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# Inter-island variation in the butterfly *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889) (Lepidoptera, Satyrinae) in the Canary Islands

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## Summary

Samples of the endemic Canary grayling butterfly, *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889), were obtained from all five of the Canary Islands where it occurs. Each island population comprises a distinct subspecies but the differences between them are quantitative rather than qualitative ; hence a system is devised by which elements of the wing pattern are scored to permit quantitative analysis. The results demonstrate significant inter-island differences in wing size and wing pattern. The underside of the hindwing shows the greatest degree of inter-island variation. This is the only wing surface that is always visible in a resting butterfly ; its coloration is highly cryptic and it is suggested that the pattern was evolved in response to selection by predators long before *H. wyssii* or its ancestors reached the Canaries. Subsequent evolution of the details of the wing pattern differed from island to island because each island population was probably founded by few individuals with only a fraction of the genetic diversity of the species. It is postulated that the basic "grayling" wing pattern is determined by natural selection, but the precise expression of this pattern on each island is circumscribed by the limited gene pool of the original founders.

## Résumé

Des exemplaires du Satyride *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889), endémique des Iles Canaries, ont été récoltés dans les cinq îles de cet archipel où ils existent. Les populations de chaque île forment une sous-espèce distincte, mais les différences entre celles-ci sont plutôt quantitatives que qualitatives. On a donc établi un système basé sur certains éléments précis des ailes permettant une analyse quantitative. Les résultats ainsi obtenus prouvent l'existence de différences significatives entre les populations de chaque

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île en ce qui concerne la taille et le dessin des ailes. Le dessous des ailes postérieures est l'élément qui présente le plus fort degré de variation d'une île à l'autre. C'est en fait la seule partie de la surface des ailes qui est visible lorsque le papillon se pose. Son homochromie extrême est un élément de camouflage par mimétisme. On peut envisager que ce dessin a évolué du fait de la sélection par les prédateurs longtemps avant que *H. wyssii* ou ses ancêtres aient atteint les Canaries. L'évolution ultérieure des détails dans ce dessin des ailes fut différente d'une île à l'autre parce que la population de chaque île avait probablement été fondée par un petit nombre d'individus qui n'étaient chacun porteurs que d'une fraction de la diversité génétique de l'espèce. On peut donc penser que si le dessin typique «*Hipparchia*» du dessous des ailes postérieures est déterminé par sélection naturelle, la réalisation concrète de ce dessin sur chaque île se trouve différenciée du fait du stock de gènes incomplet des premiers arrivés «fondateurs».

## Zusammenfassung

Der Augenfalter *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889) ist auf den Kanaren endemisch. Untersuchungen an Material von allen fünf Inseln des Archipels, auf denen die Art vorkommt, ergaben, daß jede Inselpopulation eine eigenständige Unterart darstellt, die sich aber eher quantitativ als qualitativ von den anderen unterscheidet. Daher wurde ein System entwickelt, das durch die Untersuchung von Flügel-Zeichnungselementen eine quantitative Analyse erlaubt. Die Ergebnisse zeigen signifikante Unterschiede in Flügelgröße und Flügelzeichnung zwischen den Inselpopulationen. Die größte Variabilität weist die Unterseite des Hinterflügels auf. Dies ist die einzige Flügelfläche, die an einem ruhenden Falter stets sichtbar ist. Sie zeigt eine ausgeprägte Tarnfarbe, deren Muster vermutlich durch Feinddruck selektiert worden ist, bevor *H. wyssii* oder ihre Vorfahren die Kanaren erreichten. Die spätere Entwicklung der Details der Flügelzeichnung variiert von Insel zu Insel, weil jede Inselpopulation wahrscheinlich nur von wenigen Individuen -mit nur einen Bruchteil der genetischen Vielfalt der Art -begründet wurde. Es wird postuliert, daß das grundlegende *Hipparchia*-Flügelmuster durch natürliche Selektion bestimmt wird, aber die genaue Ausprägung dieses Musters auf jeder Insel vom begrenzten Genpool der ursprünglichen Gründer abhängt.

## Introduction

The Canary grayling butterfly, *Hipparchia (Pseudotergumia) wyssii* (Christ, 1889) (Lepidoptera, Satyrinae) is endemic to the five Canary Islands of Tenerife, La Gomera, Gran Canaria, La Palma and El Hierro (Fig. 1). Until recently little was known of this species and even its presence on one island, La Palma, was in doubt (LEESTMANS, 1975) ; however a comprehensive review which followed several collecting trips (WIEMERS, 1991) has established that the butterfly is relatively common

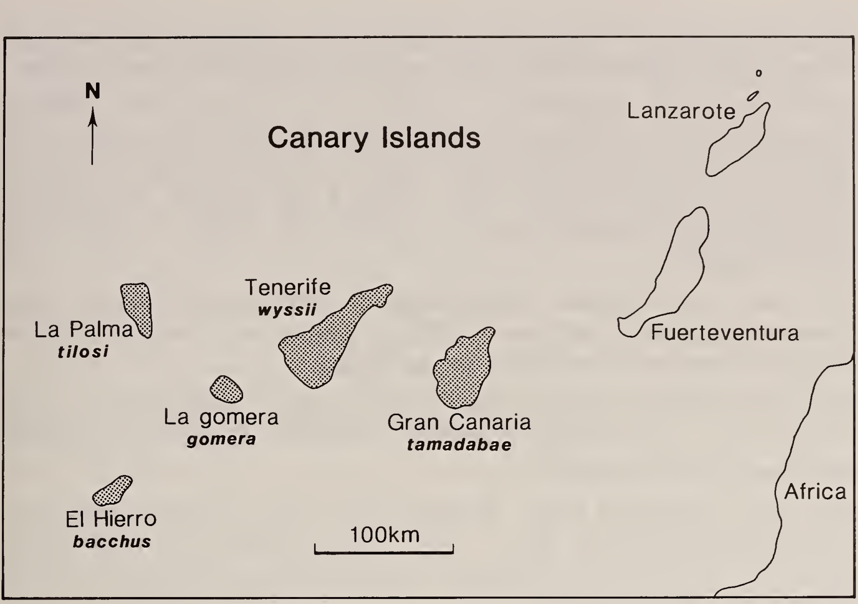

Fig. 1. The Canary Islands showing the distribution of the five subspecies of *Hipparchia wyssii*.

on Tenerife, La Gomera, La Palma and El Hierro (Herr Wiemers did not collect on Gran Canaria), and absent from the two eastern islands of Fuerteventura and Lanzarote, both of which are too dry for grass-feeding satyrine butterflies. This paper presents the results of our own sampling and field work on all five islands over the period 1987-91.

Grayling butterflies have a complex wing pattern, particularly on the underside, and the variation is difficult to quantify. Here we identify scorable and quantifiable phenotypic variation in wing pattern and coloration and use this to estimate the extent to which each island population is differentiated. Our paper is complementary to two previous analyses of variation in Canary Island satyrine butterflies : *Maniola jurtina* (Linnaeus, 1758) (Owen & Smith, 1990) and *Pararge xiphioides* Staudinger, 1871 (Owen & Smith, 1993).

## The island populations

Each island population is distinctive and we treat each as a subspecies ; in contrast Wiemers (1991) recognizes four species : *H. wyssii* (Tenerife and Gran Canaria), *H. gomera* (La Gomera), *H. bacchus* (El Hierro) and *H. tilosi* (La Palma). We recognize five subspecies, one on each island while agreeing that some or all of them may have diverged sufficiently to be designated as species ; as we discuss later, there is rarely conclusive evidence either way (from crossing) when dealing with allopatric populations and, in its absence, splitting should be avoided (Corbet & Pendlebury, 1992). Plates 1 and 2 show the complex but distinctive underside patterns of males and females of each of the five subspecies.

