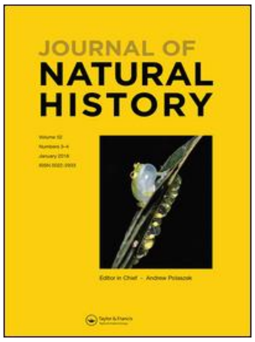

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A review of red-eye pigmentation and diel activity patterns in skippers (Lepidoptera, Papilionoidea, Hesperiidae)

Emmanuel F. A. Toussaint[a] and Andrew D. Warren[b]

[a]Natural History Museum of Geneva, Geneva, Switzerland; [b]Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

ABSTRACT
The visual systems and diel activity patterns of butterflies and moths have been studied for decades, yet understanding the underlying mechanisms that are associated with the evolution of these remains a major challenge. The order Lepidoptera is principally composed of nocturnal lineages with extreme morphological and behavioural adaptations to this lifestyle. Although most butterflies are diurnal, some clades are predominantly nocturnal, for instance, the Hedylidae. Skippers are another family that comprises multiple crepuscular and/or nocturnal lineages. Interestingly, many such lineages have red-eye pigmentation, and this morphological feature has been hypothesised to be an adaptation to the night-time lifestyle. Here, we review the occurrence and frequency of red-eye pigmentation as well as diel activity patterns in Hesperiidae. We place these data within a phylogenomic framework and provide hypotheses and predictions relative to the evolution of red-eye pigmentation in skippers with respect to diel activity. We suggest that several types of red-eye pigmentation exist in skippers, with possible structural red-eye pigmentation in some lineages of diurnal skippers. The colouration of eyes in Hesperiidae, the evolutionary mechanisms that drive these traits and the physiological underlying processes require further attention and could bring new insights into our understanding of butterfly vision systems.

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Butterfly vision; convergent evolution; Hesperiidae; nocturnality; visual system evolution

Introduction

Butterflies (Lepidoptera, Papilionoidea) are some of the most striking insects, known for their charismatic and colourful morphologies and for their close association with flowering plants that they actively pollinate. A central question in butterfly ecology and evolution is the perception of their environment and in particular their ability to perceive colours. Butterflies use vision not only to fly and avoid predators, but they also rely on vision to discriminate host plants or to detect and discriminate potential mates. Butterflies possess compound eyes made of hundreds of ommatidia, hemispherical structures comprising a lens, cone, visual pigment cells, rhabdom, photoreceptors and a tracheole (Stavenga & Arikawa 2006). When light hits the butterfly eye, it penetrates the lens and is directed by a crystalline cone to the visual pigment cells that act as protective screens. In butterflies, the visual pigment is a rhodopsin composed of a light-sensitive retinal-based

CONTACT Emmanuel F. A. Toussaint ✉ emmanuel.toussaint@ville-ge.ch

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chromophore and an opsin protein. The chromophore is isomerised when the rhodopsin absorbs photons from the light. The basic photoreceptor organisation of butterflies is similar to the one observed in bees (Hempel de Ibarra et al. 2014; Arikawa 2017), with three photoreceptor classes that have maximal sensitivity in the UV, blue (B) and green (G) (Stavenga and Arikawa 2006). However, some lineages have much more complex photoreceptor configurations with up to 15 different classes of photoreceptors (e.g. *Graphium sarpedon*, Chen et al. 2016). Interestingly, in butterflies, which are mostly diurnal, vision is operated via an apposition compound eye, as in bees for instance. This type of eye structure allows the light to be captured by the photoreceptors of each ommatidium but only from the single facet lens of their ommatidium (Warrant 2017). In other words, the light that penetrates through the facet lens of an ommatidium cannot be processed by the photoreceptors of another ommatidium, because each ommatidium is isolated from the others through a layer of light-absorbing pigment granules. However, most nocturnal insects possess a different type of eye structure called refracting superposition eye (Figure 1, Swihart 1969; Shimohigashi and Tominaga 1986; Warrant 2017). In the

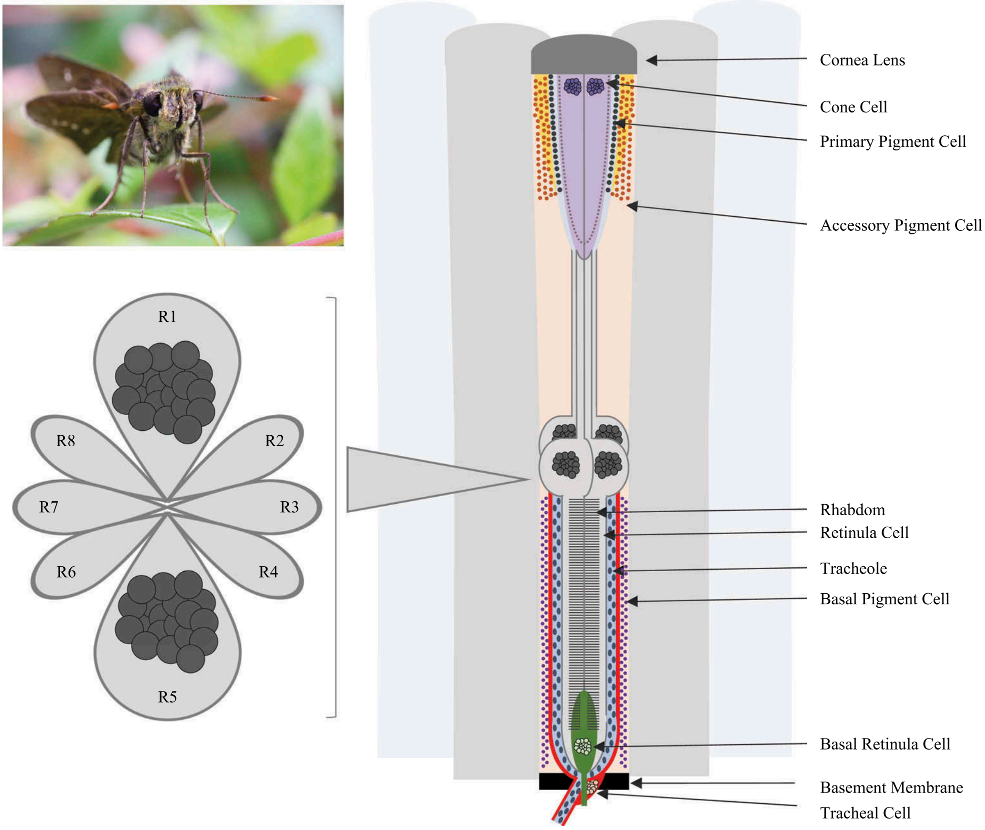

Figure 1. Morphology of an ommatidium in the superposition compound eye of a skipper.

Figure redrawn from Shimohigashi and Tominaga (1986) presenting a longitudinal view of an ommatidium in the eye of the diurnal skipper *Parnara guttata* (Hesperiidae, Hesperiinae, Baorini). The names of the major morphological structures are given in the figure. A transversal view of the retinula cells R1 to R8 is presented on the left of the figure. A picture of *Parnara guttata* is shown on the top of the figure (Credit: t-mizo).

latter, there is no such layer of pigments separating the different ommatidia, and the facet lens of each ommatidium is only separated from its photoreceptors by a clear zone that allows the light entering one ommatidium to be processed by the photoreceptors of all neighbouring ommatidia. Thanks to powerful radial gradients of refractive index, the light entering multiple lenses (i.e. up to 2000, Warrant 2017) can be focused onto a single photoreceptor in the retina. This eye structure allows for much more light to be processed and, therefore, increases the sensitivity to light (Land 1984), allowing nocturnal insects, for instance, to navigate through the night with ease and with only a couple of photons being absorbed by each photoreceptor (e.g. Warrant et al. 2004). Therefore, the eye structure seems to be tightly linked to diel activity.

