Title: Correlated evolution of multiple traits gives butterflies a false head

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TY: Conceptualisation, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Supervision, Visualisation, Writing-original draft.

UK: Conceptualisation, Funding, Investigation, Methodology, Project Administration, Resources, Supervision, Writing-review & editing.

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Correlated evolution of multiple traits gives butterflies a false head

Abstract

Many butterflies possess a combination of characters at the posterior hindwing end, superficially resembling their head. This *'false head'* has been hypothesised to deflect predator attacks towards the false head area. A clear understanding of the diversity and evolution of false head traits across butterflies is lacking. Here, we tested whether false head traits evolved from simple to complex in order to achieve a greater resemblance to a head. We also tested if false head traits formed an adaptive constellation and, thus, evolved correlatedly. Using a phylogenetic framework with 944 lycaenid species, our results illustrate evolutionary patterns of five false traits - (i) false antennae, (ii) spot, (iii) conspicuous colouration in the false head area, (iv) false head contour in the false head area, and (v) convergent lines. We found that false traits (i)–(iv) evolved in a correlated fashion across the phylogeny, likely driven by a common selective pressure. Our findings support the idea that false head functions as an adaptive constellation for predator attack deflection.

Introduction

The enormous diversity in animal colouration has fascinated humankind as early as Aristotle (1). Although some of this colour diversity is used in functions such as sexual signalling (2,3) and species identity recognition (4), many animals rely on these colour patterns to protect themselves against predators. Some of the best-studied functions of animal colouration against predator attack include the various camouflage strategies, where prey prevent detection or recognition by predators (5). Animals such as clearwing butterflies (6) and glass frogs (7) rely on the lack of body colours to achieve transparency to conceal themselves from predators (8), while background matching, where animals benefit by matching their body colours with that of their backgrounds, is widespread across taxa, from vertebrates (9) to small invertebrates (10). Many animals also use bright colouration to advertise their unprofitability, noxiousness, or both (11). In deimatism, many animals suddenly reveal their otherwise hidden conspicuous colours only when a predator approaches, causing a startle and recoiling response (12).

Deflection is another anti-predator strategy that involves employing traits to manipulate the location on the prey's body where the predator makes initial contact in a way that enhances the prey's survival likelihood (13). These deflective traits may bias the point of predator attack to the prey's body parts that are less vulnerable and can be broken off, or away from the vital body parts. For example, many lizards have brightly coloured autotomous tails, which can direct avian attacks towards this expendable body part (14). Longitudinal stripes on lizard bodies can also misdirect predator attacks towards the tail when the lizard is in motion (15). One of the best-studied examples of deflective colour patterns is the eyespot, which is a "roughly circular pattern with at least two concentric rings or with a single colour disc and a central pupil" (16), potentially resembling the vertebrate eye. These eyespots occur across various taxa, including fish (17), frogs (18) and insects, particularly in the order Lepidoptera (19). Small eyespots on the lepidopteran wing periphery may protect their bearers by deflecting attacks away from vital organs and towards the non-vital parts of the

wings (reviewed in (20)). Marginal eyespots on the hindwing of the butterfly *Bicyclus anynana* have been shown to deflect mantid predation towards the less vulnerable hindwing area (21). A deflective effect of eyespots has also been demonstrated in aquatic prey in the context of fish predation (22). Moreover, dark and roughly circular spots, which may visually resemble a reduced eyespot, can provide deflective benefits. For example, tadpoles with contrasting dark spots on their tails can direct dragonfly attacks towards the tail (23), resulting in significantly higher survival than when attacks are on the body (24).

An eyespot can be considered an individual trait. While such traits can be effective on their own, multiple traits could function together for increased efficiency to deflect predator attacks. When multiple traits function together in synergy, they are referred to as adaptive constellations (25). For example, many animals possess an eye stripe, which is a bar running through the eye, with its colour matching (part of) the eye. Such eye stripes in fishes have been suggested to impart a concealing effect on the eye (26,27). Through a comparative study of butterflyfishes, Kelley and colleagues (17) showed that all fish with eyespots also have eye stripes. Through a series of predation experiments, Kjernsmo and Merilaita (22) first provided evidence for the deflective effect of fish eyespots and the concealing benefits of eye stripes. Their results also suggested that these two traits with different functions can form an adaptive constellation to produce a combined effect that increases the probability of deflection. Similarly, some swallowtail butterflies have hindwing tails and conspicuous colouration near the hindwing tail. Chotard and colleagues (28) showed that these two traits can function together to deflect bird attacks. They also demonstrated that the hindwing area near the tail is significantly easier to tear off compared to other parts of the wing, and thus enables the butterfly to escape easily from a deflected attack. The tail, hindwing colouration and differential wing strength can be considered three traits that form an adaptive constellation to enhance the deflective effect.

