European Butterflies: A Portrait in Photographs

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Chapter 1.1

General Introduction and Reference, Provisional 1

Contents:

Version 1.0

November 2009

Introduction

This publication has been written, I suppose, for someone like me: a photographer who is not a professional lepidopterist, but who has a keen interest in butterflies and loves to be among them with a camera.

Photography is, of course, concerned with pictorial representation. The most photogenic feature of a butterfly is the pattern of colour on its wings and this is what individual pictures may portray, but having spent thirty or so years taking tens of thousands of pictures I have come to realise that the total is much more than the sum of the parts. A representative series of pictures of any species is so much more interesting than the best prize-winning individual picture, and can develop into what I dare to call a portrait of the species. I hope to present such a portrait of all the European species to the reader from my own photographs and observations.

And if one holds in one's mind the whole experience of each field trip and remember when each picture was taken, the portrait will hold a short lifetime of pleasure for the author. I will also try to communicate some of this too.

Thus, this publication contains many pictures of each species to show uppersides and undersides of each sex and how these vary across the species' geographical range and in its different forms and subspecies. All principal pictures are printed to a definite scale based on the recorded magnification of each photograph, and the number of pictures is roughly proportional to the extent of the species' distribution.

There is introductory information on each species, but thereafter each picture is accompanied by its own text in a similar way to comic books; they also have a story to tell in words and pictures. The idea is that each texted picture should illustrate one or more particular aspect of the species, and by ordering the texted pictures suitably a species' portrait will emerge in a logical way. I think the alternative of keeping words and pictures separate would lose their intimate association and, moreover, would be unbearably inconvenient for the reader as the number of pictures is large.

As implied, the primary function of each picture is to show some aspect of an individual butterfly that can be observed *objectively*, and then use it to develop the species' description, but there is bound to be a certain amount of uncertainty when extrapolating specific observations into a wider context. Therefore, I'm afraid, some sentences will be littered with qualifying adjectives, such as typically, sometimes etc. I actually think this engenders a truer perspective of butterflies than the style of many butterfly books where information is imparted as a series of *definite* statements. To be fair, though, the compact nature of field guides makes it hard for many authors to be expansive. Nevertheless, I suggest it is true that most *unqualified* general statements about Natural History (i.e. the outcomes of evolution) should be regarded warily.

There will be comments sometimes that diverge from statements commonly repeated elsewhere. In general, I intend to distinguish between comments of my own and comments that derive solely from other authors.

I will also present a systematic approach to the description of butterfly wing-patterns, some of which uses new terms etc., to allow unambiguous comments.

My own early difficulties, when I could never find enough published illustrations to help identify a slightly unusual looking photograph, are nowadays still the same for relative beginners using field guides with no real breadth of coverage. The large quantity of pictures in this publication is, I feel, bound to be helpful in this respect. But, a particular problem in distinguishing similar species is that one can easily pick up on some small difference in two illustrations which is not a consistent difference at all. I will therefore make a special effort to point out the consistent differences in similar species - but with the necessary qualifications!

The downside of having so many pictures is the large size of the publication. I have alluded to the arrangement of the descriptive text which is developed alongside the pictures and, I think, is thus satisfactory. But as a whole the publication cannot realistically be taken into the field; here a good field guide is indispensable. On the other hand, with digital camera playback one can use this publication to review a day's pictures back at base. To facilitate this, just the relevant pages can be extracted from a loose-leaf copy and spread out on a table. Another advantage of a loose-leaf version is that individual pages can be replaced if they are damaged or become updated.

At the outset I must recommend the benefits of networking. In the field, there is one thing more important than the butterflies themselves; it is any other person who seems interested in them. Talk to them, make friends and find out whatever you can. I once met a man in Sweden and found out a good site in Switzerland for a rare Fritillary! Help that I have had in this way has been so central to my butterflying that I will now acknowledge those that have helped me.