The order Lepidoptera is of particular interest in the study of vision because it comprises not only the predominantly nocturnal and paraphyletic ‘moths’, but also the predominantly diurnal and monophyletic ‘butterflies’, albeit exceptions to these diel activity patterns exist in both groups (Kawahara et al. 2018b). Among butterflies, two families have evolved a superposition eye, the nocturnal butterflies (Hedylidae) and the skippers (Hesperiidae) (Yagi and Koyama 1963; Swihart 1969; Horridge et al. 1972; Eguchi 1978; Land 1984; Yack et al. 2007; Pirih et al. 2018). Interestingly, these families are sister to each other (Mutanen et al. 2010; Heikkilä et al. 2012; Kawahara & Breinholt 2014; Espeland et al. 2018; Toussaint et al. 2018; Kawahara et al. 2019). Therefore, it seems plausible that this eye structure (i.e. superposition eye) was regained after a primary loss in swallowtails (Papilionidae) that have apposition eyes (Stavenga and Arikawa 2006) and are the sister lineage to all other butterflies (Mutanen et al. 2010; Heikkilä et al. 2012; Kawahara and Breinholt 2014; Espeland et al. 2018; Toussaint et al. 2018; Kawahara et al. 2019), but this would need to be tested in a phylogenetic comparative framework. The fact that Hedylidae have superposition eyes does not come as a surprise since these butterflies are fully nocturnal (but see Kendall 1976 regarding possible diurnal observations of *Macrosoma heliconiaria*), even exhibiting hearing organs to supposedly detect bat echolocation at night (Kawahara et al. 2018a). Hedylidae were even thought for a long time to be moths and phylogenetically placed close to Geometridae (Prout 1910). However, it is more surprising to find this eye structure in skippers, that are mostly diurnal despite some exceptions. Indeed, some skippers have been recorded as crepuscular or even nocturnal. In fact, and for a long time, skippers (Hesperiidae) were also believed to be moths, because of their bulky and ‘furry’ bodies (Toussaint et al. 2018). Behavioural and ecological information is lacking for most of the diversity among the *ca.* 4300 species of skippers, and much work is needed to understand the relationship between diel activity and eye structure in skippers. Similarly, the evolution of these diel activity patterns has not been studied in an evolutionary framework (i.e. phylogenetic framework).

A striking feature of most crepuscular and/or nocturnal skippers is often the presence of a characteristic red-eye pigmentation that is not found for instance in Hedylidae or other crepuscular butterflies and moths (Figure 2). Although some diurnal skipper lineages also present red-eye pigmentation (e.g. *Synale*), they represent an exception, and often the colouration of the eyes appears to be more structural than in crepuscular or nocturnal lineages. This is substantiated by the progressive fainting of the red-eye pigmentation in the latter compared to diurnal red-eye skippers which preserve their pigmentation long after death. As a result, the observation of red-eye pigmentation is often limited to an assessment in the field when the insects are alive or based on photographic evidence. Often, only the red-eye pigmentation of diurnal skippers can be

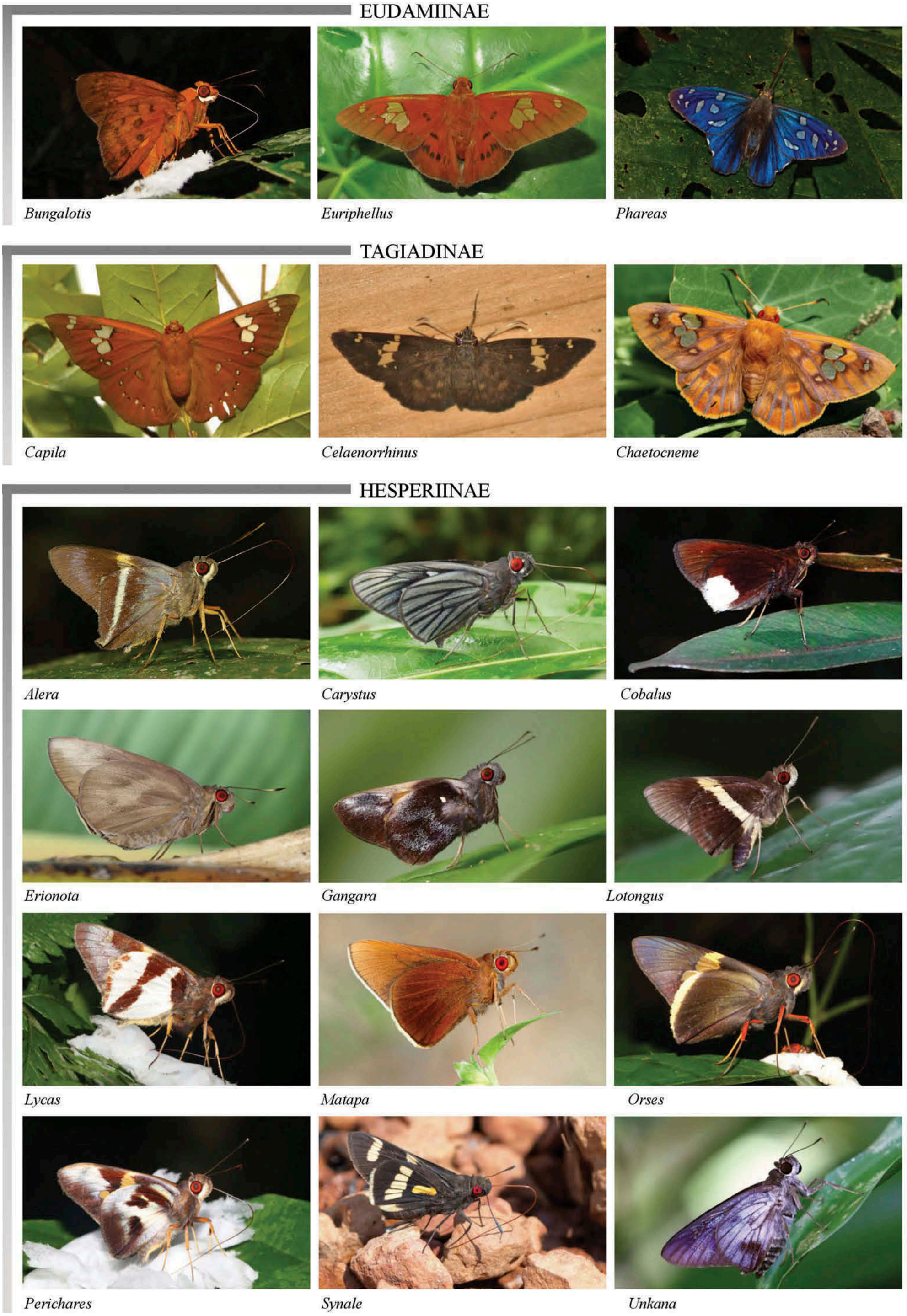

Figure 2. Phylogenetic diversity of red-eye pigmentation in skippers.