*H. wyssii wyssii* (Christ, 1890). Tenerife. Mostly confined to *Pinus canariensis* forest at altitudes of 1300 — 1700 m and also found above the pine forest zone to 2300 m at Las Cañadas.

*H. wyssii gomera* (Higgins, 1967). La Gomera. Widespread in open country and light woodland at 300 — 1200 m. (There is no natural pine forest on La Gomera.)

*H. wyssii tamadabae* Owen & Smith, 1992. Gran Canaria. Mainly in *P. canariensis* forest at 300 — 500 m but extending to 1800 m and especially associated with shallow barrancos. Known chiefly from the north-west of the island.

*H. wyssii bacchus* (Higgins, 1967). El Hierro. Strongly associated with vineyards in barrancos at 300 — 700 m and extending in small numbers to 1500 m in laurel forest, but apparently rare or absent in *P. canariensis* forest.

*H. wyssii tilosi* Manil, 1984. La Palma. Apparently widespread in deep and steep-sided barrancos above 500 m in mixed laurel/pine forest on the east and north-east side of the island, but probably absent from the extensive *P. canariensis* forest around the Caldera de Taburiente. This subspecies may be much more split up into relatively isolated populations than the others.

On all islands the butterflies are on the wing in July and August but can occur as early as May and as late as September. The early stages from four islands are described in Wiemers (1991). The larvae are grass-feeders but precisely which species of grass are utilized in the wild has not been determined. There is one breeding generation a year. Adult butterflies occasionally visit flowers but are more often seen visiting damp patches and ripe fruit, especially grapes ; on Gran Canaria, and probably also on Tenerife, they probe cracks in the bark for pine resin. On Tenerife and Gran Canaria in particular there is a marked downhill movement in the evening and an uphill movement in the morning. Most individuals involved are females. This behaviour is spectacular, especially in places where movement is funnelled by a dry barranco ; we have no explanation for it but suggest it may be associated with locating egg-laying sites or with diurnal temperature changes.

The cryptic coloration of the underside, especially of the hindwing, is superb. When at rest on a pine trunk with the forewing lowered, a butterfly is almost impossible to see. When a resting butterfly is approached it raises its forewings and exposes the eyespots and at first walks around the tree trunk, sometimes circling the trunk several times. This is presumed to be anti-predator behaviour but we have no observations of successful predation, only an attempted catch by a blue tit, *Parus caeruleus* Linnaeus, 1758, and two unsuccessful strikes by a large asiliid fly. Some of the butterflies in our samples have wing damage suggestive of unsuccessful attacks by lizards.

The existence of *H. wyssii* on four of the Canary Islands has been known since 1888-9 (review in Wiemers, 1991) but until 1966 it was well-known only from Tenerife, where it has been taken repeatedly. The rediscovery of populations on La Gomera and El Hierro in 1966 by Guichard and Ward (Guichard, 1967) was considered “unexpected and exciting...No butterflies of such distinctive appearance have been discovered in the Western Palaearctic Region for very many years” (Higgins, 1967). (Higgins was apparently unaware of earlier records for both islands dating from 1889 (Rebel & Rogenhofer, 1894) and of Nordman (1935) for La Gomera.) The La Palma population remained unknown until 1983 (Manil, 1984), possibly because its habitat is so inaccessible, while the true habitat and status of the Gran Canaria population seems to have been unknown until we discovered it in 1990 (Owen & Smith, 1992 and this paper).

## Source of samples and methods of scoring

In 1987-91 we visited all the islands where *H. wyssii* occurs and collected random samples, from single locations in the case of four islands and from six different and isolated populations, four of which are new records for the species, on La Palma. Samples were deliberately limited because of uncertainty as to exactly how common the species is on each island ; in the event we discovered that no island population is endangered except by habitat destruction resulting from increased cultivation. The butterflies were pinned and set for more detailed examination. Sample sizes for each island are given in Table 1.

Fig. 2 is a diagram of grayling wings showing the numbering system for space(s) where spots (border ocelli) may be present or absent ; it

Table 1

Inter-island variation for forewing length (mm) in *H. wyssii* in the Canary Islands

| Islands | T | G | C | P | H |
|---|---|---|---|---|---|
| | | | Males | | |
| $\bar{x}$ | 29.2 | 29.5 | 28.0 | 29.7 | 30.1 |
| $s$ | 1.7 | 1.0 | 1.0 | 1.6 | 0.5 |
| $n$ | 3 | 16 | 24 | 25 | 6 |
| | | | Females | | |
| $\bar{x}$ | 29.7 | 31.7 | 28.8 | 29.5* | 31.8 |
| $s$ | 1.8 | 1.5 | 1.4 | 3.0 | 1.0 |
| $n$ | 16 | 3 | 16 | 9 | 15 |

Island abbreviations : T = Tenerife, G = La Gomera, C = Gran Canaria, P = La Palma, H = El Hierro.

* One very small and otherwise aberrant female (22.8 mm), much the smallest individual of either sex recorded, substantially reduces the mean of this sample, without which it is 30.3 mm ($n = 8$).

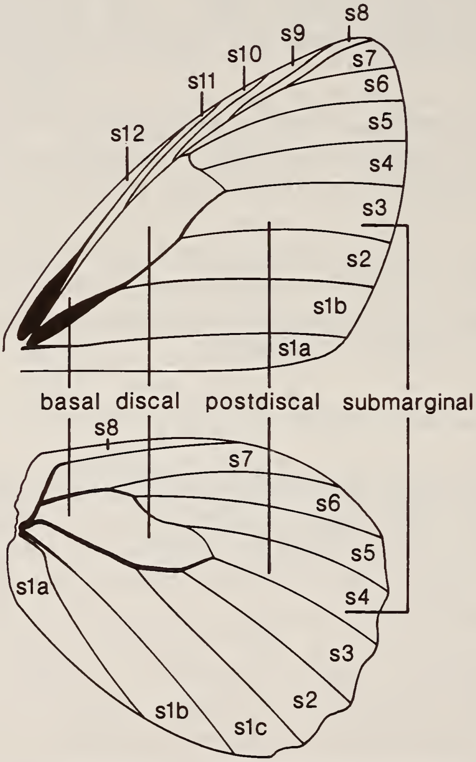

Fig. 2. Diagram of the wings of *Hipparchia wyssii* showing the nomenclature of spaces (s) and the location of other wing pattern elements mentioned in the text.

also shows the position of other elements of wing structure mentioned in the text. Each butterfly was examined by eye using a × 2 lens. All the scoring was done by one of us (DASS) to ensure consistency. The characters scored are listed in Appendix I. Forewing length was measured (with vernier calipers to an accuracy of 0.1 mm) from the apex to the point where the basal area joins the thorax. It was possible to measure forewing length in every specimen collected but for some other characters not all specimens could be scored because of damage.

## Analysis

### *Size*

Table 1 shows the mean forewing lengths for males and females. The rank order of forewing length for males is El Hierro > La Palma > La Gomera > Tenerife > Gran Canaria. If the single aberrant female from La Palma is omitted (Table 1), the rank order of forewing length for females is similar : El Hierro > La Gomera > La Palma > Tenerife > Gran Canaria.