A large number of butterflies possess a set of characters on the underside of their hindwings, popularly known as the false head due to the resemblance to the actual head of butterflies. Most butterflies rest with their wings closed, and, therefore, the false head is visible to predators when they are resting. The false head comprises a combination of traits: i) tails, which presumably resemble false antennae, (ii) dark spots, (iii) conspicuous colouration, (iv) false head contour, and (v) convergent lines (Fig. 1; detailed definition in Methods). The false head is an example of a putative adaptive constellation that deflects predator attacks (29). The false antennae, which move back and forth, are hypothesised to mimic the actual antennae, thus attracting attention towards themselves (29). The quasi-circular dark spots of the false head can influence the initial contact point of predation (30). The conspicuous colouration may help grab predators' visual attention to the false head area (29,31). Meanwhile, a modified contour of the posterior hind wing may provide a visual resemblance to the contour of a butterfly head (29). Convergent lines may act as leading lines to direct the predator's attention to the false head area (29,32).

Compared to other body parts, physical damage in the false head area is less costly to the adult butterfly in terms of survival and behaviour, including flight dynamics (33) and mating (34). From observations on wing damage in a large number of lycaenids, Robbins (35) argued

that species with more false head traits are significantly more likely to deflect predator attacks successfully. Similarly, an inspection of pinned museum specimens revealed that species with more false head traits had higher symmetrical wing damage in the false head region, suggesting that having more complex false heads decreases the rate of predation (32). Wourms and Wasserman (30) manually added false heads on the white wings of *the Pieris rapae* butterfly by painting and attaching multiple false head trait(s) singly and in combinations, and exposed these wings to birds (Great Tits – *Parus major*). Although only spots influenced the first attack contact point, the number of false head traits influenced prey handling location by the birds – models with more false head traits were more likely to be handled at the hind wing area compared to models with single or no false head traits. In contrast, López-Palafox & Cordero (36) did not find any difference in the mantid predation rates between hairstreak butterflies with intact and ablated false antennae, suggesting that, at least against some predator groups, a single false head trait independently may be ineffective in deflecting attacks.

Especially common in Lycaenidae and Riodinidae, some or all false head traits are also present in Papilionidae, Nymphalidae and Hesperiidae, i.e., in 5 of the 7 butterfly families. The presence of these false head traits varies across species, even within the same genus, as well as between sexes (32). Thus, there is extensive variation in the morphology of false heads, but an understanding of the diversity and evolution of false head traits across butterflies is lacking. Here, we use phylogenetic comparative approaches to test hypotheses about the evolution of the false head. Specifically, we formulate hypotheses to test whether the false head complex functions as an adaptive constellation for attack deflection. If a false head works to deflect attacks towards a less vulnerable area, then this less vulnerable area should be highly conspicuous in order to grab the predator's attention. Moreover, if the false head deflects predator attacks because it fools the predators into perceiving it as a head, then the false head should evolve to have many head-like characteristics. Thus, we predicted that the false head traits evolved from simple to complex, more elaborate, traits. We also reasoned that the false head traits function together as an adaptive constellation. Hence, we predicted that the false head traits evolved in a correlated pattern across the phylogeny.

It is possible that the body size of butterflies influences the evolution of the false head. Multiple comparative analyses have shown that body size can affect the evolution of body colour. Hossie and colleagues (37) demonstrated that the evolution of conspicuous eyespots in hawkmoth larvae is associated with larger body size. In the aposematic poison frogs, the evolution of larger body size was associated with increased conspicuous colouration. Moreover, the loss of conspicuous colouration in poison dart frogs likely co-evolved with a decrease in body size (38). Similarly, reduced camouflage decoration behaviour in *Majoidea* crabs correlates with larger body sizes (39). Here, we tested the evolutionary relationship between false head and wingspan. Because larger butterflies are easier to detect, they are more likely to rely on defences such as false heads. Therefore, we predicted that larger butterflies are more likely than smaller butterflies to have complex false heads.

Methods

We categorised false head traits as 5 discrete traits and collected data on the presence of these traits across 944 butterfly species by analysing images available in online databases (Supplementary: Table S1). We reconstructed the phylogeny of the species in this study using gene sequence data from NCBI (details in Methods: *Tree Building)* and performed multiple phylogenetic comparative analyses to test our hypotheses regarding the macroevolutionary pattern of false head evolution.