Acknowledgments

In the past ten years or so I have made many field trips with my friend Ted Benton, who is a most congenial and knowledgable companion. He has shared with me his knowledge about locations for many of the rarer European species. But just as importantly, I have benefited from his intelligent judgement and tried to emulate his unfailing persistence. Without him I should have achieved far less.

In Spain, Dr. Miguel Munguira, a professional lepidopterist, has been enormously kind and useful. He has told me of many interesting locations, and has advised me on numerous matters concerning identification, taxonomy etc. He has also been kind enough to read chunks of this publication and provide invaluable comments. Also in Spain, I must thank Jose Pérez and Vicente Villanueva who showed me find butterflies in Extremadura.

In Greece, Simos Icthiaroglou took time to take me on several trips in northeastern Greece to show me many of the famous locations there, and helped me with species I photographed in other parts of Greece too.

In Austria, I have been helped by Dr. Martin Lödl who allowed me access to the butterfly collection in the Natural History Museum in Vienna.

In Hungary, Hacz Tamás has shown me numerous important

locations, for many of which he had to obtain special permits, and Juhász István who accompanied us and once took me to certain sites in Transylvania. I also thank Dr. Bálint Zsolt for allowing me access to the Natural History Museum in Budapest, and Dr. Peregovits László, Szabolcs Sáfián and Petrányi Gergely for help and advice.

In Romania, Sándor Lehel has shown me several locations in the eastern Carpathians for several species.

In Sweden, Claes Eliasson has been a mine of information about species and locations and about lepidopterology generally. Also Dr. Nils Ryrholm provided information about the Arctic species, and Pär Axelson helped with information on sites in Gotland and near Stockholm.

In a general way, Tristan Lafranchis has discussed many topics in lepidopterology with me and helped with finding species in the northern Peloponnese.

I am permanently grateful to all the above men for their untiring help in the field.

The few pictures supplied by other photographers are acknowledged individually.

I am also indebted to others who have provided different kinds of support: Antoinette Young and Giles Dunmore who first encouraged me to write a book, a long time ago; Giles and Judy Dunmore who first 'found' Ted Benton and put us in touch; Eleni Paloura who took an interest in my butterflying and 'found' Simos Ichtiaroglou and introduced us; and, more recently, Alan and Chris Dawson, Roland Rogers and Mandy Gluth who have helped in the preparation of this publication in a number of ways.

Finally, I must especially thank my wife, Susan, who has never complained about my absorption in butterflying, my trips abroad in the summer and the hours I have spent every day on the computer preparing this publication the rest of the year.

Geographical Scope

The geographical region covered is Europe west of the Black Sea, Moldavia, Ukraine, Byelorussia and Russia. North Africa, the Atlantic Islands and those Greek Islands that lie close to the Turkish coast are excluded.

Not all parts of the region have been visited, particularly a belt south and east of the Baltic: northern Germany, Poland and the Baltic States. This shortcoming does not reduce the species' coverage, but does unfortunately reduce the geographical coverage of some of them.

Publication Layout and Numbering

The publication is organised into seven divisions, as listed below.

Each division is divided into numbered chapters.

Apart from division 1, each chapter concerns a group of similar butterfly species, e.g. chapter 5.12 is group 12 of division 5, which happens to be the Large Blue Group, in subfamily Polyommatinae (Blues) of the family Lycaenidae.

The pages in every chapter are numbered from 1.

Publication Divisions

1: General Introduction and Reference

2: Heperiidae (Skippers)

3: Papilionidae (Swallowtails, Festoons and Apollos)

4: Pieridae (Whites etc.)

5: Lycaenidae (Blues, Coppers, Hairstreaks and Metalmarks)

- ch. 5.0 Introduction to Lycaenidae
- chs 5.1 to 5.16 Polyommtinae (Blues)
- chs 5.17 to 5.18 Lycaeninae (Coppers)
- chs 5.19 to 5.21 Theclinae (Hairstreaks)
- ch. 5.22 Riodininae (Duke of Burgundy)

6: Nymphalidae excluding Satyrinae (Admirals, Emperors etc. and Fritillaries)

7: Satyrinae (Browns)

Divisions have an introductory chapter numbered zero, e.g. ch. 5.0 is the introductory chapter to the Lycaenidae family.