Table 2 shows the results of a one-way ANOVA for forewing length. The overall values of variance ratios ($F$) are significant for both males and females at the 0.1 per cent level, indicating that forewing length (which reflects body size) has diverged significantly among the island populations. Individual island comparisons are shown in Table 2 only where they are significant. Of the seven significant comparisons, five

Table 2

One-way analysis of variance for forewing length in *H. wyssii* from the Canary Islands

| Source of variation | Degrees of freedom | Variance ratio ($F$) | Probability |
|---|---|---|---|
| | Males | | |
| All islands | 4,69 | 7.25 | $<0.001$ |
| C v G | 1,72 | 12.51 | $<0.001$ |
| C v P | 1,72 | 22.13 | $<0.001$ |
| C v H | 1,72 | 13.67 | $<0.001$ |
| | Females | | |
| All islands | 4,54 | 6.88 | $<0.001$ |
| T v H | 1,57 | 11.39 | $<0.01$ |
| C v G | 1,57 | 6.95 | $<0.05$ |
| C v H | 1,57 | 22.79 | $<0.001$ |
| P v H | 1,57 | 9.88 | $<0.01$ |

Island abbreviations as in Table 1. Comparisons for individual island pairs are included only if statistically significant.

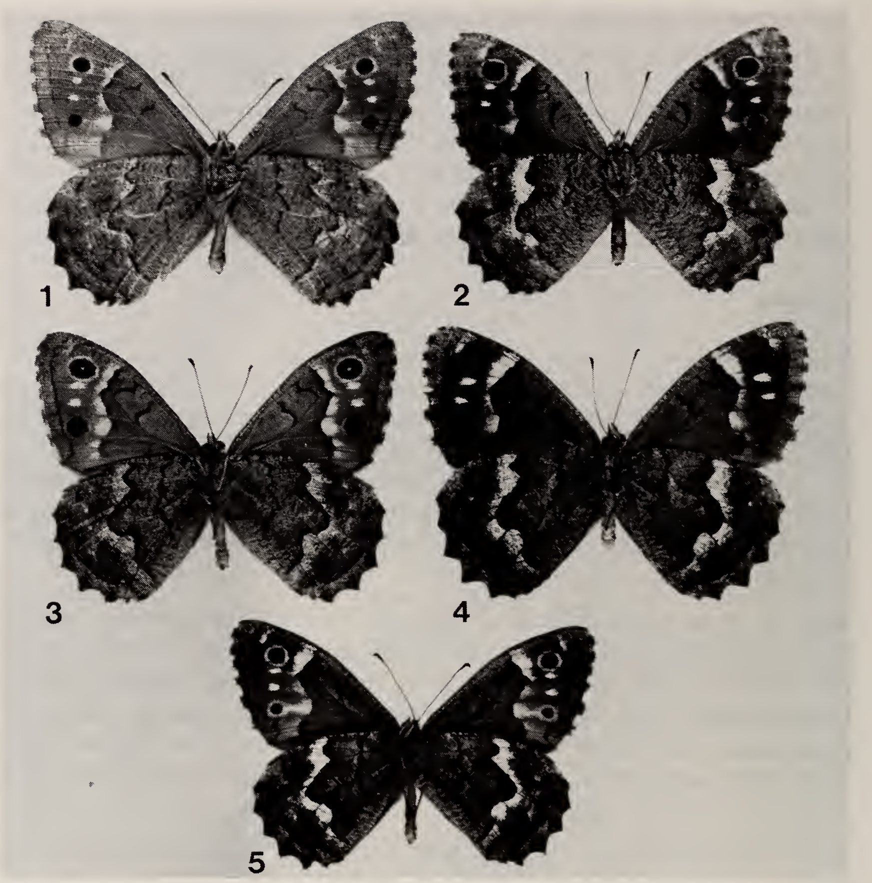

Plate 1. *Hipparchia wyssii*, undersides of males (actual size).
1 — *H. w. wyssii* (Tenerife) ; 2 — *H. w. gomera* (La Gomera) ; 3 — *H. w. tamadabae* (Gran Canaria) ; 4 — *H. w. bacchus* (El Hierro) ; 5 — *H. w. tilosi* (La Palma).

involve Gran Canaria (the smallest subspecies) and four El Hierro (the largest). Therefore, size may be a diagnostic character for at least these two islands but it is possible that larger samples would reveal that all five populations are statistically different in size. The marked difference in size between Gran Canaria and El Hierro butterflies can be seen in Plates 1 and 2.

### *Hindwing border ocellus (spotting) phenotypes*

A list of hindwing spotting phenotypes is given in Appendix III. The spots, which belong to the border ocellus system (Nijhout, 1991), are

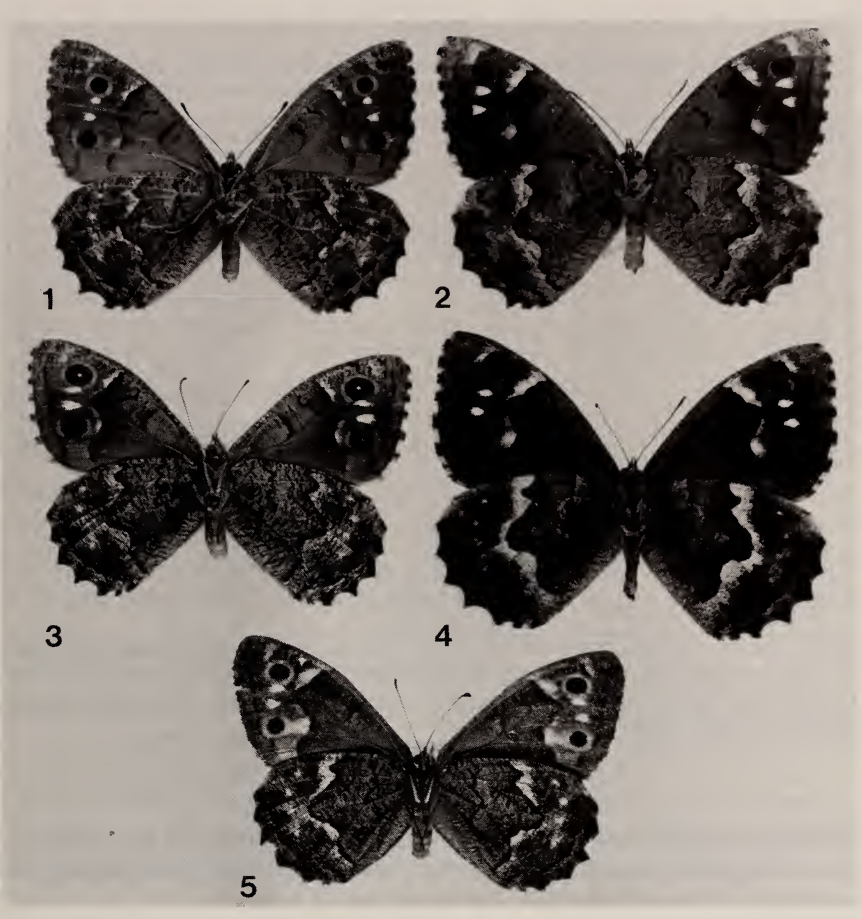

Plate 2. *Hipparchia wyssii*, undersides of females (actual size).
1 — *H. w. wyssii* (Tenerife) ; 2 — *H. w. gomera* (La Gomera) ; 3 — *H. w. tamadabae* (Gran Canaria) ; 4 — *H. w. bacchus* (El Hierro) ; 5 — *H. w. tilosi* (La Palma).

numbered antero-posterially from the costal side as follows : 1 (space 6), 2 (s5), 3 (s4), 4 (s3), 5 (s2) (the position of the spaces is shown in Fig. 2). Spots 1 — 4 are pale ochreous or white on the upperside but invariably white on the underside. Spot 5 is always black and may be white-pupilled (underlined) or ringed with a yellowish halo (superscript bar).

Table 3 shows the distribution of hindwing spotting phenotypes on each of the five islands. As shown, we recorded 18 upperside (UPH) phenotypes (A-R), and 22 underside hindwing (UNH) phenotypes (1-22).

