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A supposition: structural colours resulting from both natural and sexual selection on an individual wing in the butterfly genus Cyanophrys (Lepidoptera: Lycaenidae)

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Abstract – Spectral measurements of 29 individuals from five superficially similar species of *Cyanophrys* Clench, 1961 reveal that the blue structural colour of the dorsal fore wings is species and sex dependent, while the green structural colour of the ventral hind wings is mutual. The results suggest that the blue colouration functions as a conspecific signal during courtship and/or mate recognition, considering also that several species of *Cyanophrys* co-exist in the same environment and appear morphologically similar. The resting places of the females and perching sites of the males of *Cyanophrys* are usually green leaf surfaces. While resting/perching their wings are closed. Therefore the ventral green colouration probably serves a generalized camouflage function. Consequently the nanostructures responsible for the blue colouration are most probably under the influence of sexual selection, whereas those causing the green colour are affected by natural selection. With 26 figures and one table.

Key words – Butterflies, structural colour, photonics, nanostructures, natural selection, sexual selection.

INTRODUCTION

Members of the neotropical lycaenid butterfly genus *Cyanophrys* CLENCH, 1961 (type species: *Strymon agricolor* BUTLER et DRUCE, 1872) have attracted the attention of biologists due to the stark contrast between their dorsal and ventral wing colourations. The green colour of the ventral wing surfaces is shared by many species, and has been used to imply phylogenetic relationship. The genus was considered to be related to the lycaenid genus *Callophrys* BILLBERG, 1820 (type species: *Papilio rubi* LINNAEUS, 1758) because it displays the same matt green colour in the ventral surfaces of the wings (*cf.* SCOTT 1975: 297). The structures producing physical colour were examined by GHIRANDELLA (1989) also in the species "*Thecla herodotus*" (= *Cyanophrys herodotus* (FABRICIUS, 1793)), but the biological role of the colours was not tackled. Later the genera *Cyanophrys* and *Callophrys* were considered to be monophyletic on the basis of structural characters ("Callophrys Section" of ROBBINS 2004; in this context see JOHNSON & KRUSE 1997: 5), but the intrageneric relationships within the group remain unresolved (ROBBINS & DUARTE 2005: 413).

ROBBINS & DUARTE (2005) recognized 15 species of *Cyanophrys* during a cladistic revision, using 14 characters provided by the bodies (frons in the head and genitalia in the abdomen) and wings (androconia, shape and venation) of the imagines. In this paper it was mentioned that "exposure to humidity, particularly during preparation, or to physical abrasion can change scale colour from green to brown" (ROBBINS & DUARTE 2005: 400 and 411), suggesting that the colour is structural. Recently KERTÉSZ *et al.* (2006) revealed the physical properties of the contrasting wing surfaces of a single individual of *Cyanophrys remus* (HEWITSON, 1868). It was demonstrated that both dorsal and ventral wing colourations are generated by photonic crystal-type structures of the scales that varied in architecture on the nanoscale. The physical mechanism of the colour change from green to brown was also explained, where individual light waves reflected from the various optical interfaces interfere constructively. When one of the two materials in the scale, i.e. chitin and air, changes, i.e. from air to water, the refractive index difference is also changed, and this affects the optical properties of the structure.

No publications dealing with *Cyanophrys* or the optical phenomena generated by wing scales present any data for understanding how synchronic and sympatric taxa can discriminate each other, or how reproductive isolation can work *in situ* where superficially indistinguishable taxa cohabit. In this paper we are interested in the question whether the photonic properties of the wings play a role in such discrimination by examining several, related species, including some from the same environment. Former observations and generalized statements suggest that (a) dorsal blue wing surfaces play an important role in sexual communication (LUNDGREN 1977, SILBERGLIED 1984) and (b) that the ventral surfaces of the wings provide cryptic colouration or camouflage (NIJHOUT 1991). However, it is important to consider spectral measurements rather than appearances to the human eye. We aim to test the two working hypotheses and measure the optical variables which can be associated to them. We remark here that our working hypotheses are not dependent from each other; consequently hypothesis (1) does not implies hypothesis (2), nor *vice versa*:

(1) If the dorsal surfaces of the wings play an important role in the communication of individual butterflies, then closely related taxa occurring synchronically and syntopically should reveal different, species-specific spectral properties (Fig. 1).