In the General Introduction, there is material relevant to all families: Evolution, Taxonomy and Systematics, Structure and Notation. The first two topics are not developed in this provisional version. The latter two describe, *inter alia*, a notation for butterfly wing-veins which applies to all species and serves as fundamental material for the descriptions of pattern-elements.

The notation presented here for labelling the veins and the spaces between them is self-consistent and differs in some respects from other notations.

However, even though all wing-patterns are largely controlled by the underlying veins, which are more of less constant in all butterfly species, actual wing-patterns differ greatly between subfamilies. Therefore, a particularised system of analysis of wing-patterns is given in the introductory chapter of each division for the relevant subfamilies.

In the General Reference, there are several sections: Bibliography and References; Glossary of names and abbreviations (most of the terms needed in chs 5.1 to 5.23 are in ch. 5.0); Alternative Scientific Names, e.g. synonyms; Index of Common Names; and an Index of Scientific Names (including alternatives). The last three subjects are not included in this provisional version.

Species Section Layout

Within each chapter, there is an Introduction to the group followed by separate sections for each species.

These sections have a standard layout. As already mentioned, there are two parts: broadly, an introduction to the species followed by the texted pictures.

The Introduction has a Taxonomy and Systematics subsection where subspecies are listed and appropriate comments made.

Since a major, and arguably unsolvable, problem in any book or publication on natural history is the taxonomy, there will be a general discussion of this topic in later versions of this General

Introduction. For now, I only wish to remark that the question, "What is it?", only makes sense if butterflies, at least most of them, can actually be categorised into species, subspecies or whatever. The problem is that boundaries between categories are never perfectly defined or identified.

For some readers the uncertainties of taxonomy are merely an aggravation, and their best wish is for someone to produce the ultimate and unalterable list of species etc. In this they will be disappointed. They may, however, prefer to skip anything to do with taxonomy etc. in this publication and accept my lists of species etc. without too much thought. One point for them to bear in mind, however, is that if a familiar name seems to have disappeared, it may well be because of some taxonomic consideration. In future versions of the General Reference I will take some trouble not to lose recently used names completely by producing a list of synonyms etc. Such names will also appear in an index, which will also be constructed after all other chapters are completed.

Next in the Introduction to each species, there are subsections on Distribution, Foodplant and Habitat, and Flight Time. Much of the information given has been drawn from the work of other authors, as listed in the Bibliography.

There is a section on Variation, Identification and Similar Species which is largely based on my own pictures, but partly informed by various published sources mentioned in the Bibliography. The subsequent texted pictures develop this subsection. Together these are the essence of the publication.

There is also a Photography subsection where I include a few comments concerning behaviour I have observed which relates to photography.

Finally, there is a topographical map of the region of Europe where the species flies which is marked to show the locations of the sites where the texted pictures were taken. This will give the reader a preliminary overview of the coverage of the texted pictures. When neighbouring sites are too close to be resolved a *single* symbol is used to cover them.

The picture magnification is stated at the bottom of the relevant pages. It applies to all pictures, unless stated otherwise, but not to the decorative pictures in the introductory subsections except for one right at the start which is scaled to exact life-size.

The pictures only appear at the correct scaled sizes if the page is printed or displayed at A4 size.

The scaled sizes are calculated from the magnification of the original photograph, and are subject to small errors, say 5%. In a few case, when the magnification was not recorded or when the picture was provided by another photographer, they have been scaled to a typical size for the species and this is commented on if something misleading could arise. The reader should be aware that a butterfly's wing can appear misleadingly small when parallax is involved, so one cannot easily use an oblique picture of a wing to measure its size.

The text always gives the exact date the picture was taken. Taken as a whole these dates add some objective information on the flight time and, possibly, its geographical variation. The text always gives a brief description of the location, too, which serves to amplify the remarks about habitat in the introductory part of the species section.