Photographs of adults from different genera of skippers presenting red-eye pigmentation. From left to right and top to bottom: *Bungalotis midas* (Credit: Shirley Sekarajasingham), *Euriphellus euribates* (Credit: Karen Nichols), *Phareas coeleste* (Credit: Ken Kertell), *Capila phanaeus* (Credit: Antonio Giudici), *Celaenorrhinus fritzgaertneri* (Credit: Tripp Davenport), *Chaetocneme denitza* (Credit: Bill Higham), *Alera manu* (Credit: David Geale), *Carystus ploetzi* (Credit: Les Catchick), *Cobalus virbius* (Credit: Marquinhos Aventureiro), *Erionota torus* (Credit: Hsing-Han Li), *Gangara sanguinocculus* (Credit: Antonio Giudici), *Lotongus avesta* (Credit: Antonio Giudici), *Lycas argentea* (Credit: Andrew Warren), *Matapa aria* (Credit: Eishwar Maanay), *Orses cynisca* (Credit: Andrew Warren), *Perichares seneca* (Credit: Andrew Warren), *Synale elana* (Credit: Rodrigo Conte), *Unkana ambasa* (Credit: Antonio Giudici).

observed in Museum collection specimens years after the death of the butterflies. There is no clear evidence as to why crepuscular and nocturnal skippers present red eyes. The evolution of such pigmentation was hypothesised to be linked to an enhanced crepuscular and nocturnal vision (De Vries et al. 2008); however, this was never tested empirically, and the underlying mechanisms allowing an enhanced vision were not identified or even hypothesised (Kawahara et al. 2018b). It is noteworthy that red-eye glow is observed in butterflies including diurnal ones. This glow hue is supposedly linked to a reflective structure found in the eye, the tracheal tapetum at the end of the rhabdom (Ribi 1979a, 1979b). This structure is found in nocturnal moths but also more surprisingly in some diurnal butterflies. Whether this structure is responsible for the red-eye pigmentation of crepuscular skippers is unknown, and if it were the case, the evolutionary mechanisms governing its appearance and disappearance between different skipper lineages would require some investigation. Therefore, a first step in the study of visual system evolution in skippers consists of identifying and characterising diel activity patterns on one hand, and red-eye pigmentation on another hand. In this study, we review these patterns in a phylogenetic context to provide a first attempt at understanding the complex vision systems of crepuscular and night skippers.

Methods

Among skippers, many lineages have been identified as crepuscular or nocturnal, with a vast majority of these clades being tropical. However, the data is scattered across decades or even centuries of notes and scientific studies, and a review is necessary to lay the foundations of a systematic study focusing on the evolution of red-eye pigmentation and its association with diel activity patterns. Here, we present a review of all skipper lineages following the current classification (Warren et al. 2008, 2009) and taking into account recent phylogenetic (Sahoo et al. 2016, 2017) and phylogenomic (Toussaint et al. 2018; Li et al. 2019) studies. We report knowledge of diel activity patterns for crepuscular and/or nocturnal skipper lineages as well as observations of red-eye pigmentation based on an extensive survey of the literature, museum specimen collections, personal observations and Flickr image screening. We summarised known information relative to red-eye pigmentation in skippers in the framework of the best phylogenetic hypotheses available (Sahoo et al. 2017; Toussaint et al. 2018; Li et al. 2019).

Results and Discussion

Subfamily Coeliadinae

The subfamily Coeliadinae comprises nine genera and *ca*. 80 species of large and often colourful skippers distributed in the Old-World tropics (Chiba 2009). This clade is sister to the remainder of skippers but intra-subfamilial phylogenetic relationships remain largely unknown. Many species from the Indo-Australian region have been recorded as being crepuscular although none appears to be strictly nocturnal (Parsons 1991, 1999; de Jong and Treadaway 2007; Kimura et al. 2011). The African genera do not seem to be crepuscular although their life history is not as well known as Indo-Australian species. Species from the Indo-Australian genera *Burara* and *Hasora* are widely accepted as being crepuscular, although *Bibasis* seems to be diurnal (Maruyama 1991; Eliot 1992; Vane-Wright and de Jong 2003; Hsu and Huang 2008; Kimura et al. 2011; Braby 2016; but see de Jong and Treadaway 2007 on *Bibasis*). However, Sondhi and Kunte (2018a, 2018b) list all Indian Coeliadinae (*Badamia, Bibasis, Burara, Choaspes* and *Hasora*) as crepuscular, being active in the early morning and/or evenings. In his extensive review of New Guinean butterflies, Parsons (1999) mentions that the New Guinean Coeliadinae genera *Allora, Badamia* and *Hasora* are diurnal while *Choaspes* (i.e. *C. hemixanthus* and *C. illuensis*) is exclusively and markedly crepuscular. This behaviour might be the result of mimicry complexes involving different lineages of toxic moths as suggested by Parsons (1999). Therefore, there might be a different diel activity pattern across and among Indo-Australian Coeliadinae genera along their geographic ranges. There is no clear mention in the literature of red-eye pigmentation in Coeliadinae; however, De Vries et al. (1987) compared the purplish tinge of Neotropical *Celaenorrhinus* eyes (see below) to that observed in *Hasora*. Observations from live photographs of specimens belonging to Indo-Australian Coeliadinae, and in particular to *Hasora* and *Burara*, suggest that such a pigmentation might exist, but it is often reduced to a discrete tinge and is by no means as bright as in other red-eye skippers of the subfamilies Eudaminae and Hesperiinae for instance (see below).

Subfamily Euschemoninae

The subfamily Euschemoninae comprises the monotypic species *Euschemon rafflesia* whose diel activity has been well characterised. This species flies in the late afternoon and early morning as well as dusk (Braby 2016) and does not seem to present visible red-eye pigmentation. The genus *Euschemon*, along with a few species of Coeliadinae and Tagiadinae (i.e. *Chaetocneme*, see below), is the only crepuscular skippers in Australia, the rest of the fauna being strictly diurnal (Braby 2016), including for instance the endemic subfamily Trapezitinae, whose eye structure was the topic of a seminal study on the superposition eye structure in skippers (Horridge et al. 1972).

Subfamily Eudaminae

Tribe Phocidini

The subfamily Eudaminae and in particular the tribe Phocidini (sensu Li et al. 2019) comprises multiple lineages of crepuscular and/or nocturnal skippers, some of which have been called ‘night skippers’ (Austin 2008), including some striking examples of red-eye pigmentation (e.g. *Bungalotis*, Figure 2) (de Jong 1983; Ackery et al. 1999). In a seminal study on diel activity patterns in Neotropical skippers, De Vries et al. (2008) presented statistical support for the somewhat crepuscular activity of several Eudaminae genera including *Bungalotis, Cephise, Dyscophellus, Nascus, Salatis* and *Sarmientoia*. All these genera were observed to fly on average after 4:00 pm, and *Bungalotis* and *Sarmientoia* were observed to fly on average after 5:00 pm, which corresponds to a crepuscular activity at these latitudes. Other reports, studies and field guides (e.g. Canals 2000), as well as personal observations, support the classification of these genera as crepuscular. In addition, the genus *Porphyrogenes* was reported as crepuscular by Austin and Mielke (2008) and Burns et al. (2010), and the recently described monotypic genera *Euriphellus* and

Pseudonascus are also crepuscular (Austin 2008; Sourakov and Houlihan 2017). Interestingly, most species belonging to these genera have red eyes (Figure 2), albeit with different intensities, and a large fraction of them (*Bungalotis, Dyscophellus, Euriphellus, Pseudonascus* and *Salatis*) belong to a clade well supported by molecular data (Sahoo et al. 2017; Toussaint et al. 2018; Li et al. 2019).