(2) If the ventral wing surfaces of the wings play an important role in the camouflage of individual butterflies, then taxa occurring synchronically and syntopically should reveal similar spectroscopic properties, because it is likely that they target the same visual systems (of generalist predators) (Fig. 2).

Figs 1–2. 1 = Male *Cyanophrys acaste* (PRITTWITZ, 1865) individual in perching position, before taking flight and emitting blue signals, 2 = Female *Cyanophrys remus* (HEWITSON, 1868) individual in camouflaging pose during overcast periods (photos: A. MOSER)

MATERIALS AND METHODS

Species and individuals sampled

Five species of *Cyanophrys* were selected for the following reasons. Three occur syntopically and synchronically in the forests of SE Brazil including *Cyanophrys remus* (Hewitson, 1868), the scales of which have been the subject of thorough structural and optical analyses (Biró *et al.* 2006, Kertész *et al.* 2006). Another species, widely distributed in the Andes, has been chosen as a complementary taxon of the SE Brazilian triad. According to the results of Robbins & Duarte (2005) this Andean taxon is one of the hypothetical sister species of *C. remus*. A further *Cyanophrys* species also from the Andes, considered to be rare by Robbins & Duarte (2005: 405) has been included in our analyses for recording variability.

We measured 29 specimens from the Hungarian Natural History Museum (HNHM) and the private collection of Alfred Moser. Material examined is listed according to species and individual specimens with localities and collecting data (and numbers corresponding with spectrographs given in the Figures); all specimens are deposited in the HNHM. The representative individuals of each species measured are illustrated as Figs 3–20. Their scientific names with authorities, collecting data and database register are as follows.

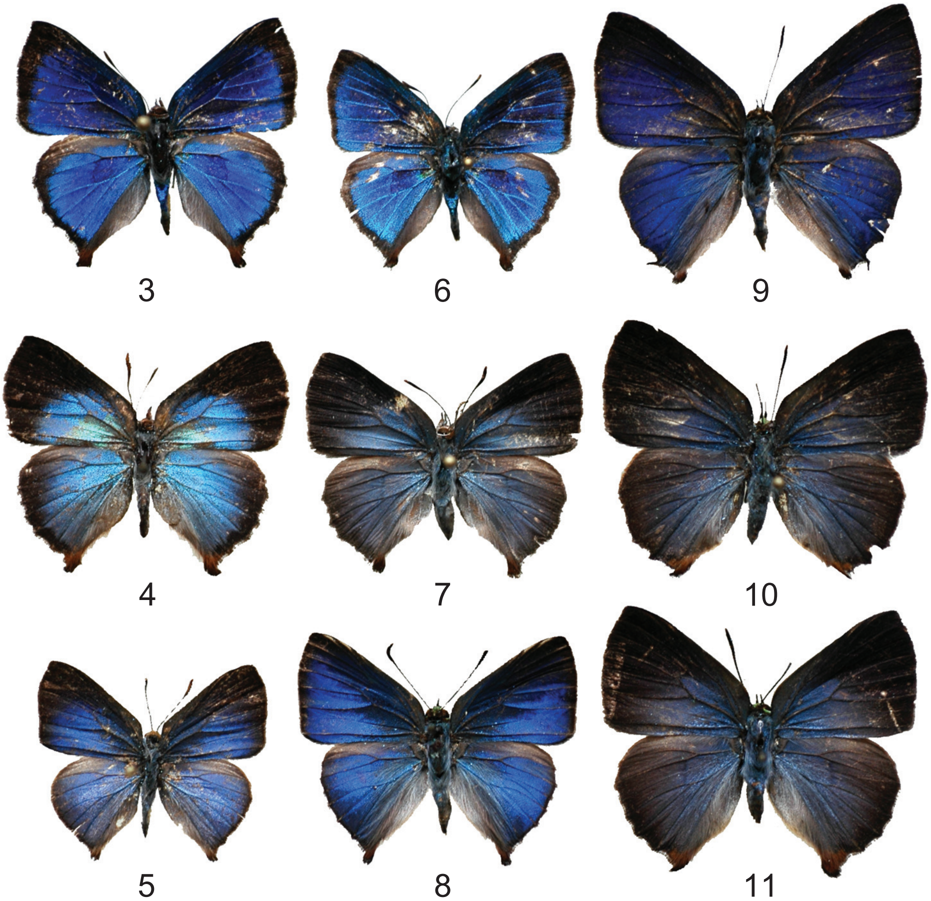
Cyanophrys acaste (Prittwitz, 1865) d'Abrera, 1995 – BRASIL-RS, Morro Reuter, 700 m, 15.III.1998 (nos 11–12: males); BRASIL-RS, Morro Reuter, 700 m, 14.IV.1996 (no. 14: male); BRASIL-PR, Pién, 900 m, 7–14.III.2000 (no. 15: male); BRASIL-RS, Dois Imãos, Picada Verão, 300 m, 25.III.1998 (no. 27: female); BRASIL-SC, São Bento do Sul, Serra Rio Natal, 600 m, 6–9.IV.2000 (no. 28: female).