I have also included habitat pictures here and there which I hope will be informative and give an idea of what the habitat feels like. This is a part of the whole experience.

The cover page of every chapter has a list of contents: species, subspecies, forms etc.

I have made a considerable effort to organise the pictures and text to fit the pages neatly, but with pictures produced to a definite scale there are occasional layout problems, such as wasted spaces or text that runs over a page end. These are fairly infrequent and I hope will be acceptable.

I shall always use scientific names for species etc. because they are systematic, but the English common name will be added in brackets when the name first appears on any page, and every section on a particular species will have the scientific and English common name in the page headings.

The aggravation of changing scientific names is perennial and unavoidable. As mentioned before, I will, in later versions of the General Reference, produce a list of all the recent alternatives and index them.

Glossary and Abbreviations

At present, there is no glossary as such, but the important general words and phrases are highlighted in the following subsection on structure and notation. More particular words and phrases are similarly highlighted in ch. 5.0.

The following abbreviations (plurals in brackets) are used throughout the publication:

uns (unss): underside of wings

ups (upss): upperside of wings

unhw (unhws): underside of hindwing

unfw (unfws): underside of forewing

uphw (uphws): upperside of hindwing

upfw (upfws): upperside of forewing

pd: postdiscal

sm: submarginal

ad: antediscal

sp (spp): species

ssp (sspp): subspecies

f.: form

Introduction

On inspection, a butterfly's wing appears as a number of **pattern-elements** on a background. The background colour is often fairly even in appearance, and when this makes it appropriate to do so, it is referred to as the **ground-colour**.

A most important fact is that the positions of the pattern-elements are largely controlled by the so-called veins. In consequence, the pattern-elements may be divided into three main types: localised elements positioned between veins; localised elements on veins; and extended (linear) elements on veins.

It is convenient to describe the venation of the wings here, because it is similar in all families. I shall also define the notation used for labelling the wing-veins.

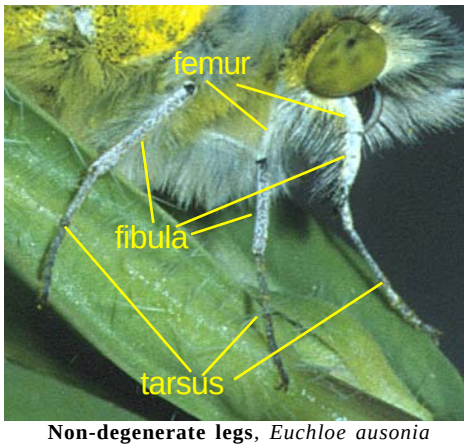
Despite the organising role of the veins, however, the resulting surface patterns of colour and shape in different taxa may be very different. For this reason, as already mentioned, wing-patterns themselves will be discussed on a subfamily basis in the introductory chapter of each division, except to mention here that the notation used to name pattern-elements stems from the notation given here to name veins.

Legs will be described here because they too are generally similar in all families, except for the forelegs which do distinguish families, and, in certain subfamilies, the sexes.

Legs

A butterfly's leg has three main sections: **femur** (thigh), **tibia** (shin) and **tarsus** (foot), which are jointed to each other. The tarsus consists generally of five articulated segments ending in a somewhat complicated **claw**, but in more recently evolved families there has been a progressive trend for the forelegs to degenerate.

Thus, in the presumably more primitive families, Hesperiidae (Skippers), Pieridae, as illustrated (Whites etc.), and Papilionidae (Apollos, Swallowtails etc.) all three pairs of legs are fully developed in both sexes. In the three major European Lycaenidae subfamilies, Polyommatinae (Blues), Lycaeninae (Coppers) and Theclinae (Hairstreaks), the tarsus on the foreleg of the male, but not the female, is degenerate structurally. This discriminates the sexes in appropriate photographs. The degeneration of the forelegs is more complete in the Nymphalidae (Vanessids etc., Fritillaries and Browns) to the extent that the forelegs are useless for walking in both sexes. Actually the male's legs are the more degenerate, but the forelegs are more-or-less concealed by body 'hairs' and usually cannot be recognised in photographs. Lycaenidae subfamily Riodininae, (Metalmarks), are intermediate between the other Lycaenidae subfamilies and the Nymphalidae, there being some foreleg degeneration in both sexes.