Collection of false head data

The dataset on the presence and absence of the five false head traits – 1) false antennae, 2) spot, 3) conspicuous colour, 4) false head contour and 5) convergent lines (Fig. 1) - was built as binary data with 1 representing presence and 0 absence. Data were coded from images of butterfly individuals with the false head region clearly visible and without wing damage. Images were sourced from online sources and databases (Supplementary: Table S1). We relied on published descriptions with images and illustration plates for two species: *Arhopala tyrannus* (Taf. XXIXX, Fig. 1 & 2 in (40)) and *Eirmocides ardosiacea* (PIate I, Fig. 122-123, PIate 2, Fig. 133-134 in (41)). We chose species for which at least one clear image of the undamaged underside of the butterfly was available. Whenever multiple images were available for a species, a minimum of two images were analysed. With these criteria, images representing 944 species were analysed by the authors, and the presence and absence of the false head traits were recorded as discrete traits. Some species exhibited sexual dimorphism in the presence of false head traits. In such cases, we considered data from the sex which possessed more false head traits. We first restricted our analysis to the family Lycaenidae, which has the highest number of species with false heads. The included species represented all major clades and broad regions of the distribution of Lycaenidae (42). We also conducted similar analyses using a higher-level phylogeny (42) of 183 species, representing all families and 98% of butterfly subtribes. We acknowledge that colour patterns should ideally be assessed from images taken under controlled conditions. However, the scope of the study necessitated the availability of a large number of images from species from many countries across multiple continents. Therefore, it was not logistically possible for us to photograph all species under controlled conditions. Other studies with a similar scope as ours have employed human observers to grade animal colour patterns based on images (17,43–46).

We defined the false head area of a butterfly as the hindwing tornal area enclosed from above by the hindwing vein M3 and laterally by 50% of the hindwing inner margin. We defined the false head traits (Fig. 1) by modifying previously used definitions (31,32,35).

- **False antennae**: Thin antennae-like elongated protrusions in pair(s) from the false head region of both hindwings were defined as false antennae.
- **Spot**: A spot was recorded present if a species has a quasi-circular dark spot in the false head area. However, if multiple such spots are present in other parts of the wing, a spot is not marked present (e.g., in the case of serial marginal eyespots as in *Mycalesis mineus*).

- **Conspicuous colour**: Conspicuous colour was recorded present if a species had a salient colour patch in the false head area, not present in the other wing areas, and had a diameter larger than that of the spot.
- **False head contour**: False head contour was recorded present if the tornal wing area is modified by a protrusion of the wing shape, visually mimicking the contour of a butterfly head.
- **Convergent lines**: Convergent lines were defined as the presence of at least two lines running continuously across the ventral side of both wings and converging and meeting at the false head area.

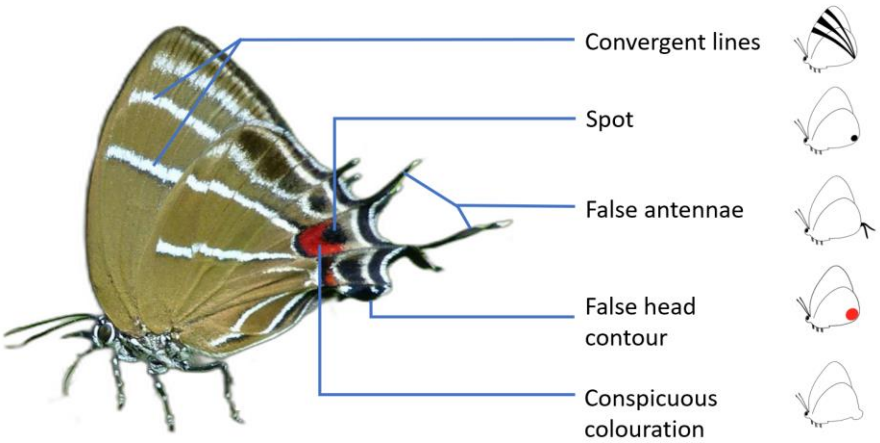

Figure 1. Photograph of *Airamanna columbia* depicting the five false head traits characterised in this study. Photo by Mark Eising (www.markeisingbirding.com).

Tree building

Sequence data for nine genes, carbomylphosphate synthase domain protein (CAD) gene, cytochrome c oxidase subunit I (COI), elongation factor 1 alpha (EF1a), dopa decarboxylase (DDC), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), histone H3 (H3), malate dehydrogenase (MDH), ribosomal protein S5 (RpS5) and wingless, were downloaded for 943 Lycaenidae and 1 Riodinidae species from Genbank (47) using the NSDPY package *v0.2.3* (48). The riodinid served as the outgroup. Each gene dataset was aligned independently through the MAFFT web server (https://mafft.cbrc.jp/alignment/server/) with the default setup (49). The aligned sequences were transformed into sequential nexus files using the ALTER web server (50). Since some species had missing sequence data for particular genes, we adopted a constrained tree-building approach using a recently published phylogeny of butterflies as the backbone. We reconstructed a maximum-likelihood phylogeny (Fig. 2) using the constrained tree search approach in IQTREE *v2.2.2.6* (51). The constrained tree file was built by pruning a recent global butterfly phylogeny (52) and retaining species which were common with our species list with false head data. The best substitution model (GTR+F+I+R8) was selected using the *ModelFinder* option, and the best partition model, using the recommend *-p* command. Branch support of the tree was inferred using 1000 replicates of ultrafast bootstraps using *-B 1000* (53).