The genus *Cephise* was included by Sahoo et al. (2017) but was not recovered as belonging to the 'red-eye clade', a result confirmed by Li et al. (2019) who recovered it within the tribe Eudamini. Several species of *Cephise* have red eyes and are crepuscular, some being occasionally caught at light traps (Austin and Mielke 2000). However, the species of *Cephise* sampled in these phylogenies, *C. aelius*, does not seem to have red eyes. It is possible that this genus is not monophyletic and that red-eye *Cephise* species are nested in the 'red-eye clade' within Phocidini. This will need to be tested in a phylogenetic framework. The genus *Porphyrogenes* which was not included in Sahoo et al. (2017) was recovered within the 'red-eye clade' in Li et al. (2019) along with the monotypic genus *Emmelus* whose physiology is unknown and the genus *Aurina* that seems to have red eyes based on photographic evidence. Three additional genera, *Ocyba, Phareas* and *Phocides*, were placed in the 'red-eye clade' by Sahoo et al. (2017) and Li et al. (2019). *Ocyba* and *Phareas* are both crepuscular and have red eyes (Figure 2), but the genus *Phocides* does not comprise red-eyed or crepuscular species. It is possible that red-eye pigmentation along with crepuscular and nocturnal diel activity evolved only once in Eudaminae with a potential loss but additional taxon sampling and observations would be necessary to test this hypothesis.

Subfamily Tagiadinae

Tribe Celaenorrhinini

The subfamily Pyrginae does not seem to comprise examples of crepuscular behaviour or red-eye pigmentation; however, the recently delineated subfamily Tagiadinae presents a few cases. The genus *Celaenorrhinus* (Hesperiidae, Tagiadinae, Celaenorrhinini) was one of the first examples of gregarious roosting and nocturnal diel activity documented in skippers (De Vries et al. 1987; but see Reichholf 1973 for an earlier report of roosting in the skipper *Sarbia damippe* in highlands of Santa Catarina, Brazil). In this seminal study, De Vries and colleagues reported the nocturnal activity of *Celaenorrhinus fritzgaertneri* from Guanacaste Province in Costa Rica. Nevertheless, the crepuscular behaviour of members of the genus *Celaenorrhinus* was known long before this study. Bailey (1880) found *Celaenorrhinus fritzgaertneri* during the day within 'an old deserted mine … at a depth of eighty feet', and we have frequently found this species under highway culverts during the day in western Mexico, where large numbers of adults congregate and remain mostly inactive. Watson (1891) noted that the Oriental *Celaenorrhinus leucocera* was flying long after sunset in India. Real (1968) and MacNeill (1975) both reported collecting of *Celaenorrhinus* in the early morning and late afternoon in Central America as well as using mercury vapour lamps on Barro Colorado Island. De Vries et al. (1987) mention that crepuscular adults of *Celaenorrhinus* have reddish eyes. An extensive review of live photographs allowed us to verify this claim with some photographed specimens presenting a purplish tinge as observed in Coeliadinae for instance. However, the red pigmentation of the eyes is very different from the bright-red colouration observed in Eudaminae lineages such as *Bungalotis* and *Salatis* (Figure 2).

Tribe Tagiadini

In addition to *Celaenorrhinus*, two other Tagiadinae genera within the tribe Tagiadini have red-eye pigmentation and have been suggested as crepuscular. The Oriental and Australian genera *Capila* and *Chaetocneme*, respectively, both have representatives with bright-red eyes (Eliot 1978; Parsons 1991; 1999; Osada et al. 1999; Kimura et al. 2011). These genera are rather similar in morphology and have been suspected to be phylogenetically closely related (Müller 2016), although no study to date has sampled both genera, and *Chaetocneme* was never placed in a phylogenetic framework. The genus *Chaetocneme* is distributed in Australia and New Guinea exclusively (Parsons 1991, 1999). Adults have bright-red eyes and have been collected at or after dusk as well as at house lights at night (Parsons 1991). The genus *Capila* is distributed in Indomalaya, from eastern India to China and Sumatra (Kimura et al. 2011). Although there is mention of some species presenting bright-red eyes (Eliot 1978; Osada et al. 1999; Kimura et al. 2011), we could not find evidence of crepuscular behaviour in the literature. In fact, Maruyama (1991) lists the representatives of this genus as diurnal without additional information. This might be due to the extreme rarity of species in this genus, albeit this apparent rarity could be caused by an undocumented crepuscular behaviour. Live photographic review supports the view that adults of some species in the genus *Capila* have bright-red eyes, at least in *C. phanaeus* (Figure 2). *Capila* was found in Li et al. (2019) as sister to the genus *Gerosis*, whose species do not present red-eye pigmentation.

Subfamilies Pyrginae and Pyrrhopyginae

These two diverse subfamilies do not seem to present red-eye pigmented skipper lineages or conspicuously crepuscular species, but a more in-depth review of these clades using a broader taxon sampling would be needed to refine this observation.

Tribe Pyrgini

A unique mention of potential crepuscularity in the genus *Xenophanes* was reported in De Vries et al. (2008). In this study of Neotropical skipper diel activity, it was noted that *Xenophanes tryxus* was observed flying late in the afternoon, indicating a potential crepuscularity. We could not find other studies mentioning a crepuscular habit for *Xenophanes*, and our observations throughout the Neotropics support the idea that this genus is diurnal; likewise, a review of live photographs suggests that red pigmentation is absent in *Xenophanes*. Therefore, we argue that the unique record from De Vries et al. (2008) is likely an outlier data point and does not represent the diel activity of this genus.

Subfamilies Heteropterinae and Trapezitinae

The two small subfamilies Heteropterinae and Trapezitinae both comprise strictly diurnal species and no report in the literature or evidence in photographic reviews could indicate either a potential crepuscular activity or red-eye pigmentation.

Subfamily Hesperiinae

Tribe Hesperiini

Within the subfamily Hesperiinae, many lineages have evolved red eyes and/or crepuscular diel activity. An extensive genus-level photographic review allowed us to document red-eye pigmentation in the tribe Hesperiini, more specifically in a clade comprising the genera *Wahydra* and *Zalomes*. The genus *Wahydra* is endemic to the Neotropics with an Andean distribution from Venezuela to Argentina and was erected by Steinhauser (1991) to include several species of the genus *Zalomes*; therefore, it is not surprising that red-eye pigmentation is found in both these phylogenetically closely related genera. Species of *Wahydra* and *Zalomes* have not been documented as crepuscular and available data on diel activity gleaned from species descriptions (e.g. Carneiro et al. 2018) indicates that the genera are most likely diurnal. This is particularly interesting since *Wahydra* and *Zalomes* possess bright-red eyes. However, these species occur in montane cloud forest habitats where low light levels are common during daytime hours, so while technically diurnal their visual systems may operate similar to those of crepuscular species; however, this remains to be tested in an empirical setting. Another genus, *Mnaseas* seems to include species with a reddish tinge in the eye colour, but this is less striking than in the two above-mentioned genera and could only be observed on a few live photographs. Additional data are needed to understand the role of red-eye pigmentation in this clade.

A clade found in Warren et al. (2008, 2009) as well as in Sahoo et al. (2016, 2017) is comprised of the following exclusively red-eye pigmented genera: *Aides, Dubiella, Cobalus, Talides* and *Thracides*. Based on preliminary phylogenomic data (Toussaint et al. unpublished), the two genera *Carystina* and *Carystus* are likely placed in the same clade. All these genera are Neotropical and present red-eye pigmentation, from dark carmine (e.g. *Dubiella*) to striking ruby colours (e.g. *Carystus*) (Figure 2). The genera *Aides, Cobalus* and *Dubiella* have darker eye pigmentation, and are diurnal, flying in the middle of the day (De Vries et al. 2008; pers. Obs. ADW). The genus *Carystina* also presents a dark red-eyed pigmentation but there is no evidence of its diel activity in the literature, although live photography review seems to indicate that this species is at least active during the day. Among crepuscular species of this group is the genus *Talides*, whose representatives have bright ruby red eyes. Although Austin (1998) did not note that *Talides* species were crepuscular in his detailed review of the genus, data from De Vries et al. (2008) indicates that some species are flying late in the afternoon, and our personal observations in Brazil corroborate this. In addition, *Talides* was observed to nectar on parrot's beak flowers (*Heliconia psittacorum*) before sunrise in the Atlantic Forest of Brazil (Cruz et al. 2014), and Rios et al. (2010) reported *Talides sergestus* nectaring on *Aechmea* bromeliad inflorescences at 6:00 am. The genus *Thracides* also presents some red-eye pigmentation although the study from De Vries et al. (2008) supports the idea that this genus is mostly diurnal. More data are needed to understand the diel activity of this genus.