Non-degenerate legs, *Euchloe ausonia* (Eastern Dappled White)

Wings

The following brief description of wing development is based on Nijhout (1991), a book that deals extensively with the science of butterfly wing-patterns.

In broad terms, the adult wing consists of two lamellae (sheets of cells) which form the ventral (underside) and dorsal (upperside) wing-surfaces. Although the inner faces of the sheets are stuck together, there are certain **lacunae**, tube-like spaces, between them which form the so-called **wing-veins**. The lacunae are, in the main, radial from the wing-root to the outer periphery of the wing. The lacunae carry haemolymph, a fluid that is roughly equivalent to the blood and lymph of mammals. Also, inside the lacunae are fine **trachea** (air tubes) that supply oxygen to the wings. The outer surfaces of the lamellae carry the **wing-scales** or **scales**.

The early development of wing-lamellae, in the later part of the larval stage, is accompanied by development of lacunae. One is the **bounding lacuna** near, but inside, the periphery of the lamellae. The others radiate from the root of the lamellae, some branched, to the bounding lacuna. The two ends of the bounding lacuna are at the root of the lamellae just anterior to and just posterior to the bunch of radial lacunae. The overall pattern is recognisably similar to the venation of the adult wing. The lacunae, with the exception of the bounding lacuna, are penetrated by what can be called the **primary tracheation**.

Later, as the wing-lamellae grow, the primary tracheation is replaced by **secondary tracheation** in which certain of the earlier lacunae are abandoned and some new connectivities are created. The adult venation is the secondary system, composed of what may be called **developed veins**, plus a few **atrophied veins** left over from the primary system. Furthermore, the cells outside the bounding lacuna die and it then becomes the boundary of the adult wing. Any feature that involves a butterfly's wing-outline, such as a tail, results directly from a corresponding kink in the bounding lacuna.

Wings are, of course, covered in scales. The colours on a butterfly's wing are entirely due to the colour of the scales, except that the underlying **membrane** is usually brown, when it is not colourless, and may become visible in very worn individuals. Scales are of two principal types: **under scales** (also known as **ground scales**) and **cover scales**. Commonly they are arranged in rows roughly transverse to the radial veins, with the two types of scale alternating, though in a few instances they are more random, e.g. in the Parnassiinae (Apollos). Usually, too, the cover scales are larger and more brightly coloured than the under scales and cover them.

Thus, it is usually the case that the pattern and colour of a butterfly's wing are due to the cover scales. When the cover scales are lost, through wear for example, most butterflies become more drab as the under scales become more apparent.

Each scale is a single colour, and in many cases the colour is a pigment. Pigments produce colours from whitish, through yellows and oranges to red, and also browns and blacks.

Blues, purples and greens are **structural colours**, as are all the iridescent colours. A structural colour arises from some repeated structure in or on a wing-scale, such as parallel ribs on the surface or a repeating layer structure in the bulk (many more possibilities are known). If the repetitions are suitably spaced they will reflect certain colours more than others and so seem coloured. And, in particular, the effect can depend on the direction of the light falling on the scale and the direction in which the reflected light is viewed. Thus it is that many iridescent colours come and go depending on these relative directions. It may be noted that purple/violet gleams on the Apaturinae (Purple Emperors) and the Lycaeninae (Coppers) are generally produced by structured, black-pigmented scales.

In addition to under scales and cover scales, male butterflies carry modified scales, **androconia**, that produce pheromones. Androconia are generally different in structure from normal scales and are extremely variable between species. In cases where they are aggregated into patches, androconia can produce a distinctive appearance that is part of the overall wing-pattern.

Notation

Wing-regions

The edges of the wing are: the **costa**, the anterior (front) edge; the **outer margin** or just **margin**, the distal (outer) edge; and the **inner margin**, the posterior (rear) edge. I shall refer to the whole wing-edge as the **periphery**.

