the populations of *Papilio* butterflies, even though they are not poisonous. The species of the genus can look totally different, and many different colours and pattern can be found within this genus. Because the species is not poisonous, their own colour pattern does not contain warning colours. That is why they have to mimic the warning colour of a poisonous species, to look like they are toxic.

2.3 Mimicry

The wing pattern and colouration in the *Papilio* genus evolved as Batesian mimicry. This type of mimicry is very common, but mimetic polymorphism is relatively rare. The *Papilio* genus is one of the best studied cases with mimetic polymorphism (Joron & Mallet, 1998). The reason why there are not many species with mimetic polymorphisms is not exactly known. Only some suggestions are done. It could be that there is a strong selection on mimics for one specific model species. It could also be that a very peculiar genetic architecture is required in order to get a mimetic polymorphism, a supergene, and that is found a very few species. The mimicked species has the possibility to escape it mimic by evolving a new warning pattern, but that would not work because the mutants will attract new mimics, and rare variant will be disfavoured. Recently it is shown that cyclical coevolution of model species and its mimic is possible if interspecific interactions are stronger than intraspecific interactions, but in nature the intraspecific effect is mostly stronger than the interspecific effect. (Joron & Mallet, 1998). When the interactions within one species are very strong, the mimic and model will not interact, and therefore not mimic each other, so cyclical evolution will not occur. Escaping the model is possible in two ways: one way is mimicking another more protected mimic or evolving a wing pattern out of the league of the mimic.

There are multiple mimics found within the population of *Papilio dardanus*, which means there is a polymorphism. Balancing selection maintains polymorphism (Timmermans et al., 2014). Mimicry is only seen in the females, who differ a lot from the males (Timmermans et al., 2014). The males cannot possess mimicry. In a lot of *Papilio* species the mimicry is limited to the females. There are at least 14 wing pattern morphs found in *Papilio dardanus*. In de *Papilio dardanus* from Madagascar the females look a lot like males and are non-mimetic.

Papilio memnom butterflies mimic unpalatable models like *Atrophaneura polyeuctes*. The males are non-mimetic, and non-mimetic females are found within the population as well. The *Papilio polytes* exhibits a similar pattern of polymorphism as *Papilio memnom* (Iijima et al., 2018).

Papilio glaucus has two forms of females, a black type and a yellow type. The proportions black and yellow females differs between the populations. For example in Canada all the *Papilio* butterflies are yellow, but in regions where the model *Battus philenor* is present, the black form occurs a lot. Both forms compete against each other that makes it interesting to figure out why both forms still live next to each other. It seems like the frequency of the black form is controlled by the abundance of *Battus philenor*. When the mimicking species becomes too common, the hiding effect gets lost, because predators would soon learn to ignore the colouration of the preys (Joron & Mallet, 1998). For the unpalatable species it is better to be common, because then their wing-pattern is recognized. Therefore it is expected that these species are monomorphic (Joron & Mallet, 1998). Another explanation might be migration, in areas with such a great abundance of the model, the yellow form is not expected anymore, but due to migration also the yellow butterflies occur there (Clarke & Sheppard, 1962b).

2.4 Genetics

Creating mimetic polymorphism requires tightly linked new colour genes, and the genes have to be linked from the beginning. Otherwise recombination will destroy the adaptive polymorphism before it is stabilized. Probably most genetic architecture are not fitting and therefore monomorphic mimicry had developed in most species (Joron & Mallet, 1998).

The phenotypic variation in *Papilio dardanus* is mostly due to a single Mendelian locus, termed *H*. "The various alleles exhibit a dominance hierarchy such that most of them are inherited without producing intermediate phenotypes" (Clarke & Sheppard, 1960a. Clarke & Sheppard, 1962a. Clarke & Sheppard, 1960b. Clarke & Sheppard, 1959). Crossing of different subspecies results in partial breakdown of the dominance. *H* co-segregates with the gene coding for the transcription factor *invected*, and its paralogue *engrailed* as well. The engrailed locus can possibly control development transcriptionally (Timmermans et al., 2014). The research of Thompson et al (2014) predicts that similar phenotypes will share alleles at *H*, in spite of their geographic origin. Therefore individuals of a specific morph are expected to be phylogenetically closely related at loci determining the phenotype. Genetic work has shown that the mimetic pattern of hybrids is less perfect, indicating that within a race the gene complex is adjusted by natural selection, so a good mimetic pattern is produced (Clarke & Sheppard, 1960c, d).

In *Papilio polytes* a single locus is found, called *doublesex* (*dsx*), that determines the wing pattern. This gene is well-known as a highly conserved component of the sex determination cascade in both invertebrates and vertebrates. In *Papilio*, it also appears to be regulating wing patterns. A combination of regulatory mutations and amino acid substitutions determines the wing pattern (Kunte et al., 2014). Possibly through differential expression of isoforms of *doublesex* (Thompson et al., 2014). Genetic work has shown that the mimetic pattern of hybrids is less perfect, indicating that within a race the gene complex is adjusted by natural selection, so a good mimetic pattern is produced (Clarke & Sheppard, 1960c, d).