Table 3

Distribution of the hindwing upper and underside border ocellus phenotypes of *H. wyssii* (see Appendix III for codes) on the five Canary Islands where it occurs

| Phenotype | T | G | C | H | P | Phenotype | T | G | C | H | P | Phenotype | T | G | C | H | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| § A01 | | | + | | | # B17 | + | | | + | | § H15 | | | | | + |
| § A02 | | | + | | | # B18 | + | | | + | | § H17 | | | | | + |
| § A07 | | | + | | | * B19 | + | | | | | § H20 | | | | | + |
| # A09 | + | | + | | | # B20 | + | + | + | + | | * I21 | | | + | | |
| § A12 | | + | | | | # B21 | | | + | | | * J20 | | | | | + |
| § A13 | | + | | | | * B22 | + | | | | | * K07 | | | | + | |
| § A17 | | | + | | | * C20 | + | | | | | * K20 | | | | + | |
| # B01 | + | + | + | + | | § C21 | | | | | + | * L07 | | | | | + |
| § B02 | | | + | | | * D18 | + | | | | | * L20 | + | | | | |
| # B03 | + | + | | + | + | § E09 | | | | | + | # L21 | | | + | | + |
| § B04 | | | + | | | * E15 | + | | | | | * M20 | | | | | + |
| # B05 | + | | + | | | * E17 | | | | | + | * N02 | | | + | | |
| * B06 | + | | | | | § E20 | | | | | + | * O20 | | | | | + |
| # B07 | | + | + | + | | § E21 | | | | | + | * P08 | | | + | | |
| # B08 | | + | + | | | * F07 | | | | + | | * P16 | | | + | | |
| § B09 | | | | | + | * F14 | | | + | | | * P20 | | | | | + |
| § B10 | | | | + | | * F15 | | | | + | | * P21 | + | | + | | |
| * B11 | + | | | | | § F20 | | | | | + | * Q20 | | | | | + |
| § B15 | | + | | | + | * G20 | | | | | + | * R21 | | | + | | |
| * B16 | | | + | | | | | | | | | | | | | | |
| | | | | | | | | | | | | Total phenotypes | 16 | 8 | 22 | 11 | 20 |

§ recorded in males only (19), * recorded in females only (28), # recorded in both sexes (11). Island abbreviations as in Table 1.

58 different combinations were recorded ; the theoretical maximum is 396 though the actual number is probably far less. Considering the small size of some samples, however, many more phenotypes would be expected in larger samples, especially in males from Tenerife (n = 3) and females from La Gomera (n = 3). Nineteen phenotypes occur in males only, 28 in females only and 11 in both sexes : females are thus more variable than males.

Table 4 summarizes inter-island differences in the distribution of hindwing phenotypes and compares hindwing diversity on each of the five islands. Of the 58 hindwing phenotypes recorded only 12 (≃ 20%) occur on more than one island, none is found on all five islands and only three (≃ 5%) occur on four islands. This alone suggests considerable inter-island diversification.

The distance coefficients for phenotypes shared with other islands (Table 6D) show that La Palma has the most distinct population, followed by Gran Canaria, Tenerife and La Gomera/El Hierro. La

Table 4

Analysis of the inter-island distributions (Table 3) of the hindwing phenotypes of *H. wyssii* (Appendix III) in the Canary Islands, with the phenotypic diversity on each island

| Islands | T | G | C | H | P | *N* |
|---|---|---|---|---|---|---|
| Number of phenotypes (both sexes) | 16 | 8 | 22 | 11 | 20 | 58 |
| Sample size | 18 | 18 | 36 | 21 | 30 | 123 |
| Number phenotypes shared between 4 islands | 3 | 3 | 2 | 3 | 1 | 3 |
| Number phenotypes shared between 3 islands | 0 | 1 | 1 | 1 | 0 | 1 |
| Number phenotypes shared between 2 islands | 5 | 2 | 5 | 2 | 2 | 8 |
| Total shared phenotypes | 8 | 6 | 8 | 6 | 3 | 12 |
| Mean % phenotypes shared with other islands | 15.0 | 16.4 | 11.0 | 16.3 | 4.1 | — |
| Mean phenetic distance from other islands | 0.42 | 0.42 | 0.47 | 0.45 | 0.52 | |
| Total unique phenotypes | 8 | 2 | 14 | 5 | 17 | 46 |
| Per cent unique phenotypes | 50.0 | 25.0 | 63.6 | 45.5 | 85.0 | — |
| Margalef Diversity Index ($D_{Mg}$) | 5.19 | 2.42 | 5.86 | 3.29 | 5.59 | |
| Berger-Parker Diversity Index ($1/d$) | 4.50 | 2.25 | 5.14 | 4.20 | 7.50 | — |

Island abbreviations as in Table 1.

Palma is also the most distinctive population in terms of the percentage of unique phenotypes, followed again by Gran Canaria and Tenerife.

Small sample size in one or the other sex from some islands necessitates combining sexes to estimate phenotypic diversity. Although this procedure inevitably involves the loss of some resolving power, the results are nevertheless unambiguous. We use two contrasting measures of diversity, the Margalef Index and the Berger-Parker Index (MAGGURAN, 1988). The former is primarily a measure of richness (number of phenotypes) (CLIFFORD & STEPHENSON, 1975) and has the disadvantage that it is strongly influenced by sample size (SOUTHWOOD, 1978) ; the latter emphasises evenness (or dominance) and is little affected by sample size (MAY, 1975). In this case, where all samples are fairly small, the Berger-Parker Index is preferred although encouragingly the rankings for the two indices are in substantial agreement. The La Palma (Berger-Parker) and Gran Canaria (Margalef) populations have the highest diversity, El Hierro and La Gomera (especially) the lowest, with Tenerife intermediate (both indices agree on the ranking of the latter three islands).

In general the larger islands (Tenerife, Gran Canaria and La Palma) are more diverse than the smaller (El Hierro and La Gomera), as could be predicted from biogeographical theory (MACARTHUR & WILSON, 1967). The high diversity on La Palma, in particular, is enigmatic : it may result from independent evolution of sub-populations in relative isolation within deep barrancos, a situation which probably does not prevail on the other islands.

Table 5
Mean values for spots, pupils and halos comprising the hindwing border ocellus system in *H. wyssii* from the Canary Islands

| Islands | T | G | C | H | P |
|---|---|---|---|---|---|
| | Males | | | | |
| UPH spot average (max. 5) | 1.0 | 0.9 | 0.7 | 1.0 | 1.7 § |
| UNH spot average (max. 5) | 3.5 | 2.8 | 2.7 | 1.8 | 4.3 § |
| Pupil average (max. 6) | 0.0 | 0.1 | 2.0 § | 0.0 | 0.2 |
| Halo average (max. 6) | 1.7 | 1.7 | 0.5 | 1.0 | 2.2 § |
| *N (N*)* | 3 (2) | 16 | 24 (21) | 6 | 25 (22) |
| | Females | | | | |
| UPH spot average (max. 5) | 1.6 | 1.0 | 2.7 | 1.8 | 3.8 § |
| UNH spot average (max. 5) | 3.9 | 2.5 | 3.9 | 3.3 | 4.8 § |
| Pupil average (max. 6) | 0.5 | 0.0 | 3.1 § | 0.0 | 0.1 |
| Halo average (max. 6) | 2.4 | 2.0 | 2.3 | 1.2 | 4.7 § |
| *N (N*)* | 16 | 3 (2) | 16 (15) | 15 | 9 (8) |

* Numbers in parenthesis are sample sizes for spot averages reduced due to hindwing damage in some specimens. § Sample means significantly different (in *t* tests) from others in the same row. Island abbreviations as in Table 1.