Cyanophrys amyntor (Cramer, 1775) d'Abrera, 1995 – BRASIL-RS, São Leopoldo, 1.XI.1995 (nos 16, 19: males); BRASIL-RS, Montenegro, 16.XII.1995 (no. 17: male); BRASIL-RS, São Leopoldo, 22.IX.1994 (no.18: male); BRASIL-PR, Pién, 900 m, 1.IV.2000 (no. 20: male); BRASIL-SC, São Bento do Sul, Serra Rio Natal, 700 m, IV.2003 (no. 29: female).

Cyanophrys argentiniensis (Clench, 1946) d'Abrera, 1995 – COLOMBIA, Caldas, Cerro Aguacatal, 1600 m, 1.IV.1994 (no. 13: male).

Cyanophrys pseudolongula (Clench, 1946) d'Abrera,, 1995 – COLOMBIA, Caldas, El Aquila, 3.III.1996 (no. 6: male); COLOMBIA, Cerro Calvijo, 9.XII.1994 (nos 8–9: males); COLOMBIA, Guatapé, 11.III.1992 (no. 10: male); COLOMBIA, Caldas, Riosucio, Cerro Ingrumá, 2270 m, 19.VII.1994 (no. 7: male; no. 24: female); COLOMBIA, Caldas, Quebrada el Aquila, Mpio de Manizales, 1750 m, 24.VI. 1994 (no. 25: female); COLOMBIA, Caldas, Manizales, 12.VI.1994 (no. 26: female).

Cyanophrys remus (Hewitson, 1868) d'Abrera, 1995 – BRASIL-PR, Pién, 900 m, 22–25.III. 2000 (nos 1, 4–5: males); BRASIL-PR, Pién, 900 m, 1. IV. 2000 (no. 2: male); BRASIL-SC, São Bento do Sul, Serra Rio Natal, 600 m, 6–9.IV.2000 (no. 3: male; no. 22: female); BRASIL- SC, São Bento do Sul, Serra Rio Natal, 600 m, 16.IV.2000 (no. 21: female); BRASIL-PR, Pién, 7–14.III.2000 (no. 23: female).