Some additional genera of Hesperiini present red-eye pigmentation, although their phylogenetic placement is uncertain. For instance, most species of the genus *Carystoides* are crepuscular and/or are active at low light levels (ADW pers. obs.). They also present bright-red-eye pigmentation. This is also the case of the genus *Evansiella* which is crepuscular (ADW pers. obs.; De Vries et al. 2008). Some species of the genera *Lychnuchus, Moeros, Pseudorphe, Sacrator, Tisias* and *Turesis* seem to present dark-red pigmentation, these skippers being active either in cloud forests at low light levels or being diurnal but often in deep forests and at low light levels. The placement of these genera is mostly unknown, and additional data are needed to understand their phylogenetic ties.

Other genera of the tribe Hesperiini present a crepuscular or nocturnal diel activity although they do not seem to present red-eye pigmentation. This is the case of the genus *Argon* distributed in South America from Mexico to Uruguay and Argentina. The only species of the genus *Argon iota* is potentially crepuscular (Bustos and Güller 2010), although red pigmentation is not obvious in this genus. The genus *Calpodes* is another example. It was recorded as flying in the early morning and late afternoon (Smith et al. 1994), as well as being caught on vapour lights in Trinidad (Cock 2003). However, members of this genus do not present red-eye pigmentation.

A remarkable genus within Hesperiini is *Synale*, whose species are notably diurnal and present one of the brightest shades of red among skippers (Bustos et al. 2011, Figure 2). They are also some of the few skipper genera whose members retain their red-eye pigmentation after death and this for decades as can be observed in museum collections. Understanding the relationship between red-eye pigmentation and diurnality in *Synale* might be important to pinpoint the evolutionary mechanisms at play in vision evolution among skippers.

In a different clade, is found the monotypic *Flaccilla*, whose unique species *F. aecas*, the aecas ruby-eye is a deep forest inhabitant, mostly flying at low light levels in Neotropical forests (ADW pers. obs.). Similarly, the Neotropical genera *Venas* and *Vertica* fly in deep forests and with low light levels. Species belonging to these genera present a red-eye pigmentation despite a diurnal activity (De Vries et al. 2008). In their phylogeny, Toussaint et al. (2018) recovered *Flaccilla* as sister to *Anthoptus*, a diurnal genus whose members do not present red-eye pigmentation, while the other genera *Venas* and *Vertica* have not been included in a phylogenetic framework to date.

Erionotini

Many genera of grass skippers within Erionotini present red-eye pigmentation, with some of these genera being exclusively crepuscular or nocturnal. This is the case for instance of the Old World tropical genera *Erionota, Gangara, Matapa, Unkana* and *Zela* (Toussaint et al. 2018). The genus *Erionota* comprises several species known as pests of palms including the widespread banana skipper or palm red-eye *E. thrax* (Patrick and Patrick 2012). Species belonging to this genus are generally crepuscular (Ackery et al. 1999; Cock 2015), and all present bright-red eyes (Figure 2). This species is attracted to lights at night, and in particular to boat lights, which might explain its invasive capacity and its introduction on several Pacific islands including Hawaii (Cock 2015). The genus *Erionota* is phylogenetically close to other red-eye-pigmented skipper genera including *Gangara, Matapa* and *Zela* (Sahoo et al. 2017; Toussaint et al. 2018). The genera *Gangara, Matapa* and *Zela* are amongst the most striking example of red-eye pigmentation within skippers (Figure 2). These are large grass skippers with a crepuscular or nocturnal activity, broadly distributed in Southeast Asia, from India to Wallacea (Best 1956; Wynter-Blyth 1957; Donahue 1962; de Jong 1983, 1992). These four genera form a robust clade that is closely related to the genera *Lotongus* and *Unkana* (Sahoo et al. 2017; Toussaint et al. 2018), the latter comprising species with a somewhat dark-reddish eye pigmentation (Figure 2), but apparently with a diurnal activity (e.g. Haidar et al. 2014). We posit that this clade, coined *Plastingia*-group in some studies when including other related genera such as *Ge, Pirdana* or *Plastingia*, is of primary interest to study the transition from diurnality to crepuscularity and the emergence of a possibly associated red-eye pigmentation. Analyses of visual gene (i.e. opsins) expression and arrangements in these genera would likely provide crucial insights into our understanding of the link between diel activity patterns and eye pigmentation in skippers.

Pericharini

Among Pericharini grass skippers, a few Neotropical genera are worth mentioning. The genera *Alera, Lycas, Orses* and *Perichares* all present red-eye pigmentation and are or are thought to be largely crepuscular. They are closely related based on morphological characters (Warren et al. 2009) and molecular data (Li et al. 2019). The rare genus *Alera* is crepuscular or flies during cloudy days (ADW pers. obs.) in ombrophile forests (Mielke and Casagrande 2004). The genus *Lycas* flies in the late afternoon and is also crepuscular (ADW pers. obs.). The unique record in De Vries et al. (2008) indicating a diurnal activity is likely an outlier. *Lycas* species present a red-eye pigmentation based on a photographic review. The genera *Orses* and *Perichares* are largely crepuscular (ADW pers. obs.) and are closely related (Sahoo et al. 2017). De Vries et al. (2008) indicate that *Orses* flies indeed in the late afternoon while *Perichares* seems to also have a diurnal activity. This could be explained by the fact that not all *Perichares* species have red-eye pigmentation, and in fact, the genus itself might not be monophyletic (Toussaint unpublished). Finally, the genera *Lychnuchoides* and *Orphe* placed in Li et al. (2019) in Pericharini present dark-red pigmentation. Skippers from these genera are usually active either in cloud forests at low light levels or are diurnal but often in deep forests and at low light levels.

Megathymini

Among giant-skippers (Megathymini), only *Megathymus cofaqui* is known to have red eyes. This species is active during the day but prefers very shady habitats and adults rest almost exclusively in the shade.