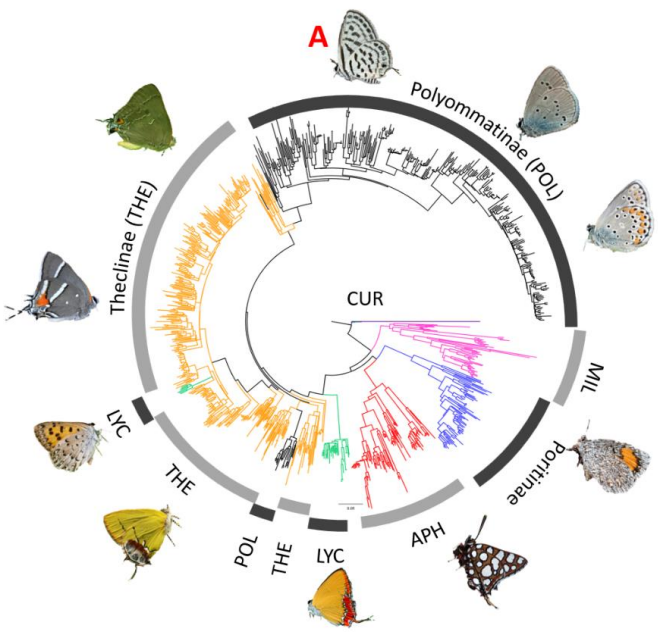

Figure 2. Maximum likelihood tree estimated in IQTREE using the constrained tree search approach. Clades belonging to a particular subfamily are represented using light and dark grey arcs with abbreviations as follows – APH: Aphnaeinae, CUR: Curetinae, LYC: Lycaeninae, MIL: Miletinae, POL: Polyommatinae, THE: Theclinae. Photo credits starting clockwise from A: Fahim Khan, Ramón, Baranyi Tamas, Fahim Khan, mr_fab, steveball, portiod, adam187, Ken-ichi Ueda, Edward Perry, juancarlosgarciamorales1.

Markov models for modelling false head evolution and ancestral state reconstruction

All analyses were conducted using the package *phytools v.2.3.0* (54) in R *v4.2.1* (55) through Rstudio *v2023.03* (56). We fitted equal rates (ER) and all rates different (ARD) time-continuous Markov (Mk) models to each false head trait. We used maximum likelihood to fit the models using *the fitMk* function, and the best-fitting model was selected based on the Akaike Information Criteria score. Furthermore, all the models were fitted with two different root priors. Models with a "flat" prior treat all states as having equal probabilities at the root (57) whereas those with a "fitzjohn" root prior regard the root state as a nuisance parameter and implement an alternative root assignment by weighing each root state by its probability of giving rise to the extant data, considering the tree and model parameters (58). Ancestral state reconstruction of the five false head traits was performed using Bayesian stochastic character mapping using the *make.simmap* function in the R package *phytools v.2.3.0* (54) with 1000 simulations for both flat and fitzjohn root priors. The 1000 stochastic maps were summarised to calculate each state's probability at the nodes, and the transition numbers were counted using the *countSimmap* function and averaged.

Correlated evolutionary patterns between discrete traits

Evolutionary correlation analyses among the five discrete traits were performed using BayesTraits *v4.0.1* (available at www.evolution.reading.ac.uk), which implements the method proposed by Pagel (59). We built an *independent* model (assumes no correlation between traits analysed) and a *dependent* model (assumes a correlated evolutionary pattern between the two traits) and obtained the model parameter estimates using the reverse jump Markov chain Monte Carlo (RJ MCMC) method (60). We built such models for all possible pairwise combinations of the five false head traits. The best-fitting model was selected based on the log Bayes factor given by log BF = 2 (log-likelihood of the dependent model – log-likelihood of the independent model). A large value of the log Bayes factor indicates support for the *dependent* model over the *independent* model. A log BF < 2 implies weak evidence, while values between 5 to 10 and >10 suggest strong positive and very strong evidence, respectively (61).

Adopting the same methods described above, we also tested the correlated evolutionary pattern of false head traits across all butterfly families using a phylogeny with 183 species representing all subtribes except Pseudopontiinae (42).

Evolutionary transition between character states

We inferred the probable order of evolution of the false head traits using transition state analyses by building a *dependent* model, where transitions between each state of the traits are allowed, and blocked models where the possible transitions (one by one) are restricted to zero. These analyses were done for all transitions between character states of pairwise traits. The best-fitting model was selected based on the log Bayes factor, where values < 2 indicate the particular transition rate was not different from zero (60,61).

Phylogenetic path analyses to estimate the sequence of trait evolution

To complement the transition states analysis, we inferred the probable order of evolution of the three most common false head traits – spot, false antennae and conspicuous colouration – using the phylogenetic path analysis based on the d-separation method (62). We performed the analysis using the R package *phylopath v1.1.3* (63), employing the phylogenetic linear regression approach and Pagel's lambda evolution model. Best-fitting models were picked based on the model ranking quantified using the C-statistics information criterion (CICc). Models with ΔCICc ≤ 2 were considered equally best-fitting and, therefore, averaged (62) using the *mds* algorithm.