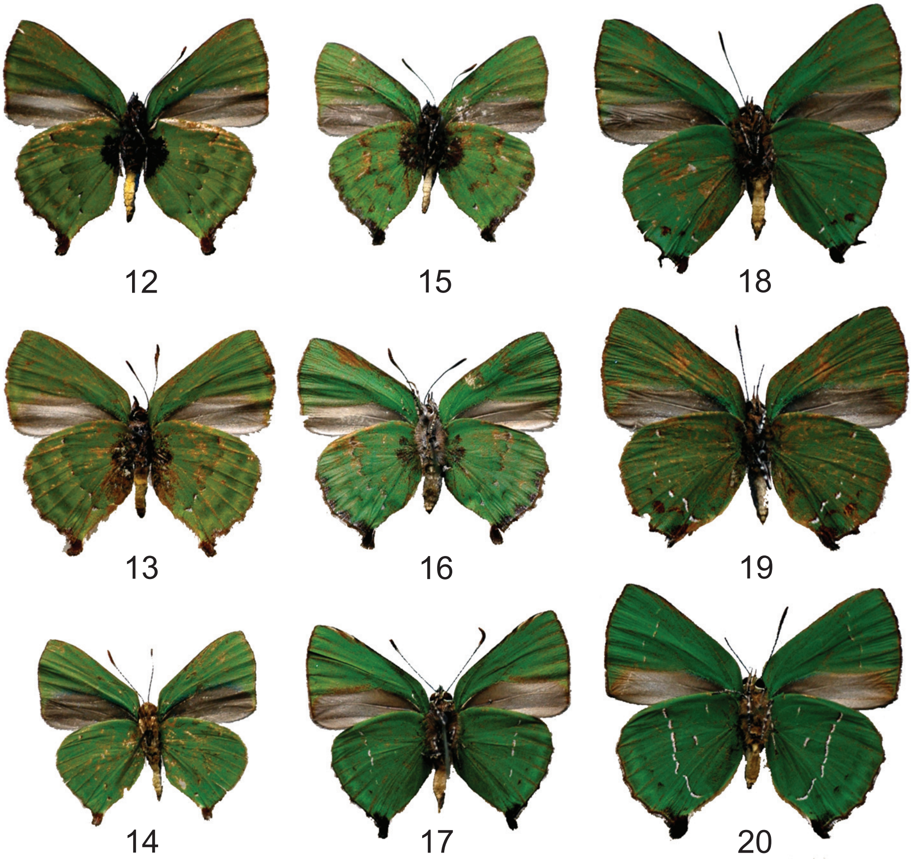


Figs 3–11. Specimens in dorsal aspect representing all *Cyanopyhrys* species examined (with individual number of the specimen): 3 = *C. pseudolongula* (Clench, 1946) male (7), 4 = *C. pseudolongula* female (25), 5 = *C. argentiniensis* (Clench, 1946) male (13), 6 = *C. remus* (Hewitson, 1868) male (4), 7 = *C. remus* female (22), 8 = *C. acaste* (Prittwitz, 1865) male (14)., 9 = *C. amyntor* (Cramer, 1775) male (19), 10 = *C. amyntor* female (29), 11 = *C. acaste* female (28). Scale (all specimens in the same magnification): fore wing length of specimen 7 (Fig. 3) measured from fore wing costal basis to apex 15 mm

Reflectance spectra measurements

Reflectivity measurements were made using an Avaspec 2048/2 fiber-optic spectrometer in specular arrangement, with unpolarized white (200–850nm wavelength) incident light. Reflectance was measured with the same incident light at the normal, at 5 mm distance from the central discalis of the fore wing dorsal surface and hind wing ventral surface of every butterfly examined, using a short (approximately 500μs) integration time. An Avaspec diffuse, white standard was used as a comparison sample for reflection factor measurements.

Numerical results of the measurements are listed in Table 1, and they are not necessarily exactly referred under Results or Discussion.



Figs 12–20. Specimens of *Cyanophrys* CLENCH, 1946 in ventral aspect, as shown in Figs 3–11. Scale as in Fig. 3

Table 1. Summary of measurements for the five *Cyanophrys* species

Species	Sex (number of individuals)	Type of reflectance spectrum	Figures (reflectance peak and reflectivity)
Cyanophrys acaste	male (4)	unimodal	485 nm / 36%
Cyanophrys acaste	female (2)	unimodal	450 nm / 26%
Cyanophrys amyntor	male (5)	unimodal	445 nm / 22%
Cyanophrys amyntor	female (1)	unimodal	450 nm / 31%
Cyanophrys argentiniensis	male (1)	unimodal	450 nm / 15%
Cyanophrys pseudolongula	male (5)	bimodal	250 nm / 8% and 440 nm / 22%
Cyanophrys pesudolongula	female (3)	bimodal	310 nm /12% and 510 nm /31%
Cyanophrys remus	male (5)	bimodal	290 nm / 7% and 490 nm / 17%
Cyanophrys remus	female (3)	unimodal	480 nm / 30%

RESULTS

Intraspecific reflectance comparisons

Cyanophrys remus individuals of the same sex produced identical spectra from their dorsal wing surfaces according to their sexes (Fig. 21).

Male-female dorsal wing surfaces – The spectral properties of conspecific male and female dorsal wing surfaces were dissimilar. They always differed in the position of their spectral wavelength peaks and the intensity of their reflectances. In general, males were less reflective but possessed more saturated colours with narrower wavelength peaks, while the females revealed broader reflectance peaks. The only exception was *Cyanophrys acaste*, whose males were far more reflective than the females. However, amongst the five *Cyanophrys* species examined, *C. acaste* exhibited the brightest male reflectivity (Fig. 22).

Male-male dorsal wing surfaces – Spectral properties of the male dorsal wing surfaces of different species were also dissimilar (Fig. 23). Beside the different wavelengths at which the peaks occur, and different reflectance values for the peaks, there were differences in the shape of the reflectance peaks too. The species *C. acaste* and *C. pseudolongula* displayed steep reflectance peaks compared to the broader peaks of the other three species examined. Although some species revealed a dual-peaked spectra, the second peak always lay in the ultraviolet (UV) region at or below 300 nm.