In *Papilio memnon* a nearly identical *dsx* is found, in *Papilio memnon dsx* contains 3 genes. The locus controlling wing is found at the almost the same genomic region in both *Papilio memnon* and *Papilio*

polytes. In *Papilio polytes* the mimicry locus was contained in a chromosomal inversion, and for *Papilio memnon* that is not true (Iijima et al., 2018).

In *Papilio glaucus* offspring mostly inherit the colour of the female parent. A study done by Clarke and Sheppard (1962c) confirmed that data, and concluded that the black mimetic form is not an autosomal sex-controlled dominant or recessive gene. They conclude that the inheritance of black in the Florida and Chicago race of *Papilio glaucus* are similar. In both races inheritance is Y-linked.

2.5 Speciation

Speciation is heavily influenced by mimicry. Mimicry can create new species, on the other hand butterflies can look the same but be different species. It is hard to distinguish between the species. The North American species *Papilio Canadensis* and *Papilio glaucus* are having allopatric distributions. Studies of patterns of hybridization suggest that there is a complex interaction between both species and that they might actually form a new species.

Conclusion

Papilio and *Heliconius* differ in the way mimicry occurs in the two sexes. Within the *Papilio* species the males are mostly non-mimetic and only the females possess mimicry. Within the *Heliconius* species males and females possess mimicry. That gives different selection pressures in the species from both genera. In both genera mimetic polymorphisms occur. Within both genera, the genetics causing wing pattern differ, but the important genes and loci are often found at homologous regions. The genome architecture of *H* contrasts with results in the polymorphic mimic *H. numata* (Timmermans et al., 2014). The function of the engrailed locus of the *Papilio dardanus* is in accordance to the findings in the *Heliconius* genus, where non-coding elements near the *optix* gene control the wing phenotype (Timmermans et al., 2014). Even within one genus, mimicry evolved multiple times. *Papilio polytes* and *Papilio memnom*, have a similar genetic architecture causing mimicry, but the mimetic and non-mimetic alleles diverged independently.

Papilio and *Heliconius* possess different sorts of mimicry. In *Heliconius* there is an intense selection for mimicry, because with more butterflies with the same pattern, the predator will learn to recognize the signal faster, and the changes of survival for an individual will be bigger. Which wing-pattern is favoured depends of the abundance of a specific warning signal. In *Papilio* the selection pressure depends on the abundance of the model species, when there are too many mimics, the predator will stop avoiding a specific pattern, which is unbeneficial for the mimic and the model species, a both will be eaten more.

To conclude, *Papilio* and *Heliconius* differ in the way they possess mimicry. Different genes and loci control the diversity in wing-pattern. But differences within both genera are found as well. Some species are monomorphic and some other are polymorphic. All these differences makes understanding the evolution of mimicry very hard. The wing-pattern variety is controlled by different genes, but sometimes at homologous placed. There is also known that gene flow happens and that can influence the mimicry. While hybrids have lower survival rates and their mimics are not clear, it can be suggested that mimicry in species diverges from each other. These results suggest that mimicry evolved multiple times in butterflies and that the processes of evolution differ from each other.

Both genera contain many different species. *Heliconius* and *Papilio* are two of the species richest genera of *Lepidoptera*. There is known more about the species that are not discussed, but due to time issues not all species have been taken into account for this essay. But the general statements are based on research of multiple species. It would be great to look at more species and more factors and genes that influence mimicry and because of that cause speciation. There are many more *Lepidoptera* species who possess mimicry, those genera are not taken into account for this essay, because of time. For further research it might be great to look at more genera, to see if mimicry developed in the same way and it also can make changes in the phylogenetic tree. Not all research is line with each other, a reason for that might be that a lot of statements are based on suggestions. So more research needs to be done, to be sure which regions cause the wing-pattern variation and mimicry. When more is known which genes play an important role bigger questions as understanding the processes behind evolution can be solved. New techniques might give more information about the genes controlling wing-pattern. Mimicry supergenes also control wing shape and may even control behaviour. In this essay the focus was laid on mimicry in wing colour. To get more clear results all the element controlled by mimicry supergenes should be taken into account. There has been done more research one the *Heliconius* genus in comparison to the *Papilio* genus. There is not enough information about warning colours in *Papilio* species. Speciation has as well not been a major topic of the research of *Papilio*. So it is hard to draw conclusions about warning colour and speciation, because there was not much data found.

This essay contributes to the aim of understanding evolution, as mimicry is a wonderful and complex adaptive trait. It is hard to understand polymorphisms within species and then give a clear definition of species. With this information some steps are made towards some conclusions in the bigger picture of the arising of mimicry and therefore evolution. On mimicry you can apply: it is better to copy of another, than stay yourself. So being different is not always better.

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