Effect of wingspan on false head evolution

We used wingspans as a proxy for body size. We employed phylogenetic generalised least square regression using the R packages *nlme v3.1.164* (64) and *geiger v2.0.11* (65) to test the association between wingspan and false head evolution. We derived a dataset of 355 species for which we could obtain published wingspan data from the sources listed in Supplementary Table S1 and LepTraits 1.0 (66). For species with minimum and maximum wingspan data, or sexual dimorphism in wingspan, we used the averaged measure for our analyses. We applied three evolutionary models (Ornstein–Uhlenbeck, Brownian motion and estimated lambda model) and relied on Akaike weights to choose the best-fitting model.

Results

Markov models for modelling false head evolution and ancestral state reconstruction

The ARD model was the best fitting across the models for all false head traits (Supplementary: Table S2). The average total number of transitions between the states remained similar across the two different root priors (Supplementary: Table S3). Similarly, the evolutionary transition rates between the presence and absence states of false head traits when fitted with fitzjohn root prior (Fig. 3(a)) did not differ from that of flat root prior (Supplementary: Fig. S1), and hence the results from 'fitzjohn' are reported hereon. The ancestral state reconstruction of false head traits recovered multiple origins of false antennae (30.006 times), spots (52 times), conspicuous colouration (63.612 times), false

head contour (20.196 times) and convergent lines (13.89 times) across the phylogeny. The analysis also recovered multiple losses of false antennae (94.441 times), spots (112 times), conspicuous colouration (90.731 times), false head contour (60.092 times) and convergent lines (57.147 times). The total number of character changes derived from models with flat root priors is given in Supplementary Table S3.

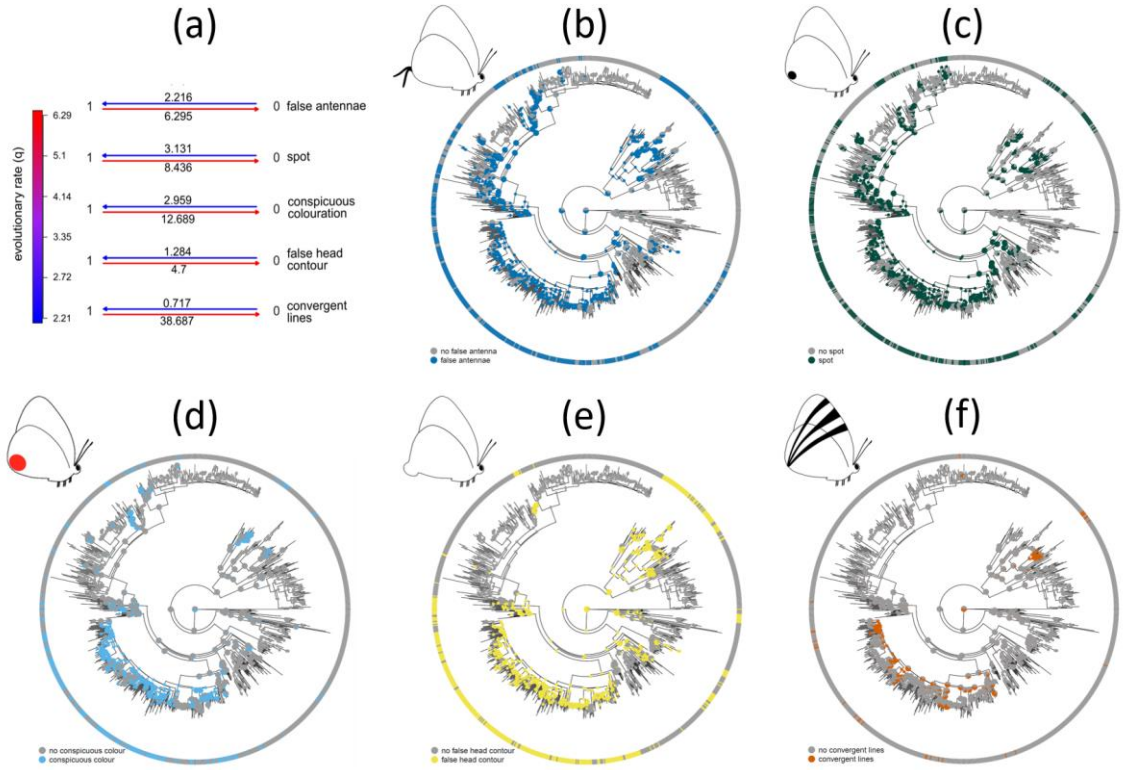

Figure 3. (a) Evolutionary transition rates between absence and presence states of each false head trait derived from Mk models with fitzjohn root prior. Ancestral state estimation using stochastic mapping with fitzjohn root prior for b) false antennae, c) spot, d) conspicuous colouration, e) false head contour and f) convergent lines. The ring at the rim of the phylogeny represents the state of the extant taxa (grey for absence, coloured for presence). Pie charts represent the marginal frequencies of the states at the internal nodes. Size of the pies represents the probability for a state to occur at the nodes. Note that pies with a probability > 0.98 are reduced in size.