Female-female dorsal wing surfaces – Female spectral properties were less divergent between species than in males, although there remained a (minor) degree of species-specificity (Fig. 24). Again, the one dual-peaked reflectance (of *C. pseudolongula*) revealed an additional peak in the UV region at 300 nm.

Dual-peaked spectra

The male and female of *Cyanophrys pseudolongula*, and the male of *C. remus* individuals revealed dual-peaked spectra, with peaks at around 300 and 500 nm respectively, of which the lower one displays a moderate 15% reflectance at normal incidence. The male *C. pseudolongula* spectrum was similar to that of *C. remus* regarding reflectance and number of peaks, but the two species differ in their maximum reflectivities. The female *C. remus* spectrum possessed a single peak at around 400 nm with higher (20%) reflectance, while the female *C. pseudolongula* possessed a bimodal spectrum. The second peaks of all dual-peaked spectra, however, always occurred at 300 nm or less, which was not significant for animal behaviour (see Discussion).

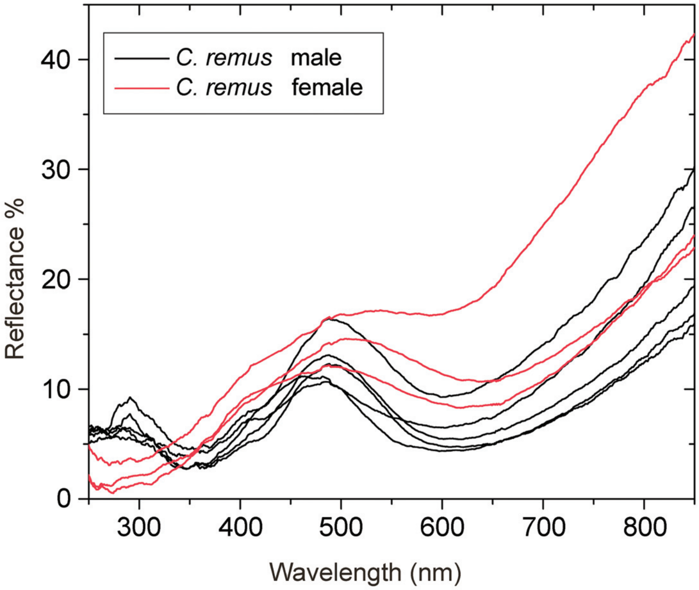


Fig. 21. Spectral properties of the five male and three female *Cyanophrys remus* (HEWITSON, 1868) individuals measured

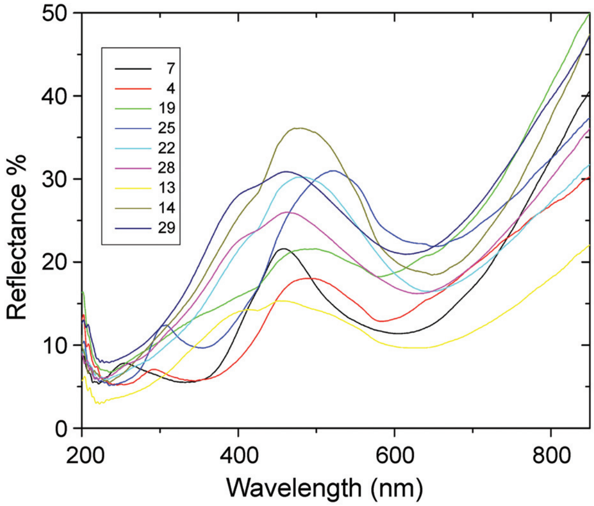


Fig. 22. Spectral properties of five *Cyanophrys* CLENCH, 1946 species representing both sexes measured in the dorsal surface of the right fore wing discal cell: *C. acaste* (PRITTWITZ, 1865) (male = 14, female = 28), *C. amyntor* (CRAMER, 1775) (male =19, female = 29), *C. argentiniensis* (CLENCH, 1946) (male = 13), *C. pseudolongula* (CLENCH, 1946) (male = 7, female = 25), and *C. remus* (HEWITSON, 1868) (male = 4, female = 22)