Table 5 shows the UPH and UNH spot averages for males and females for each island. Correlation for UPH and UNH spot number in individuals is low and not significant in either males ($r = 0.070$, $n = 68$) or females ($r = 0.073$, $n = 55$) ; Nijhout (1991) has emphasised that dorsal and ventral wing coloration patterns develop from epithelial monolayers within separate compartments and that correlation between them is by no means inevitable. As shown, La Palma has the highest values for spot average for both UPH and UNH. El Hierro and La Gomera have the lowest values with Tenerife and Gran Canaria intermediate.

The frequency of white pupils in the six black spots (border ocelli) (UPF/UNF s6 and s3 and UPH/UNH s2) and of the yellow halos around the same spots, provides a set of characters additional to hindwing spotting which can be used to differentiate populations. Table 5 gives pupil and halo averages for males and females for each island. The sum of pupils (maximum 6) and halos (maximum 6) for an individual butterfly gives a measure which we call spot enhancement (maximum 12) ; both pupils and halos render the black spots more distinctive and conspicuous. Males and females from La Palma and Gran Canaria have significantly higher enhancement values than the other populations but it is obtained by different means : mainly by pupillation on Gran Canaria (a consistently diagnostic feature of ssp. *tamadabae*) and by the development of halos in ssp. *tilosi* from La Palma. Both features are recorded from some of the other islands but less distinctly and much less frequently. On La Palma and Gran Canaria, the black spots tend to be larger and, when combined with white pupils and yellow halos, they are rendered much more apparent.

The ssp. *bacchus* phenotype is also highly distinctive in a quite different way from ssp. *tilosi* or ssp. *tamadabae*, because of the intense contrast between the postdiscal black line (element **f** of the central symmetry system (Nijhout, 1991)) and the band of white background immediately distal to it, especially on the UNH (Plates 1 and 2) ; ssp. *bacchus* has low values for spot average and much the lowest development of spot enhancement (Table 5). As the background of the *bacchus* wing is extensively melanised, several other black pattern elements (**d**, **e** and **i** (Nijhout, 1991)) are also relatively obscured. Subspecies *gomera* is intermediate between ssp. *bacchus* and ssp. *wyssii* in all the above respects (Plates 1-2).

Table 6
Matrices showing mean Euclidean distances (*MED*)
for five *H. wyssii* OTUs in the Canary Islands :
(A) males, (B) females, (C) combined sexes,
(D) hindwing spotting phenotypes (both sexes) (Table 3, Appendix III).
A-C are based on 34 non-metric characters and D
on numbers of phenotypes shared between islands (Table 4)

| | | T | G | C | H | P | |
|---|---|---|---|---|---|---|---|
| A | T | — | 0.359 | 0.409 | 0.371 | 0.544 | B |
| | G | 0.410 | — | 0.522 | 0.321 | 0.585 | |
| | C | 0.296 | 0.434 | — | 0.519 | 0.580 | |
| | H | 0.484 | 0.330 | 0.469 | — | 0.588 | |
| | P | 0.483 | 0.399 | 0.507 | 0.509 | — | |
| C | T | — | 0.842 | 0.839 | 0.750 | 0.970 | D |
| | G | 0.386 | — | 0.846 | 0.733 | 0.923 | |
| | C | 0.355 | 0.479 | — | 0.900 | 0.976 | |
| | H | 0.433 | 0.326 | 0.494 | — | 0.967 | |
| | P | 0.513 | 0.497 | 0.544 | 0.548 | — | |

Kendall's rank correlation for A and B is not significant ($\tau = 0.4$, $P = 0.11$) ; C and D are significantly correlated ($\tau = 0.822$, $P = 0.04$). Island abbreviations as in Table 1.

*Phenetic distance coefficients*

The phenotypes of all members of the genus *Hipparchia* Fabricius, 1807 are difficult to measure as much of the variation is quantitative and therefore judgment of it subjective. Hence for the calculation of phenetic distance coefficients (Table 6), we have chosen 34 non-metric characters (Appendix I) which are discrete (i.e. can be consistently scored as present or absent) and variable in frequency within or between islands. This statement does not imply that these characters are the only ones by which the five island populations can be compared and differentiated, nor that they are necessarily even the most distinctive. Many characters are manifested only or mainly in males (9) or females (7) ; those which are variable in both sexes (18) nevertheless differ in frequency and so they are scored separately for males and females. Therefore the matrices (Table 6) are based on 27 characters for males, 25 for females and 52 for the combined sexes. As shown in the character matrix (Appendix II), few characters are absolutely diagnostic, most differing only quantitatively between islands. Hence each character score is weighted (0-100%) for its comparative frequency. The data in Table 6 represent the Euclidean distance *MED* (Sneath & Sokal, 1973) between pairs of island populations (OTUs). *ED* is calculated for each OTU (subspecies) pair using the formula :

$$ED_{jk} = [\Sigma(X_{ij} - X_{ik})^2]^{1/2}$$

where $X_{ij}$ and $X_{ik}$ are the scores of OTUs (subspecies) j and k for character i. Mean Euclidean distances (*MED*) over all characters are calculated as :

$$MED_{jk} = \sqrt{[\Sigma(X_{ij} - X_{ik})^2]/n}$$

where *n* is the number of characters.
Comparing the distance values (*MED*) between sexes (Table 6A, B, Fig. 3A, B) it is clear that females have in general diverged further than males. In the case of La Palma this applies to the female *MED* values compared to all other islands ; for Gran Canaria it is confined mainly to the comparison with Tenerife. Furthermore, the differences between the male and female phenograms (Fig. 3), and the absence of any significant rank correlation between their inter-island phenetic distances (Table 6), strongly suggest that there has been a degree of independence in the evolution of the phenotype of the two sexes, the male being the more conservative .

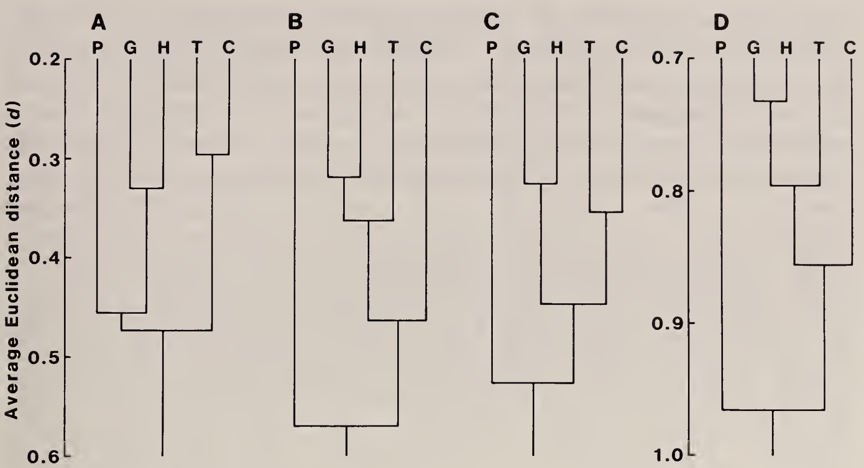

Fig. 3. Phenograms, derived by UPGMA, showing the mean Euclidean distances (*MED*) (Table 6) between the five subspecies of *Hipparchia wyssii* : A, males ; B, females ; C, combined sexes ; D, hindwing border ocellus phenotypes (both sexes) shared between islands (Table 3). Island abbreviations as in Table 1.

Considering combined sexes (Table 6C), La Palma (mean distance = 0.523) is the most distinctive followed by Gran Canaria (0.468). El Hierro (0.450) is intermediate, with Tenerife and La Gomera (both 0.422) the least distinctive on average. The two most similar populations are El Hierro and La Gomera. However, there is no rank correlation (Siegel & Castellan, 1988) between the geographical distances separating islands and phenetic distances (Kendall's $\tau$ (tau) = 0.422 ; $P = 0.11$).