The **fw apex** is the pronounced angle in the wing-periphery where the costa and the margin meet. The **anal angle**, on forewing and hindwing, is an abrupt turn where the margin and the inner margin meet, but in some groups the anal angle is not well-defined.

The wing-surface may be divided roughly into three parts: the **basal area**, nearest to the thorax; the **discal area**, in the central region of the wing; and the **submarginal area**, beyond the discal area up to the wing-margin. Also, the **apical region** is the wing-surface close to the fw apex.

Wing-veins

As regards the so-called veins, it is simpler to start with the hindwing. In the adult there are five developed **root-veins** radiating from the wing-root, some of which branch to produce altogether nine developed **peripheral veins** at the wing-periphery (and there are also certain atrophied veins). Some species have a short **precostal vein**, labelled pc, which will not be discussed further.

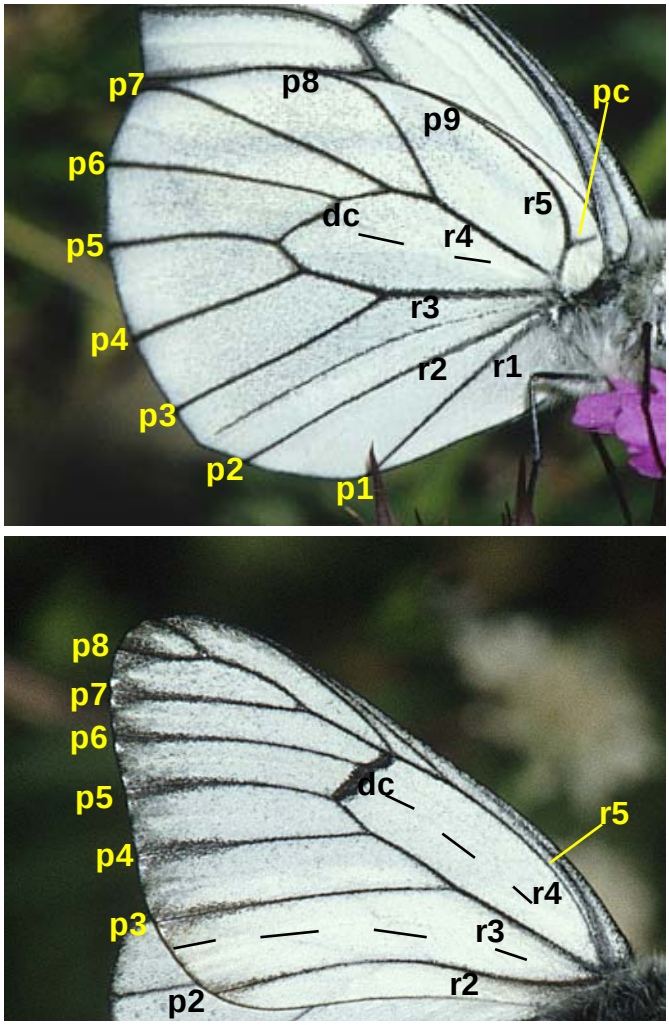
The natural scientific approach to notation is to give primacy to the root-veins and treat the peripheral veins as secondary. In such notations there may be conventional names for root-veins, e.g. costal, medial, radial, anal etc. The branches are then given names such as radial 1, radial 2 etc. There can be several variants of this approach depending on whether the tracheae or lacunae, or indeed the primary or secondary system, are treated as principal.

For wing-pattern description and recognition, however, it is convenient to adopt a non-fundamental *ad hoc* notation. The system used here is indicated in the illustrations.

The **developed veins** are numbered, starting from the inner margin. Thus the root-veins are labelled r1 to r5. Of the nine veins reaching the periphery, the first two are the ends of the unbranched root-veins r1 and r2. The next six are branches of root-veins 3 and 4, and the last is the continuation of the unbranched root-vein r5.