Incertae sedis

Within Hesperiinae, several Afrotropical genera are crepuscular, and they usually present a dark-red eye pigmentation. It is the case, for example, in the genera *Gretna* and *Zophopetes*, respectively, the giant crepuscular skippers and palm nightfighters. The genus *Gretna* is possibly associated with the *Plastingia*-group, although its phylogenetic placement is uncertain, while the genus *Zophopetes* does not seem closely related to any other genera and is placed as sister to a clade comprising other genera with red-eye pigmentation and/or crepuscular habits (Sahoo et al. 2017, see below). Both genera comprise large grass skippers with a crepuscular activity at dusk and dawn (Kielland 1994; Penney 2009; Safian 2011; Williams et al. 2015; de Jong 2017). Other African skippers present a red-eye pigmentation and a somewhat crepuscular diel activity pattern. For instance, the genus *Pteroteinon* presents red-eye pigmentation although its diel activity is not particularly well known (it seems to be mostly diurnal). This genus is supposedly closely related to the Oriental genus *Hidari* whose members are also red-eye skippers (Sahoo et al. 2017). In fact, species of both *Hidari* and *Pteroteinon* present a bright-red-eye pigmentation, one that reminds the one observed in *Matapa,* for example (Figure 2). More data are needed on diel activity patterns in these two genera and a broader taxon sampling will be compulsory to understand the evolution of red-eye pigmentation in these lineages. Two other genera found in the Afrotropics, *Artitropa* and *Gamia*, are crepuscular (Riley 1925; Miller and Collins 1997) and seem to exhibit red-eye pigmentation based on photograph reviews, although this morphological feature is not obvious from the literature. Both genera are closely related, potentially being sister, and belong to a large clade that also comprises the earlier mentioned genera *Hidari, Pteroteinon* and *Zophopetes*, along with *Chondrolepis, Leona, Monza, Mopala* and *Semelea* (Sahoo et al. 2017). None of the five latter genera are known to be crepuscular or to present red-eye pigmentation, except maybe for *Chondrolepis*, the putative sister genus to *Artitropa* and *Gamia* (Sahoo et al. 2017), noted by de Jong (1986) as possibly presenting a red-eye pigmentation. Additional data will be needed to understand the diel activity and eye pigmentation in this part of the skipper tree-of-life. We hypothesise that this clade might represent the snapshot of the early stages in the transition from diurnality to crepuscularity with red-eye pigmentation being significantly less marked than in other groups that also present much more clear-cut patterns of diel activity.

Conclusion

In this review, we summarised all known information on diel activity and red-eye pigmentation in skippers based on the literature, field notes and Flickr live photograph screening. We investigated these features in every single genus of skipper for which data were available and only reported the genera that presented one and/or the other focal feature. This comprehensive review of red-eye pigmentation and diel activity pattern in skippers allows us to shed light on a surprisingly complex array of morphological and behavioural patterns. Our review indicates that in some clades, the crepuscular activity of skippers is apparently decoupled from red-eye pigmentation, while in others, diurnal skippers present red-eye pigmentation. However, in the vast majority of cases, crepuscular activity is linked to some degree to a red-eye pigmentation. Interestingly, the red-eye pigmentation is not identical among lineages, indicating either different evolutionary mechanisms and pathways driving the evolution of this colouration in the development of the eyes, and/or different evolutionary stages in the setup of this pigmentation, where some lineages having recently shifted from diurnality to crepuscularity would have less developed pigmentation mechanisms than lineages being crepuscular for a much longer period of time on a geological timescale. We identify more than a dozen independent origins for red-eye pigmentation linked to crepuscularity in skippers, indicating a striking case of convergent evolution. Based on our results, we hypothesise that red pigmentation of the eyes in skippers is directly linked to their diel activity. We postulate, in agreement with earlier studies (e.g. de Jong 1983), that red-eye pigmentation in skippers allows for a better vision at night, possibly through adaptations of the tracheal tapetum lucidum although more data are needed to test this hypothesis (Ribi 1979a, 1979b). We also suggest that this pigmentation is a continuous evolutionary process that takes place over geological time. As a result, the transition from diurnality to nocturnality is a progressive mechanism, and taxa belonging to clades presenting this feature and in which the shift to crepuscularity is comparatively old should have more pigmented eyes, whereas recent shifts from diurnality to crepuscularity/nocturnality should be associated with less pigmented eyes. These hypotheses should be tested using a combination of phylogenetic/phylogenomic and transcriptomic tools to understand the evolutionary processes linked to the development of red-eye pigmentation and the setup of optic genes from the opsin family. Our study allows us to pinpoint clades that would be ideal candidates for such studies, including for instance the lineage comprising the genera *Erionota, Gangara, Lotongus, Matapa, Unkana* and *Zela*, which present different diel activity patterns and red-eye pigmentation levels and are concentrated on a single biogeographic region.

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References

Ackery PR, de Jong R, Vane-Wright RI. 1999. The butterflies: Hedyloidea, Hesperioidea and Papilionoidea. Lepidoptera, moths and butterflies. 1. Evolution, systematics, and biogeography. In: Kristensen NP, editor. Handbook of Zoology. Vol. 4, Part 35. Berlin: Walter de Gruyter; p. 263–300.

Arikawa K. 2017. The eyes and vision of butterflies. J Physiol. 595(16):5457–5464. doi:10.1113/JP273917.

Austin GT. 1998. Hesperiidae of Rondônia, Brazil: notes on *Talides* Hübner (Lepidoptera: Hesperiidae: Hesperiinae). Trop Lepid Res. 9:26–32.

Austin GT. 2008. Hesperiidae of Rondônia, Brazil: taxonomic comments on “night” skippers, with descriptions of new genera and species (Lepidoptera: Eudaminae). Insecta Mundi. 0029:120.

Austin GT, Mielke OH. 2000. Hesperiidae of Rondônia, Brazil: *Cephise* Evans (Pyrginae), with descriptions of new species from Mexico and Brazil. Revista Brasileira De Zoologia. 17(3):757–788. doi:10.1590/S0101-81752000000300021.

Austin GT, Mielke OH. 2008. Hesperiidae of Rondônia, Brazil: *Porphyrogenes* Watson (Lepidoptera: Pyrginae: Eudamini), with descriptions of new species from Central and South America. Insecta Mundi. 0044:572.

Bailey JS. 1880. Description of a new species of Pleusioneura from Central America. Bull Brooklyn Entomologic Soc. 3:62–63.

Best AEG. 1956. Further notes and additions to the list of butterflies from Bombay and Salsette. J Bombay Nat Hist Soc. 54:215–216.

Braby M. 2016. The complete field guide to butterflies of Australia. Melbourne (Australia): Csiro Publishing.

Burns JM, Janzen DH, Hallwachs W. 2010. Of many similar species in the neotropical genus *Porphyrogenes* (Lepidoptera: Hesperiidae), a new one, repeatedly reared in Costa Rica, is relatively distinct. Proc Entomol Soc Wash. 112(1):32–42. doi:10.4289/0013-8797-112.1.32.

Bustos EN, Güller R. 2010. Mariposas de la Ciudad de Buenos Aires y alrededores. Buenos Aires (Argentina): Vazquez Mazzini Editores.

Bustos EON, Favre P, Bertolini MP, Turner JD, Sourakov A. 2011. Mariposas diurnas (Lepidoptera: Papilionoidea y Hesperioidea) de la reserva privada Osununú-parque provincial Teyú Cuaré y alrededores de San Ignacio, provincia de Misiones, Argentina. Trop Lepid Res. 21(1):34–42.

Canals GR. 2000. Mariposas bonaerenses. Buenos Aires: LOLA.

Carneiro E, Dolibaina DR, Grishin NV, Warren AD. 2018. A new species of *Wahydra* from Ecuador (Hesperiidae, Hesperiinae, Anthoptini). Zootaxa. 4392(1):196–200. doi:10.11646/zootaxa.4392.1.

Chen P-J, Awata H, Matsushita A, Yang E-C, Arikawa K. 2016. Extreme spectral richness in the eye of the common bluebottle butterfly, *Graphium sarpedon*. Front Ecol Evol. 4:1–12. doi:10.3389/fevo.2016.00018.

Chiba H. 2009. A revision of the subfamily Coeliadinae (Lepidoptera: Hesperiidae). Bull Kitakyushu Mus Nat Hist Hum Hist (A Nat Hist). 7:1–51.

Cock MJ. 2003. The skipper butterflies (Hesperiidae) of Trinidad. Part 11, Hesperiinae, genera group O. Living World. J Trinidad and Tobago Field Naturalists' Club. 2003:14–48.