Correlated evolutionary patterns between discrete traits

The Bayestraits analyses provided strong support (i.e., the *dependent* models were favoured over *independent* models of evolution) for the correlated evolution of four false head traits, *viz.* spot, false antennae, conspicuous colouration and false head contour (Table 1). However, BayesTraits analyses between the pairs of convergent lines and the rest of the false head traits provided no support for the correlated evolution of convergent lines with any of the remaining false head traits (Table 1).

Evolutionary transition between character states

Our transition state analysis with Bayestraits for spots and false antennae revealed that the transition rate q31, i.e., from spot with no false antennae to no spot without false antennae, was not different from zero (Supplementary: Table S4). In contrast, all the other possible

transitions between character states of these two traits are evolutionarily likely. The zero-transition rate of q31 suggests that loss of spot is unlikely if it is gained before the evolution of false antennae. However, all other character state transitions suggest that the loss and gain of the spot are possible if false antennae preceded the evolution of the spot.

For the trait pair spot and conspicuous colouration, the zero-transition rate q13 (Supplementary: Table S5) – from no conspicuousness and no spot to conspicuousness and no spot – suggests that the gain of conspicuousness occurred after the gain of spots. Similarly, the transition rate q34 – from conspicuousness and no false antennae to conspicuousness and false antennae – was not different from zero (Supplementary: Table S6), suggesting that the gain of false antennae is unlikely if conspicuousness is already gained. However, the gain and loss of false antennae in transition between all other character states suggests that false antennae likely preceded the evolution of conspicuousness.

Phylogenetic path analyses to estimate the sequence of trait evolution

We built six phylogenetic path models to test the order of evolution of false antenna, spot and conspicuous colouration (Fig. 4). Models six and one were the best-fitting models (Fig. 4, Table 2) and were averaged. Although the averaged model selected both paths to and from false antennae and spot, the evolutionary path from false antennae to spot had a larger coefficient (0.921, standard error = 0.065) than the reverse path (0.721, standard error = 0.154). Similarly, the path from spot to conspicuous colouration had a larger coefficient (0.389, standard error = 0.034) than the corresponding reverse path (coefficient = 0.303, standard error = 0.027). Together, these results suggest that the probable direction of the evolution of traits is from false antennae to conspicuousness via spot.

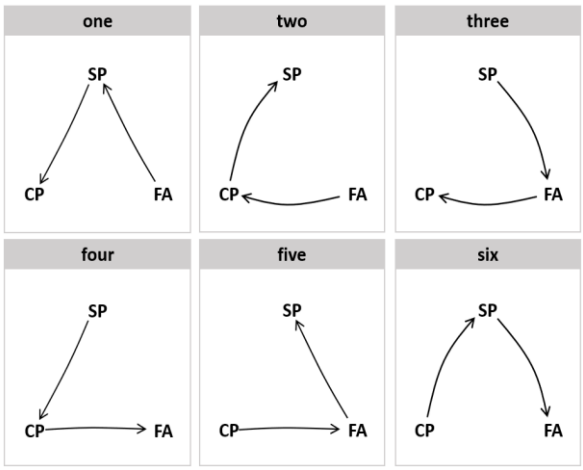

Figure 4. Schematics of the alternative models tested in the phylogenetic path analysis. Each model represents a hypothesised directionality among three false head traits: SP: spot, FA: false antennae and CP: conspicuous colouration. Please refer to this figure in relation to Table 2.

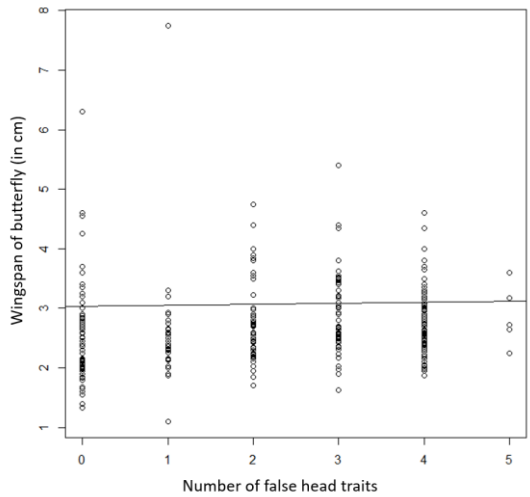

Figure 5: Plot showing no phylogenetic association between the number of false head traits a butterfly has with its wingspan under the lambda model of evolution.

Effect of wingspan on false head evolution

The phylogenetic generalised least square regression analysis tested the effect of the wingspan of butterflies on the evolution of false heads. The lambda model ($\lambda = 0.9649$) was most favoured among the three evolutionary models (Ornstein–Uhlenbeck, Brownian motion and estimated lambda model). However, there was no phylogenetic association between an increase in wingspan and an increased number of false head traits (coefficient = 0.017241, $p = 0.4385$, Fig. 5).