In Table 6D we compare the islands by numbers of shared hindwing phenotypes. The isolation of La Palma and the closeness of La Gomera and El Hierro are again clear and, as above, there is no rank correlation between the physical distance separating islands and the number of shared phenotypes ($\tau = 0.244$ ; $P = 0.38$). Encouragingly, however, the two methods of inter-island comparison (Table 6C, D) are themselves significantly correlated by rank ($\tau = 0.822$ ; $P = 0.04$).

## Interpretation of inter-island variation

The phenograms in Fig. 3 are derived by the UPGMA method (Sneath & Sokal, 1973) from the data in Table 6. The relative isolation of the La Palma subspecies is evident in all the phenograms ; La Gomera and El Hierro form a cluster ; Tenerife and Gran Canaria may also form a cluster, possibly for male phenotypes only (Table 6A, 6C), but 6B and 6D suggest that Tenerife is closer to La Gomera/El Hierro with Gran Canaria more isolated. The raw data for males (Table 6A) indicate that ssp. *tilosi* (La Palma) is closer to ssp. *gomera* (La Gomera) than to any other but this is not the case for females. The phenetic distance of *ssp. tilosi* females from all other subspecies would suggest either a comparatively early dichotomy from the ancestral stock or more recent but rapid evolution. To explain this anomaly it is necessary to postulate different rates of evolution in males and females, the former being relatively conservative and the latter evolving rather rapidly, especially on La Palma. All data sets (Table 6) show that *ssp. tamadabae* (Gran Canaria) is closest to *ssp. wyssii* (Tenerife). In this case too, however, there is a sex difference, the males being much closer than the females. The El Hierro subspecies (ssp. *bacchus*) is undoubtedly closest to ssp. *gomera* and is equally distinctive, mainly due to the dark background (unscored) (Plates 1 & 2), in both sexes. It should be noted, however, that Wiemers (1991) observed that the eggs of these two subspecies are quite dissimilar.

## The origin and relationships of *H. wyssii*

There are three other species belonging to the subgenus *Pseudotergumia* Agenjo, 1947 (Kudrna, 1977). If examined comparatively in the manner advocated by Harvey & Pagel (1991), they are the outgroup for reconstructing ancestral character states. *H. fidia* (Linnaeus, 1767) is a west Mediterranean species ranging from Morocco, Algeria and Tunisia through Portugal, Spain and S. France to Italy ; *H. pisidice* Klug, 1832 occurs in the Middle East from Sinai through Jordan, Palestine, Lebanon and Syria to south Turkey ; *H. tewfiki* (Wiltshire, 1949) is a relict endemic restricted to Yemen and southwest Arabia. All three species share with *H. wyssii tamadabae* the white pupilling of the two forewing ocelli in s6 and s3 (UPF and UNF). These characters are likely to be primitive for the subgenus and their absence from most individuals of the other subspecies of *H. wyssii* is probably due to loss. There are several other similarities between ssp. *tamadabae* and the other *Pseudotergumia* species (the nomenclature of the following pattern elements follows Nijhout (1991) : first, the bold black proximal band of the central symmetry system (element **d**), which bisects the discal cell (UNF) ; second, bold discal spots (element **e**) on the discoidal vein (UNF) and, third, bold proximal (medial) and distal (postmedial) bands (elements **d** and **f**) of the central symmetry system (UNH), given in our original description of ssp. *tamadabae* (Owen & Smith, 1992). All things considered, it seems likely that *H. wyssii tamadabae* is closest to the ancestral *Pseudotergumia* (and *Hipparchia*) phenotype. In other words, the states of some of the above characters in most individuals of *H. wyssii* ssp. *wyssii, gomera, bacchus* and *tilosi* are derived.

The origin of *H. wyssii* itself is a matter for conjecture. On the evidence of present distributions, an origin for *H. wyssii* from *H. fidia* stock, which inhabited the western Mediterranean area, seems the most plausible. Indeed, while admitting that *Hipparchia* phenotypes are in general conservative, the adult phenotype of *H. fidia* is in many respects close to *H. wyssii tamadabae*. However, from a comparison of the male genitalia and androconia, Kudrna (1977) believed *H. wyssii* to be closer to *H. tewfiki* than to either *H. fidia* or *H. pisidice*. Judging from his excellent figures of the very similar genitalia and androconia of all the *Pseudotergumia* species, his conclusion requires exceedingly fine distinctions to be made, mainly on grounds of size. As is commonly the case when genitalia characters are used in insect taxonomy, no allowance was made for allometry (Gould, 1966) : *H. tewfiki* is considerably smaller than all other species of *Pseudotergumia* but, of the subspecies of *H. wyssii* examined by Kudrna, is closest in body size to ssp. *wyssii* (which he believed inhabited both Tenerife and Gran Canaria). The above remarks notwithstanding, as the only worker to have examined all known museum specimens of the four *Pseudotergumia* species, we tentatively accept Kudrna's conclusion that *H. wyssii* is closer to *H. tewfiki* than to *H. fidia*. In view of the conservatism of *Hipparchia* adult phenotypes and the considerable continuous variation between individuals within taxa, a protein or DNA study is needed to reach more robust conclusions.

If *H. wyssii* and *H. tewfiki* are indeed closely related then their present distributions, in the Canaries and southwest Arabia, respectively, are highly disjunct. To account for the presence of *H. wyssii* in the Canary Islands, it is therefore necessary to invoke both vicariance and several island-hopping events. We argue that neither is improbable as both are prevalent features of the flora and fauna of the Canary Islands. First, during the Miocene, southern Europe and the present Sahara Desert area were covered with subtropical to tropical evergreen forests (Axelrod, 1986). As drier climates spread through the Upper Miocene and Pliocene, disjunctions in range developed, which are well-documented for the flora (Bramwell, 1976) resulting in highly disjunct distributions between, on the one hand, the Canary Islands and, on the other, far-distant locations such as Arabia, Socotra, Mauritius, the East African highlands, the Himalayas and south Asia. Two of these disjunctions are particularly relevant to a possible scenario for the origin of *H. wyssii* : *Pinus canariensis* may be most closely related to *P. roxburghii* of the western Himalaya, with fossil relatives in southwest Asia (Axelrod, 1986) ; the genus *Appollonias* (Lauraceae), one of the four lauraceous species found in the *laurisilva*, has only two living species, *A. barbajuna* in the Canaries and *A. arnotti* in south India (Sunding, 1979). Moreover, there are parallel examples among butterflies : the distribution of *Vanessa indica* (Herbst, 1794) (Nymphalidae), with distinct subspecies in Macaronesia (the Canaries and Madeira) and south Asia, has attracted recent attention (Leestmans, 1978 ; Shapiro, 1992a, 1992b) ; the genus *Cyclyrius* Butler, 1897 (Lycaenidae), which has only two living species, *C. webbianus* (Brullé, 1840) in the Canaries and *C. mandersi* (Druce, 1907) from Mauritius, presents a similar case (Owen & Smith, 1993).

There is considerable evidence that many genera of butterflies from several families and subfamilies, including some satyrines (Porter & Geiger, 1988 ; Porter & Shapiro, 1991), are slow-evolving or bradytelic (Simpson, 1944). We believe that *Hipparchia*, in particular the ancestor of *tewfiki-wyssii* is probably a bradytelic taxon and that *H. wyssii* has a relatively ancient origin (Larsen, 1984) in the Miocene, say 10 — 15 Ma. The first dispersal event, presumably from North Africa, was probably to the eastern islands of Gran Canaria and Fuerteventura, possibly at the same time as the invasion of the *laurisilva* and *P. canariensis* forest and before these islands became arid. The second dispersal event may have been from Gran Canaria to La Gomera. However, the low phenotypic diversity on La Gomera, compared to Gran Canaria, and indeed all other islands, suggests a bottleneck effect at introduction which is still reflected in the modern population. Subsequent island hops would follow, first to Tenerife, not earlier than 6 Ma (Schminke, 1976) and then to El Hierro and La Palma during the Pleistocene (2 — 0 Ma). The increasing aridity of the Sahara region during the Pliocene would then produce the vicariance event which split the *tewfiki-wyssii* ancestor into two relict species.