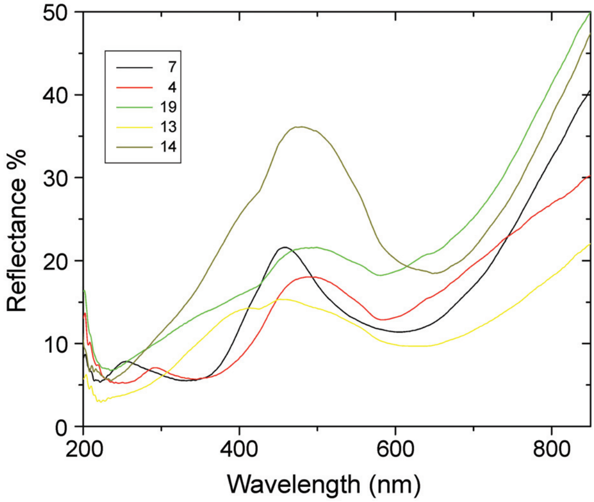


Fig. 23. Spectral properties of five *Cyanophrys* species representing only males measured in the dorsal surface of the right fore wing discal cell: *C. acaste* (PRITTWITZ, 1865) = 14, *C. amyntor* (CRAMER, 1775) = 19, *C. argentiniensis* (CLENCH, 1946) = 13, *C. pseudolongula* (CLENCH, 1946) = 7, and *C. remus* (HEWITSON, 1868) = 4

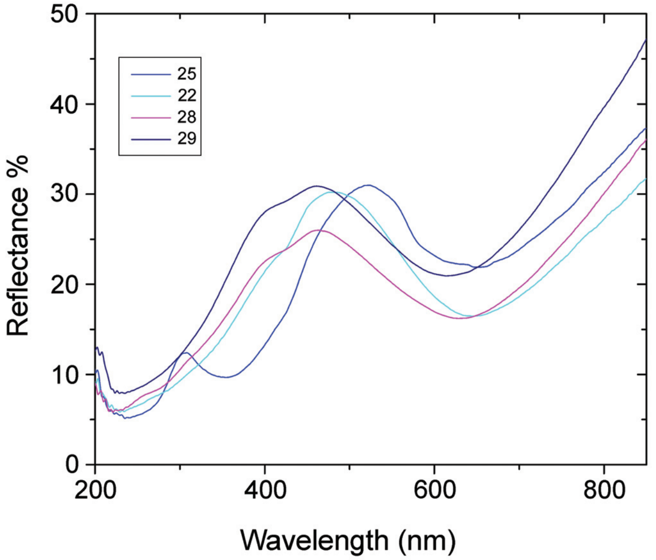


Fig. 24. Spectral properties of four *Cyanophrys* species representing females measured in the dorsal surface of the right fore wing discal cell: *C. acaste* (PRITTWITZ, 1865) = 28, *C. amyntor* (CRAMER, 1775) = 29, *C. pseudolongula* (CLENCH, 1946) = 25, and *C. remus* (HEWITSON, 1868) = 22

Ventral wing surfaces

The green ventral wing surfaces were almost equal in all species and sexes. Reflectance spectra in all the species revealed single peaks (Fig. 25). The UV and blue range reflectance remained below or at around 10%, then the reflectance curve increased sharply to reach a reflectance peak at around 585 nm – corresponding to the green colour observed by naked eye – then after a slight descent it ascended at wavelengths above 600–650 nm. These high reflectances beyond 600 nm may be due to a melanin pigment (see BÁLINT *et al.* 2005, PRUM *et al.* 2006). The only difference between species and sexes is the intensity of their reflectance peaks. *Cyanophrys argentiniensis* revealed the lowest spectral reflectance peak, but in general this species is the less reflective anyway, with a relatively low dorsal wing reflectivity also. In general, the only difference between species and sexes is the intensity of their reflectance peaks.