Cock MJ. 2015. A critical review of the literature on the pest *Erionota* spp. (Lepidoptera, Hesperiidae): taxonomy, distribution, food plants, early stages, natural enemies and biological control. CAB Rev. 10(007):1–30. doi:10.1079/PAVSNNR201510007.

Cruz D, Silva M, Alburquerque S. 2014. Floral syndrome, resources and pollinator guilds: a case study of *Heliconia psittacorum* L. f. (Heliconiaceae). Série Botânica, Porto Alegre. 69(2):303–312.

de Jong R. 1983. Revision of the Oriental genus *Matapa* Moore (Lepidoptera, Hesperiidae) with discussion of its phylogeny and geographic history. Zool Med. 57:243–270.

de Jong R. 1986. Systematics, phylogeny and biogeography of the chiefly afromontane genus *Chondrolepis* Mabille (Lepidoptera: Hesperiidae). Zoologische Verhandelingen. 231:1–40.

de Jong R. 1992. A new species of *Gangara* Moore (Lepidoptera: Hesperiidae), with a note on the genus. Zool Med Leiden. 66:183–188.

de Jong R. 2017. A new species of *Zophopetes* Mabille, 1904 (Lepidoptera: Hesperiidae) from Cameroon. Metamorphosis. 28:11–15.

de Jong R, Treadaway CG. 2007. Hesperiidae of the Philippine Islands. Butterflies of the world, Suppl. 15:1–72.

De Vries PJ, Austin GT, Martin NH. 2008. Diel activity and reproductive isolation in a diverse assemblage of Neotropical skippers (Lepidoptera: Hesperiidae). Biol J Linn Soc. 94(4):723–736. doi:10.1111/(ISSN)1095-8312.

De Vries PJ, Schull J, Greig N. 1987. Synchronous nocturnal activity and gregarious roosting in the neotropical skipper butterfly *Celaenorrhinus fritzgaertneri* (Lepidoptera: Hesperiidae). Zool J Linn Soc. 89(1):89–103. doi:10.1111/j.1096-3642.1987.tb01345.x.

Donahue JP. 1962. Observations and records of butterflies attracted to light in India. J Lepid Soc. 16 (12):131–135.

Eguchi E. 1978. Comparative fine structure of lepidopteran compound eyes, especially skippers (Hesperioidea). Zool Mag. 87:32–43.

Eliot JN. 1978. [descriptions and revisions]. The butterflies of the Malay Peninsula. 3rd ed. (A. S. Corbet and H. M. Pendlebury). Kuala Lumpur (Malaysia): Malayan Nature Society.

Eliot JN. 1992. The butterflies of the Malay Peninsula. 4th revised ed. (originally by AS Corbet and HM Pendlebury). Kuala Lumpur: Malayan Nature Society.

Espeland M, Breinholt J, Willmott KR, Warren AD, Vila R, Toussaint EFA, Maunsell SC, Aduse-Poku K, Talavera G, Eastwood R, et al. 2018. A comprehensive and dated phylogenomic analysis of butterflies. Curr Biol. 28(5):770–778. doi:10.1016/j.cub.2018.01.061.

Haidar IKA, Rahman MM, Ahsan MF, Islam MA, Tania NJ, Banick PR, Ahmed S. 2014. Records of three new butterfly species from the Chittagong University Campus of Chittagong in Bangladesh. J Entomol Zool Stud. 2(5):178–181.

Heikkilä M, Kaila L, Mutanen M, Pena C, Wahlberg N. 2012. Cretaceous origin and repeated tertiary diversification of the redefined butterflies. Proc R Soc B. 279:1093–1099. doi:10.1098/rspb.2011.1430.

Hempel de Ibarra N, Vorobyev M, Menzel R. 2014. Mechanisms, functions and ecology of colour vision in the honeybee. J Comp Physiol A. 200:411–433. doi:10.1007/s00359-014-0915-1.

Horridge GA, Giddings C, Stange G. 1972. The superposition eye of skipper butterflies. Proc R Soc Lond B. 182(1069):457–495.

Hsu YF, Huang HC. 2008. On the discovery of *Hasora mixta limata* ssp. nov. (Lepidoptera: Hesperiidae: Coeliadinae) from Lanyu, Taiwan, with observations of its unusual immature biology. Zool Studies-Taipei. 47(2):222.

Kawahara AY, Breinholt JW. 2014. Phylogenomics provides strong evidence for relationships of butterflies and moths. Proc R Soc B. 281(1788):20140970. doi:10.1098/rspb.2014.0970.

Kawahara AY, Breinholt JW, Espeland M, Storer C, Plotkin D, Dexter KM, Toussaint EFA, St Laurent RA, Brehm G, Vargas S, et al. 2018a. Phylogenetics of moth-like butterflies (Papilionoidea: Hedylidae) based on a new 13-locus target capture probe set. Mol Phylogenet Evol. 127:600–605. doi:10.1016/j.ympev.2018.06.002.

Kawahara AY, Plotkin D, Espeland M, Meusemann K, Toussaint EFA, Donath A, Gimnich F, Frandsen PB, Zwick A, Dos Reis M, et al. 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. Proc Natl Acad Sci USA. 116(45):22657–22663.

Kawahara AY, Plotkin D, Hamilton CA, Gough H, St Laurent R, Owens HL, Homziak NT, Barber JR. 2018b. Diel behavior in moths and butterflies: a synthesis of data illuminates the evolution of temporal activity. Org Divers Evol. 18(1):13–27.

Kendall RO. 1976. Larval foodplants and life history notes for eight moths from Texas and Mexico. J Lep Soc. 30(4):264–271.

Kielland J. 1994. Butterfly collecting in North-Western Tanzania II. Volume 5 March 1994 Number.

Kimura Y, Aoki T, Yamaguchi S, Uémura Y, Saito T. 2011. The butterflies of Thailand. Based on Yunosuke KIMURA collection. Vol. 1. Hesperiidae, Papilionidae, Pieridae.

Land MF. 1984. The resolving power of diurnal superposition eyes measured with an ophthalmoscope. J Comp Physiol A. 154(4):515–533.

Li W, Cong Q, Shen J, Zhang J, Hallwachs W, Janzen DH, Grishin NV. 2019. Genomes of skipper butterflies reveal extensive convergence of wing patterns. Proc Natl Acad Sci. 116(13):6232–6237. doi:10.1073/pnas.1821304116.

MacNeill CD. 1975. Celaenorrhinus. In: Howe WH, editor. *The butteflies of North America*. New York, NY: Doubleday.

Maruyama K. 1991. Butterflies of Borneo 2 (2), Hesperiidae. Tokyo: Tobishima Corporation. i–ix, 1–77; 40 pls.

Mielke OH, Casagrande MM. 2004. Two new species of *Alera* Mabile (Lepidoptera, Hesperiidae, Hesperiinae). Revista Brasileira De Zoologia. 21(4):913–918. doi:10.1590/S0101-81752004000400028.

Miller LD, Collins SC. 1997. A review of the genus *Gamia* Holland, 1896 (Lepidoptera: Hesperiidae: Hesperiinae), with the description of a new species. Metamorphosis. 8(4):147–159.

Müller CJ. 2016. A new species of Chaetocneme Felder, 1860 from Papua New Guinea (Lepidoptera: Hesperiidae). Trop Lep Res. 26(1).

Mutanen M, Wahlberg N, Kaila L. 2010. Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. Proc R Soc B. 277(1695):2839–2848. doi:10.1098/rspb.2010.0392.