Comparative morphology and high phenotypic diversity, as well as the antiquity of Gran Canaria (Schminke, 1976), support the proposed ancestral status of ssp. *tamadabae*. Whether ssp. *wyssii* on Tenerife originated from La Gomera or Gran Canaria (or both) remains an open question, each being almost equally likely on grounds of comparative morphology (Table 6). The data indicate that ssp. *bacchus* (El Hierro) originated from La Gomera, the nearest source, at a date which must have been ≤ 2 Ma ago.

The case of ssp. *tilosi*, however, appears anomalous and defies simple interpretation. While it is undoubtedly closest to ssp. *gomera* (Table 6), it is the most distinct of all five subspecies (Fig. 3) and shares the smallest number of hindwing phenotypes with other subspecies ; it also shows the highest phenotypic diversity (Table 4). We suggest above that the fragmented distribution of ssp. *tilosi* into many small isolated populations, a situation which does not apply to the other subspecies, may have resulted in numerous founder effects with unusual and differing starting sets of alleles ; sub-population differences might further intensify under subsequent genetic drift. Our collection is much too small to hope to find quantitative differences between the six sub-populations from La Palma represented, but the high phenotypic diversity in the bulked sample may reflect heterogeneity arising from the fragmented population structure of this subspecies.

However, the fact that ssp. *tilosi* is the most distant (phenetically) from all other subspecies and occurs on the island known to be the youngest (≤ 2 Ma) (Schminke, 1976) and furthest from a continental source of recruitment, suggest two other possible interpretations of the evolutionary history of *H. wyssii.* First, the species may have colonised the Canary archipelago only within the last two million years, in which case the diversification we describe occurred within the Pleistocene or later. If this is the case, then rapid evolution has occurred on El Hierro and (especially) La Palma. It follows from this that the pre-Pleistocene geological history of the islands would be irrelevant to any attempt to reconstruct the evolution of *H. wyssii.* Alternatively, the species may have reached the eastern islands a long time ago but dispersed to La Palma and El Hierro, where it has undergone rapid evolution, comparatively recently. This last interpretation best fits the facts.

## Discussion

Graylings are essentially "underside" butterflies. Only rarely is the upperside visible and it is the underside that has the intricate and characteristic patterning. When a butterfly comes to rest, the underside of the forewing is well-exposed and its spots are conspicuous. After a short interval, the forewing is lowered and hidden by the hindwing, and the butterfly is beautifully camouflaged against the background of rock or tree trunk. If alerted, it raises the forewing and the eyespots are again visible. This behaviour is widespread among members of the Satyrinae but is particularly well-developed in *Hipparchia* and it is usually interpreted as anti-predator strategy. The forewing eyespots catch the attention of a predator which may then strike at a non-vulnerable part of the wing (Brakefield, 1984), enabling the butterfly to escape by flying away. If there is no strike, the butterfly assumes the resting position with the forewing concealed. Our observations on all subspecies of *H. wyssii* suggest that this presumed anti-predator behaviour is the norm. The rarely exposed upperside is rather uniformly dark and may function in thermoregulation, though only in flight, as *Hipparchia* group species are exclusively lateral baskers at rest (Shreeve & Dennis, 1992) : it is probably never involved in anti-predator behaviour.

Hence, we view the ground plan of the underside pattern of all five subspecies as having evolved in response to selection by predators ; most of this evolution must have occurred before what is now *H. wyssii* reached the Canary Islands. Assuming a mainland origin for *H. wyssii*, the initial colonisation of any one of the islands may have involved few individuals ; indeed a single fertilised female is all that is required. Subsequent colonisation of other islands might similarly involve few individuals. Each colonisation has produced relatively large but isolated populations which could easily have been founded with only a fraction of the genetic diversity of its source population(s) leading to selective and epigenetic constraint. The restricted gene pool of each founder population would thus be unique to each island and differ stochastically from all other islands : this alone could account for most of the inter-island differentiation we have described. Genetic drift in the initially small populations of founders would be expected to lead to a further loss of genetic diversity and to the fixation of inter-island differences, which are mainly so minor that their influence on survival may be trivial.

Nijhout (1991) emphasises that small changes in the source or steepness of diffusion gradients for theoretical morphogens, thresholds for the expression of alternative pigment genes and pattern elements and the timing of the sequence of morphogenetic events, can produce quite profound changes to the visible phenotype. We believe that developmental constraint, probably involving very few gene loci with alternative alleles, has produced the high proportion of unique character combinations that now occur on each island. The overall result is that the distinct grayling phenotype is retained but its precise expression on each island is different and dependent on the genetic history of each population. The hindwing underside is the most complex of a grayling's wing surfaces and it is this which is most often exposed to potential predators : it is a cryptic wing surface but the precise means by which crypsis is attained differs from island to island.

Of the 30 species of butterfly found on the Canary Islands, four (including *H. wyssii*) exhibit inter-island differentiation in wing pattern morphology, while others probably do so but have not been subjected to detailed analysis. In all four cases, the island differences are quantitative rather than qualitative. In two species, *Maniola jurtina* and *Pararge xiphioides*, subspecific names have not been given, while in the other two, *Gonepteryx cleopatra* (Linnaeus, 1767) and *H. wyssii*, subspecific (or specific) status is based on small differences in adult size, wing pattern and the structure of genitalia (Kudrna, 1975, 1977), and in the latter case, also on egg and larval morphology (Wiemers, 1991). While these features differ slightly between islands, they vary only to an extent, as in comparisons between Palaearctic and Nearctic *Aglais* Dalman, 1816 and *Nymphalis* Kluk, 1802, that either species or subspecies might be expected to differ (Miller & Miller, 1990). To demonstrate speciation more positively would require cross-breeding or better, analysis of mtDNA. However, our view is that, although it hardly matters whether the island populations of *H. wyssii* are designated as species or subspecies, we have found no compelling evidence for full speciation and are thus persuaded to leave them as well-differentiated subspecies.

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# APPENDIX I

## Characters used for analysis of inter-island differences in *Hipparchia wyssii* in the Canary Islands

UPF
1. Small ochreous border ocellus (**h**) in s7. #
2. Black border ocellus in s6 (**h**) with white pupil.
3. Black border ocellus in s6 (2) ringed with yellowish halo.
4. Pale submarginal spot (**h**) in s5. *
5. Pale spot in s5 (4) white (+) or brown. *
6. Pale submarginal spot (**h**) in s4. *
7. Pale spot in s4 (6) white (+) or brown. *
8. Black border ocellus (**h**) in s3. *
9. Black border ocellus (8) in s3 with white pupil. #
10. Black border ocellus (8) in s3 ringed with yellowish halo.
11. Pale postdiscal spot in s6. *
12. Above spot (11) in s6 white (+) or pale brown. #
13. Pale postdiscal spot in s3. *

UPH
14. Pale ochreous or white border ocellus (**h**) in s6 (spot 1).
15. Similar ocellus (**h**) in s5 (spot 2).
16. Similar ocellus (**h**) in s4 (spot 3). #
17. Similar ocellus (**h**) in s3 (spot 4).
18. Small submarginal black border ocellus (**h**) in s2 (spot 5). *
19. Spot 5 (18) with minute white pupil. #
20. Spot 5 (18) ringed with narrow yellowish halo. #

UNF
21. Large black border ocellus (**h**) in s6 with white pupil.
22. Spot in s5 fused with halo of border ocellus in space 6.
23. Black border ocellus (**h**) in s3 with white pupil. #
24. Black border ocellus (**h**) in s3 ringed with yellowish halo.
25. s3 between elements **f** (postmedial line) and **h** ochreous (+) or brown.
26. Postdiscal area of s2 ochreous (+) or brown.
27. Diffused ochreous spot proximal to element **d** in discal cell. *

UNH
28. Diffuse white submarginal border ocellus (**h**) in s6 (spot 1).
29. Similar spot (**h**) in s5 (spot 2).
30. Similar spot (**h**) in s4 (spot 3).
31. Similar spot (**h**) in s3 (spot 4).
32. Black spot in s2 with minute white pupil.
33. Pale patches immediately lateral to postmedial line (**f**) flecked white (+) or grey.
34. Above patches (33) fused to form irregular but uninterrupted stripe.