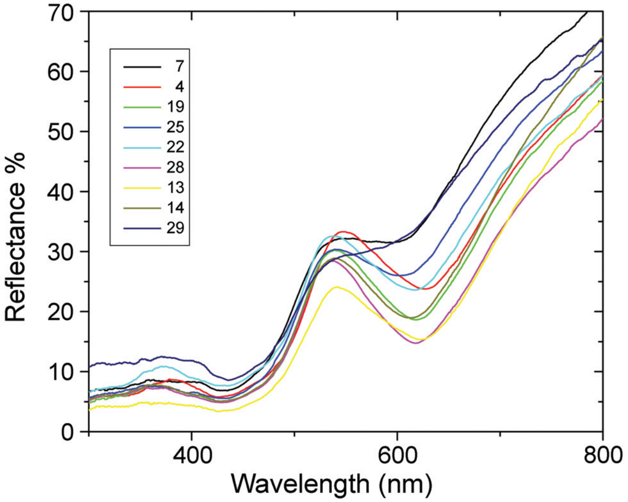


Fig. 25. Spectral properties of five *Cyanophrys* species representing both sexes measured in the ventral surface of the right hind wing discal cell: *C. acaste* (PRITTWITZ, 1865) (male = 14, female = 28), *C. amyntor* (CRAMER, 1775) (male = 19, female = 29), *C. argentiniensis* (CLENCH, 1946) (male = 13), *C. pseudolongula* (CLENCH, 1946) (male = 7, female = 25), and *C. remus* (HEWITSON, 1868) (male = 4, female = 22)

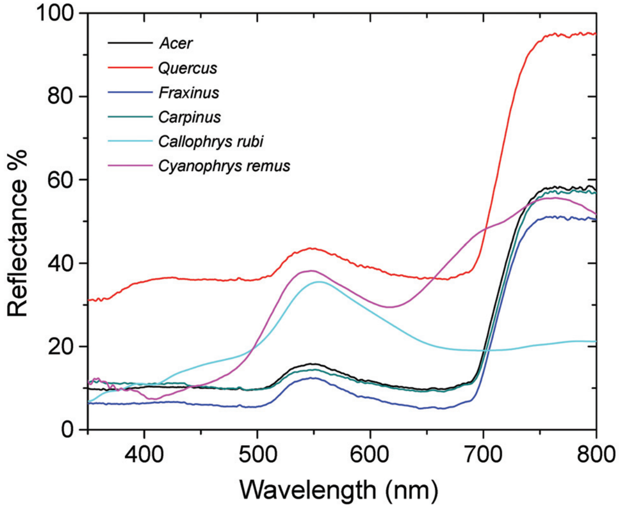


Fig. 26. Spectral properties of male *Cyanophrys remus* (HEWITSON, 1868) and *Callophrys rubi* (LINNAEUS, 1758) measured in the ventral surface of the right hind wing discal cell, plus various leaves measured

DISCUSSION

Dorsal wing surfaces

In this paper we posed two working hypotheses, which were positively supported with spectroscopic measurements taken from 29 *Cyanophrys* specimens from five species.

It emerged that the spectral properties of the male dorsal wing surfaces of *Cyanophrys* butterflies were species specific. This is in accordance with previous studies, which demonstrated for various lycaenid genera that the spectral properties of the male dorsal surface vary with species (BÁLINT, BOYER *et al.* 2006, BÁLINT, HORVÁTH *et al.* 2007, BÁLINT, KERTÉSZ *et al.* 2006, BÁLINT, WOJTUSIAK *et al.* 2007, BÁLINT *et al.* 2008).

It is probable that these species specific signals in males play a major role (along with pheromones) in mate recognition in the case of the three SE Brazilian species, considering that they appear morphologically similar and cohabit the same environments (for example in São Bento do Sul), and keep mating territories and perch practically at the same time of day (ROBBINS & DUARTE 2005). For example, in two cohabiting species, the very common *C. acaste* males possess the highest reflectivity measured in *Cyanophrys* at 480 nm, whilst the equally common *C. amyntor* is less reflective and its peak reflectance is shifted to 500 nm. The males of the mountanious forest species *C. remus* are the least reflective ones among the Brazilian triad and their spectral peaks occur at 490 nm. Since butterflies possess four types of cone cells that provide colour vision (SISON-MAGUS *et al.* 2006), it is possible that *Cyanophrys* butterflies have co-evolved (with the structural colour) sensitivity in the blue region that can discriminate between such subtle differences. Consequently, it is indeed probable that, the blue colour of male *Cyanophrys* butterflies is under the influence of sexual selection.