Osada S, Uemura Y, Uehara J. 1999. An illustrated checklist of the butterflies of Laos PDR. Tokyo (Japan): Mokuyo-sha.

Parsons M. 1991. Butterflies of the Bulolo-Wau valley. Honolulu (HI): Bishop Museum Press.

Parsons M. 1999. The butterflies of Papua New Guinea: their systematics and biology, Vol. 736. London: Academic Press.

Patrick B, Patrick H. 2012. Butterflies of the South Pacific, Vol. 240. Dunedin: Otago University Press.

Penney D. 2009. Field guide to butterflies of the Gambia, West Africa. Manchester (UK): Siri Scientific Press.

Pirih P, Ilić M, Rudolf J, Arikawa K, Stavenga DG, Belušič G. 2018. The giant butterfly-moth Paysandisia archon has spectrally rich apposition eyes with unique light-dependent photoreceptor dynamics. J Comp Physiol A. 204(7):639–651.

Prout LB. 1910. Lepidoptera Heterocera, Fam. Geometridae, Subfam. Oenochrominae. In: Wytsman P, editor. Genera insectorum. Belgium (Brussels); p. 1–119.

Real H. 1968. Notes on the crepuscular nature of the species of the Celaenorrhinus group (Lepidoptera: Hesperiidae). Pan-Pacifit Entomologist. 44:81–82.

Reichholf J. 1973. Gemeinschaftliches Schlafen beim neotropischen Dickkopffalter *Sarbia damippe* Mabille et Bullet (Lepidoptera, Hesperiidae). Dtsch Entomol Z. 20(4–5):355–356. doi:10.1002/mmnd.19730200408.

Ribi WA. 1979a. Structural differences in the tracheal tapetum of diurnal butterflies. Zeitschrift für Naturforschung C. 34(3–4):284–287. doi:10.1515/znc-1979-3-421.

Ribi WA. 1979b. Coloured screening pigments cause red eye glow hue in pierid butterflies. J Comp Physiol. 132(1):1–9. doi:10.1007/BF00617727.

Riley ND. 1925. VIII. A revision of the Continental African species of the genus *Artitropa* (Lep. Hesperiidae). Trans R Entomol Soc London. 73(1–2):281–288. doi:10.1111/j.1365-2311.1925.tb02864.x.

Rios, PAF, da Silva JB, Moura FDBP. 2010. Visitantes florais de Aechmea constantinii (Mez) LB Sm. (Bromeliaceae) em um remanescente da Mata Atlântica do Nordeste Oriental. Biotemas. 23(4):29–36.

Safian S. 2011. Butterflies across the river. Report on the rapid butterfly surveys for the 'Across The River Project' in Sierra Leone and Liberia in 2011.

Sahoo RK, Warren AD, Collins SC, Kodandaramaiah U. 2017. Hostplant change and paleoclimatic events explain diversification shifts in skipper butterflies (Family: Hesperiidae). BMC Evol Biol. 17 (1):174. doi:10.1186/s12862-017-1016-x.

Sahoo RK, Warren AD, Wahlberg N, Brower AV, Lukhtanov VA, Kodandaramaiah U. 2016. Ten genes and two topologies: an exploration of higher relationships in skipper butterflies (Hesperiidae). PeerJ. 4:e2653. doi:10.7717/peerj.2653.

Shimohigashi M, Tominaga Y. 1986. The compound eye of parnara guttata (Insecta, Lepidoptera, Hesperiidae): fine structure of the ommatidium. Zoomorphology. 106(3):131–136.

Smith DS, Miller LD, Miller JY. 1994. The butterflies of the West Indies and South Florida. Oxford (UK): Oxford University Press; p. 264 p.

Sondhi S, Kunte K. 2018a. Butterflies and moths of Pakke Tiger Reserve. 2nd ed. Titli Trust (Dehradun, India), National Centre for Biological Sciences, (Bengaluru, India), and Indian Foundation for Butterflies (Bengaluru, India); vi + 242 pp.

Sondhi S, Kunte K. 2018b. Butterflies of Uttarakhand a field guide. M/s Bishen Singh Mahendra Pal Singh (Dehradun), Titli Trust (Dehradun), National Centre for Biological Sciences (Bengaluru) & Indian Foundation of Butterflies (Bengaluru); x+ 310 pp.

Sourakov A, Houlihan PR. 2017. Note on nocturnal activity of a skipper, *Pseudonascus paulliniae*, in French Guiana. Trop Lepid Res. 27(1):26–27.

Stavenga DG, Arikawa K. 2006. Evolution of color and vision of butterflies. Arthropod Struct Dev. 35 (4):307–318. doi:10.1016/j.asd.2006.08.011.

Steinhauser SR. 1991. Taxonomic notes and descriptions of new taxa in the Neotropical Hesperiidae. Part 2, Heteropterinae and Hesperiinae, *Vinius* group. Bull Allyn Mus. 132:1–79.

Swihart SL. 1969. Colour vision and the physiology of the superposition eye of a butterfly (Hesperiidae). J Insect Physiol. 15(8):1347–1365. doi:10.1016/0022-1910(69)90196-6.

Toussaint EF, Breinholt JW, Earl C, Warren AD, Brower AV, Yago M, Dexter KM, Espeland M, Pierce NE, Lohman DJ, et al. 2018. Anchored phylogenomics illuminates the skipper butterfly tree of life. BMC Evol Biol. 18(1):101. doi:10.1186/s12862-018-1216-z.

Vane-Wright RI, de Jong R. 2003. The butterflies of Sulawesi: annotated checklist for a critical island fauna. Zoologische Verhandelingen. 343:3–267.

Wahlberg N, Wheat CW, Peña C. 2013. Timing and patterns in the taxonomic diversification of Lepidoptera (butterflies and moths). PLoS One. 8(11):e80875. doi:10.1371/journal.pone.0080875.

Warrant EJ. 2017. The remarkable visual capacities of nocturnal insects: vision at the limits with small eyes and tiny brains. Philos Trans R Soc B. 372(1717):20160063. doi:10.1098/rstb.2016.0063.

Warrant EJ, Kelber A, Gisle´n A, Greiner B, Ribi W, Wcislo WT. 2004. Nocturnal vision and landmark orientation in a tropical halictid bee. Curr Biol. 14(15):1309–1318.

Warren AD, Ogawa JR, Brower AV. 2008. Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperiidae (Lepidoptera: Hesperioidea). Cladistics. 24(5):642–676. doi:10.1111/cla.2008.24.issue-5.

Warren AD, Ogawa JR, Brower AV. 2009. Revised classification of the family Hesperiidae (Lepidoptera: Hesperioidea) based on combined molecular and morphological data. Syst Entomol. 34(3):467–523.

Watson EY. 1891. *Hesperiidae indicae*: being a reprint of the descriptions of the Hesperiidae of India, Burma and Ceylon. Madras (India): Vest.

Williams MC, Pringle EL, Greyling J, Mayer A. 2015. Annotated checklist of the butterflies of the Dwesa and Cwebe nature reserves, Eastern Cape Province, South Africa. Metamorphosis. 26:83–93.

Wynter-Blyth MA. 1957. Butterflies of the Indian region. 72 pls. (27 col.). Bombay: Bombay Natural History Society; p. xx + 523 pp.

Yack JE, Johnson SE, Brown SG, Warrant EJ. 2007. The eyes of *Macrosoma* sp. (Lepidoptera: Hedyloidea): a nocturnal butterfly with superposition optics. Arthropod Struct Dev. 36(1):11–22. doi:10.1016/j.asd.2006.07.001.

Yagi N, Koyama N. 1963. The compound eye of Lepidoptera. Tokyo: Shinkyo Press; p. 319.