Letters in bold type identify the probable homologies of pattern elements according to the nymphalid ground plan (Nijhout, 1991). s = space (Fig. 2) UPF = upperside forewing ; UPH = upperside hindwing ; UNF = underside forewing ; UNH = underside hindwing ; + = present ; characters expressed or variable only in one sex are marked * for males (9) and # for females (7) ; all other characters (18) are scored in both sexes.

## APPENDIX II

Character matrix for *H. wyssii* from the Canary Islands.
The data are expressed as percent occurrence

| Character number | | Males | | | | | Females | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | T | G | H | P | C | T | G | H | P |
| UPF | 1 | — | — | — | — | — | 25.0 | 12.5 | 0.0 | 0.0 | 0.0 |
| | 2 | 50.0 | 0.0 | 0.0 | 0.0 | 0.0 | 93.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 3 | 8.3 | 0.0 | 0.0 | 0.0 | 0.0 | 50.0 | 0.0 | 0.0 | 0.0 | 100.0 |
| | 4 | 91.7 | 66.7 | 75.0 | 100.0 | 80.0 | — | — | — | — | — |
| | 5 | 36.4 | 0.0 | 16.7 | 83.3 | 15.0 | — | — | — | — | — |
| | 6 | 91.7 | 100.0 | 100.0 | 100.0 | 100.0 | — | — | — | — | — |
| | 7 | 45.5 | 0.0 | 37.5 | 100.0 | 80.0 | — | — | — | — | — |
| | 8 | 87.5 | 100.0 | 100.0 | 100.0 | 100.0 | — | — | — | — | — |
| | 9 | — | — | — | — | — | 31.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 10 | 0.0 | 0.0 | 0.0 | 0.0 | 20.0 | 0.0 | 18.8 | 0.0 | 0.0 | 100.0 |
| | 11 | 8.3 | 0.0 | 93.8 | 100.0 | 16.0 | — | — | — | — | — |
| | 12 | — | — | — | — | — | 18.8 | 43.8 | 66.7 | 93.3 | 25.0 |
| | 13 | 20.8 | 0.0 | 87.5 | 100.0 | 96.0 | — | — | — | — | — |
| UPH | 14 | — | — | — | — | — | 33.3 | 6.3 | 0.0 | 20.0 | 42.9 |
| | 15 | 0.0 | 0.0 | 0.0 | 73.3 | 22.7 | 53.3 | 18.8 | 0.0 | 66.7 | 100.0 |
| | 16 | — | — | — | — | — | 33.3 | 18.8 | 0.0 | 0.0 | 42.9 |
| | 17 | 0.0 | 0.0 | 0.0 | 0.0 | 40.9 | 46.7 | 25.0 | 0.0 | 0.0 | 85.7 |
| | 18 | 66.7 | 100.0 | 87.5 | 100.0 | 100.0 | — | — | — | — | — |
| | 19 | — | — | — | — | — | 13.3 | 6.7 | 0.0 | 0.0 | 0.0 |
| | 20 | — | — | — | — | — | 0.0 | 6.7 | 0.0 | 0.0 | 85.7 |
| UNF | 21 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 93.8 | 31.3 | 0.0 | 0.0 | 0.0 |
| | 22 | 40.0 | 0.0 | 56.3 | 0.0 | 40.0 | 81.3 | 0.0 | 66.7 | 26.7 | 75.0 |
| | 23 | — | — | — | — | — | 81.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 24 | 45.5 | 66.7 | 68.8 | 0.0 | 100.0 | 81.3 | 100.0 | 100.0 | 20.0 | 100.0 |
| | 25 | 0.0 | 0.0 | 6.3 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 |
| | 26 | 0.0 | 0.0 | 0.0 | 0.0 | 80.0 | 0.0 | 0.0 | 0.0 | 0.0 | 50.0 |
| | 27 | 4.2 | 0.0 | 31.3 | 0.0 | 76.0 | — | — | — | — | — |
| UNH | 28 | 38.1 | 33.3 | 75.0 | 0.0 | 59.1 | 93.8 | 62.5 | 50.0 | 100.0 | 100.0 |
| | 29 | 52.4 | 66.7 | 87.5 | 66.7 | 100.0 | 93.8 | 75.0 | 100.0 | 100.0 | 100.0 |
| | 30 | 28.6 | 33.3 | 18.8 | 16.7 | 77.3 | 62.5 | 75.0 | 0.0 | 6.7 | 100.0 |
| | 31 | 38.1 | 50.0 | 12.5 | 0.0 | 95.5 | 68.8 | 86.7 | 0.0 | 20.0 | 100.0 |
| | 32 | 42.9 | 0.0 | 6.3 | 0.0 | 22.7 | 93.3 | 12.5 | 0.0 | 0.0 | 0.0 |
| | 33 | 0.0 | 0.0 | 100.0 | 100.0 | 100.0 | 0.0 | 0.0 | 100.0 | 46.7 | 100.0 |
| | 34 | 0.0 | 0.0 | 93.8 | 33.3 | 45.5 | 0.0 | 0.0 | 0.0 | 80.0 | 14.3 |

# APPENDIX III

## Classification of the hindwing border ocellus (spotting) phenotypes of *H. wyssii* in the Canary Islands

| UPH Spots | Code | Spots | Code | UNH Spots | Code | Spots | Code |
|---|---|---|---|---|---|---|---|
| 00000 | A | 12005 | K | 00005 | 01 | 12300 | 12 |
| 00005 | B | 02345 | L | 0000$\underline{5}$ | 02 | 12305 | 13 |
| 0000$\underline{5}$ | C | 0234$\overline{5}$ | M | 02005 | 03 | 1230$\underline{5}$ | 14 |
| 0000$\overline{5}$ | D | 12045 | N | 0200$\underline{5}$ | 04 | 12045 | 15 |
| 00045 | E | 1204$\overline{5}$ | O | 10005 | 05 | 1204$\underline{5}$ | 16 |
| 02005 | F | 12345 | P | 00045 | 06 | 02345 | 17 |
| 0200$\overline{5}$ | G | 1234$\overline{5}$ | Q | 12005 | 07 | 0234$\underline{5}$ | 18 |
| 02045 | H | 1234$\underline{5}$ | R | 1200$\underline{5}$ | 08 | 0234$\overline{5}$ | 19 |
| 0204$\underline{5}$ | I | | | 02045 | 09 | 12345 | 20 |
| 0204$\overline{5}$ | J | | | 02305 | 10 | 1234$\underline{5}$ | 21 |
| | | | | 00345 | 11 | 1234$\overline{5}$ | 22 |

Spots are numbered antero-posterially from the costal side as follows : 1 (s6), 2 (s5), 3 (s4), 4 (s3), 5 (s2). White pupils are indicated as e.g. $\underline{5}$ and yellow halos as e.g. $\overline{5}$.

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