Other interesting results yielded by our research were the revelation that the female spectral properties are also dissimilar from those of the males, although the females of different species are similar in their reflectance spectra. They can be specifically characterized and discriminated from male spectra. This discovery suggests that female dorsal wing surfaces also play an important role in the communication of the species. It can be presumed that female dorsal surface is used for signals directed to opposite sex as males are perching high in forest edges and control the spaces below for potential mates. Hence males need species dependent signals to detect conspecific females avoiding unnecessary flights, especially in butterfly communities where several species with similar strategies coexist. Therefore female dorsal wing colours cannot be generalized as the ventral wing surfaces. Moreover the females of the three sympatric Brazilian species we examined are not identical regarding the spectral properties of their dorsal wing reflectivity, but *C. acaste* and *C. amyntor* females show almost identical spectral peak. We have to remember the highest spectral peak of *C. acaste*, which gives the clue that in this case most probably there is a strong stress in the pre mating barrier from the male sex because otherwise the two species *C. acaste* and *C. amyntor* are obviously differing in their male spectra. This phenomenon calls again the question whether butterfly females are really more attentive just to brighter males (SILBERGLIED 1984, VANE-WRIGHT 1984, KEMP 2006; *versus* WIKLUND 2003). If so, it is difficult to explain the spectral diversity of the Lycaenidae faunas (*cf.* BÁLINT, HORVÁTH *et al.* 2007).

More measurements have to be carried out to test whether female dorsal forewing reflectivity play any role in species-specific signalling. Finally we make the remark that higher female reflectivity (female brighter than male) is most probable is related to distance, hence lekking males can spot their mates more effectively.

In males of *C. remus* and *C. pseudolongula*, and in the female of the latter species, a secondary peak in reflectance occurs at 300 nm. Butterflies are known to possess ultraviolet vision but this is always in the region 350–400 nm (BRUNTON & MAJERUS 1995, TOVÉE 1995), hence the secondary reflectance peaks of *C. remus* and *C. pseudolongula* males cannot form visual signals. Moreover the wavelength 300 nm falls in the UV-B region, known to denature DNA and consequently destroy living tissues. This second peak is not artefact, certain structures – the ones in which the layered character is strong (for example in *C. remus*) – may give the phenomenon of "upper harmonics". This means a smaller amplitude reflectance maximum appearing at higher frequencies, i.e. shorter wavelengths. This is an inherent consequence of the layered structure, usually it is neglected because the small amplitude of this second maximum. These maxima appear in Fig. 22 around 280 nm, in Fig. 23 at 250 nm (black) and around 300 nm (red & blue), in

Fig. 24 (black & red), and in Fig 25 (blue). We think that this phenomenon has nothing to do with UV protection (*cf.* VIGNERON *et al.* 2005). Hence this minor reflectance peak is neither a visual signal nor a sign of a protecting mechanism, but most likely it is just a consequence of the layered character exhibited by the structure giving the structural colour.

Ventral wing surfaces

The ventral wing surfaces measured revealed almost identical spectra. We could not detect any pattern that could characterize a sex, a taxon or a certain geographical region. This indicates that the green colouration of the ventral wing surface, produced by a polycrystalline nano-architecture (KERTÉSZ *et. al.* 2006, BIRÓ *et al.* 2007), is a generalized signal, probably involved in camouflage against predators. This green colour, therefore, is under the influence of natural selection.

Further investigation is in progress to understand better this camouflage phenomenon. We have found that the spectral properties of *Acer*, *Carpinus*, *Fraxinus* and *Quercus* leaves used by perching male *Callophrys rubi* (LINNAEUS, 1758) individuals are identical with those measured for the ventral wing surfaces of the *Cyanophrys* butterflies (Fig. 26).

Diversification mechanism

Diversification at the species level requires barriers to gene exchange, and in the case of the dorsal (blue) fore wing signals the generation of pre-mating barriers is highly probable, as lycaenid eyes are calibrated to this special purpose (SISON-MAGUS *et al.* 2006). Moreover, dorsal forewing signals as pre-mating barriers can hypothetically work in all geographic models of speciation (FUTUYMA 1998). The pre-mating barriers based on dorsal fore wing signals can work in allopatric, parapatric and sympatric models, as well as in the founder effect. As it is presumed, morphological changes in colour-generating (photonic) structures can may be evolutionary less costly than evolving a new type of pigment, considering the "starting points" the butterflies possess for evolution (PARKER 2006, BIRÓ *et al.* 2008). Even in the theoretically most problematic sympatric and founder effect models, speciation can easily take place with the appearance of a new pre-mating barrier based on colour signals. Some evidence for how nanostructural changes are developed in polyommatine lycaenids of open habitats does exist (BIRÓ *et al.* 2003, LUKHTANOV *et al.* 2005). However, future research should aim to discover which kind of phenomena (*e.g.* genetic and developmental) lead to nanostructural changes in a butterfly's scale and how this change is stabilized at the population level in the case of butterflies living in forest habitats.

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