Discussion

Despite several observational studies on the diversity and behaviour of false head traits, and experiments to understand their functional significance as anti-predator defences, an understanding of the evolution of the false head in a macroevolutionary context is lacking. Our phylogenetic comparative analyses using a large data set of nearly 1000 lycaenid species shed light on the macroevolutionary trends of the evolution of various false head traits and indicate a correlated evolutionary pattern of the traits constituting the false head.

Many false head traits are evolutionary labile

Our ancestral state analyses recovered multiple gains and losses of four traits – false antennae, spot, conspicuousness and false head contour – suggesting that these traits are evolutionarily labile. The lability may be explained by differences in selection pressure on false heads. Natural predators of butterflies include birds (30,67), lizards (68), spiders (69) and mantids (36). A false head may facilitate survival from predator attacks by a predator community, and the same false head may be ineffective, or may even increase the likelihood of detection, when predated upon by a different community. When a prey population experiences relaxed selection from predators, it can lead to the reduction or loss of morphological traits used for anti-predator defences (70). On the other hand, evolutionary changes in traits due to selection imposed in a specific environment over several hundreds of generations can be reversed within a few generations when the ancestral environment is reintroduced (71). Thus, it is possible to lose and gain false head traits due to changes in the predator community. Similarly, a false may be beneficial or detrimental depending on the habitat and changes in the habitat may select for or against false heads over evolutionary timescales.

It has been postulated that complex traits, once lost, are unlikely to be regained – popularly referred to as Dollo's law (72). In the past few decades, phylogenetic comparative analyses have reported many cases violating Dollo's law (73). These include studies demonstrating the regain of lost complex traits such as phasmid wings (74), anuran tympanic middle ear (75), frog mandibular teeth (76), squamate limbs (77), etc. The reversal of a trait after its loss could be due to the preservation of the molecular blueprint associated with the trait, even during the trait's absence (78,79).

Our ancestral state reconstruction showed that convergent lines had multiple independent origins in two subfamilies – Aphnaeinae and Theclinae. Convergent lines have been hypothesised to lead predator's attention towards the false head region where the lines converge (29). This hypothesis of leading lines has received support from studies on the visual attention of human volunteers (81), and it is widely implemented as a principle in photography (82). Thus, we had predicted convergent lines to evolve correlatedly with other false head traits. However, we found that convergent lines showed no correlated evolutionary pattern with the rest of the false head traits. Hence, our results indicate that convergent lines do not share a functional association with the other traits. One possibility is that convergent lines, which often contrast strongly against the wing background colour, may act as disrupting colour patterns, as has been shown for similar patterns in the Banded Swallowtail (*Papilio demolion*) butterfly (83).

Correlated evolutionary pattern of false head traits and its significance

The four false head traits - antennae, spot, false head contour and conspicuousness - shared a correlated pattern of evolution, suggesting a functional association among these correlated traits. Our results align with the hypothesised function of false heads as anti-predator strategies that deceive predators into misrecognising the true head. Studies based on observations of butterfly wing damage patterns in natural settings (35,85), museum specimens (32) and predation experiments (30,69,84) have provided evidence that the efficacy of false heads in deflecting attacks from predators such as birds and jumping spiders significantly increases when the butterfly (model) has a higher number of false head traits. This is corroborated by the macroevolutionary patterns in our study, which suggest that having a single false head trait may not provide an effective anti-predatory function. Therefore, our results support the idea that the false head is an adaptive constellation.

A hypothesis related to the deflective function of the false head is that the false head area should be easier to tear than the rest of the wing areas. If the deflection works as an anti-predatory strategy, the wing area where attacks are deflected should be easily detachable so that the butterfly can escape (20). Hill and Vaca (86) compared the wing tear weights between a conspicuous marginal patch and a homologous non-conspicuous patch across three species of *Pierella.* They found that the species with the conspicuous hindwing patch had lower wing tearing weights than those lacking the patch. Kodandaramaiah (20) posited that a comparison of wing tear force at the eyespotted location and other non-eyespotted locations across the wing surface of species with putative deflective eyespots could provide an understanding of the mechanism involved in deflection. Using dummy butterflies with actual wings of the swallowtail *Iphiclides podalirius* and wild-caught great tits as predators, Chotard and colleagues (28) found that the location of wing damage as a result of predation was significantly higher in the hindwing area and especially higher in the tail area when compared with other regions in both forewing and hindwing. When the force required to break the wing was compared across multiple locations on the wing surface, they found that hindwings, particularly the hindwing tails, were significantly easier to damage. Thus, there is some evidence that deflective colour patterns on butterfly wings are present on regions that easily tear, although studies on wing tear strengths of lycaenid butterflies with and without

eyespots, and at different parts of the wings, are needed to test this in the context of false heads.

Our results do not support the anti-false head hypothesis, which posits that the bright, conspicuous colouration in the false head region *per se* directs attacks towards the colouration (29). This hypothesis predicts that the evolution of the salient conspicuous colouration alone should effectively provide effective anti-predator functionality. If this is the case, conspicuous colouration should have evolved independently of the other false head traits. Instead, the correlated evolutionary pattern of conspicuous colouration with other false head traits suggests that conspicuous colouration works in conjunction with other false head traits.

False head traits are also present in other butterfly families, namely Riodinidae (87,88) and Nymphalidae (85,89). In addition to the nymphalids and riodinids, we found species having at least one false head trait in Papilionidae and Hesperiidae. Using a 183 species phylogenetic tree representing 98% of all butterfly subtribes (42), we performed similar analyses as for Lycaenidae in order to understand the evolutionary patterns of false head traits on a broader scale. In agreement with the patterns that we found within Lycaenidae, we recovered correlated evolutionary patterns of spot, false antennae, conspicuous colouration, and false head contours, while convergent lines did not show a correlated evolutionary pattern with any of the other false head traits (Supplementary: Table S7, Fig. S2). These results further strengthen the interpretations of our study.

Body size does not affect false head evolution

Predation risk is positively dependent on size, where larger-sized prey are more prone to detection, whereas smaller prey gain more protection by being cryptic (reviewed in (90)). If larger butterflies are more easily detected, they may be more dependent on deflection, whereas smaller butterflies rely on crypsis alone. Thus, we predicted the evolution of more false head traits in larger butterflies compared to smaller butterflies. However, our study did not find any phylogenetic correlation between the number of false head traits a butterfly had and its wingspan. Thus, false heads may deflect attacks irrespective of size, either as the primary defence (28) or as a late-acting defence when camouflage fails, as suggested by Galicia and colleagues (32). Instead of prey body size, the crucial criteria for deflection may be the size of the deflective features. Deflection is likely to work when the deflective features have an optimal size below which the features are too small for detection and beyond which predators are not drawn to attack (19).

Summary and Conclusion

The false head in butterflies has long been hypothesised to have a deflective function against predators. We present the first phylogenetic comparative analysis of false heads. We found that most false head traits in butterflies evolved in a correlated pattern, presumably towards a functional association as a response to a common selective force. Thus, our study provides macroevolutionary support for the idea that the false head evolved as an adaptive constellation of anti-predatory traits. These false head traits together may form a complex structure that visually resembles a head to the predators. Our results are in agreement with

studies that showed that false heads deflect predator attacks efficiently when the butterfly has many false head traits. However, we also argue that multiple anti-predator hypotheses may work together synergistically along with the deflection hypothesis highlighting the importance of further predation experiments employing multiple predator types. Overall, our comprehensive analysis underscores further studies to understand the adaptive significance of false heads in butterfly defence mechanisms.

Table 1. Evolutionary correlates of pairwise discrete false head traits resulted from BayesTraits analyses. Values under columns "Dependent model" and "Independent model" are the estimated harmonic means of maximum likelihood values for the respective models. As suggested in BayesTraits, interpretation of the correlated evolution of a pair of traits was conducted based on the log Bayes factor as weak evidence if <2, positive evidence if >2, strong evidence if between 5 and 10 and very strong evidence if >10. Pairwise traits with correlated evolution models are highlighted in bold.

Trait	Dependent model	Independent model	Log Bayes factor
(a) False antennae			
Spot	-705.841837	-790.447204	169.210734
Conspicuous colouration	-707.817894	-751.932068	88.228348
False head contour	-608.197437	-654.070723	91.746572
Convergent lines	-478.372099	-473.343151	-10.057896
(b) Spot			
Conspicuous colouration	-751.524202	-803.863843	104.679282
False head contour	-653.122021	-705.926133	105.608224
Convergent lines	-529.237692	-530.184548	1.893712
(c) Conspicuous colouration			
False head contour	-642.360816	-667.348022	49.974412
Convergent lines	-493.150529	-491.60491	-3.091238
(d) False head contour			
Convergent lines	-393.647427	-393.768922	0.24299

Table 2. Summary statistics of possible models used in the phylogenetic path analysis, where C and ωCICc values indicate Fisher's C-statistic and CICc weights, respectively. The models mentioned are as in Figure 4

Model	C	CICc	ΔCICc	likelihood	ωCICc
Six	21.8	31.9	0.000	1	0.578
One	22.4	32.5	0.627	0.731	0.422
Four	42.5	52.6	20.698	0.00032	0.000185
Two	72.1	82.2	50.289	<0.00001	<0.00001
Three	72.1	82.2	50.289	<0.00001	<0.00001
Five	72.1	82.2	50.289	<0.00001	<0.00001

Ethics. Our study does not involve any live animals and requires no ethical permits.

Conflicts of interest declaration. We declare that we do not have any competing interests.

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