The nine peripheral veins are labelled p1 to p9, where p1 and p2 are, of course, the same veins as r1 and r2, and p9 is the same as r5. Veins p3 to p8 do not correspond uniquely to any root-vein. The lack of numerical correspondence between p9 and r5 is unfortunate, but is rarely confusing because patterns associated with veins at the wing-periphery and at the wing-root are usually well segregated. Indeed, it is commonly the case that rows of spots etc. are organised by either the peripheral or the root-veins, but a single row is never, I think, organised by both. Thus, having the root series and the peripheral series of labels is actually very convenient in pattern analysis.

In addition to the developed veins, **atrophied veins** can also



Labelling of wing-veins *Aporia crataegi* (Black-veined White).

The developed veins are naturally lined by black scales. One atrophied vein on the hw (between r2/p2 and r3/p3) is also lined by black scales; the other on the hw and the two corresponding atrophied fw veins are indicated approximately by thin, black dashed-lines.

influence pattern-elements. As indicated, one atrophied vein runs simply from the wing-root to the margin between the developed veins r2/p2 and r3/p3. The other runs from the wing-root, between developed veins r3 and r4, part way to the wing-margin. Where this atrophied vein ends, there are some small transverse veins. The space around the atrophied vein, bounded by veins r3 and r4 and by the small transverse veins is named the **wing-cell** or **cell**. The small transverse veins at the end of the cell are called the **disco-cellular veins**. The exact arrangement of trachea and lacunae at the cell end is complicated: there are atrophied lacunae that, in the primary system, connected the medial vein to p5 and p6 plus some newer short lacunae that link up r3 and r4 to p5 and p6 in the secondary system. This complex of veins is labelled vein dc, for simplicity.

There is also the bounding lacuna, originating from the primary system, around the periphery of the wing. None of the atrophied veins is numbered.

The forewing-veins correspond to the hindwing-veins with two main differences. The first root-vein is absent, so the four developed root-veins are labelled r2 to r5 and correspond structurally to r2 to r5 on the hw. Secondly, vein r4 has several more branches towards the costa than does vein r4 on the hw. Thus there may be up to twelve veins at the periphery. The number of branches does, however, vary between families, and even between species in the same family. In the illustration there are eleven developed veins, which is normal for the Pierinae (Whites).

As regards the peripheral veins, the first seven on the fw correspond to veins p2 to p8 on the hw (as already remarked, there is no vein r1 and therefore no vein p1 on the fw). There is no correspondence between the next 2, 3 or 4 (depending on species) veins, these being the extra vein branches on the fw. The final peripheral vein on the fw, being root-vein r5, does correspond with the hw.

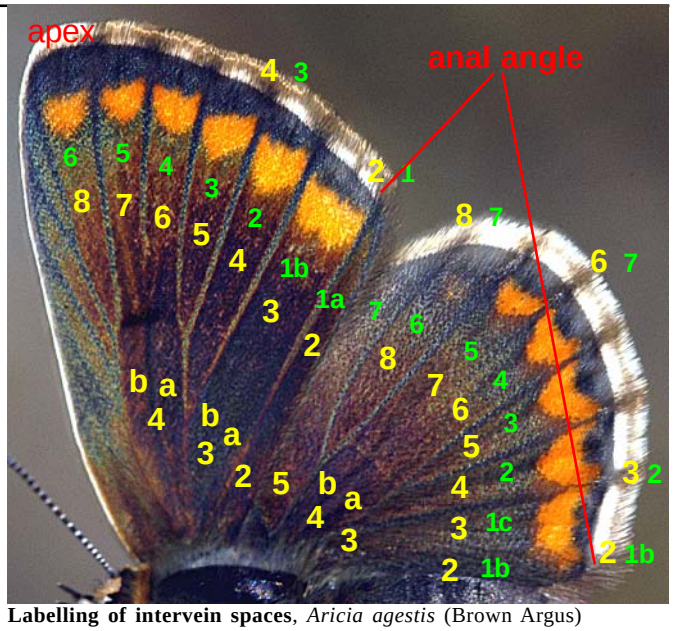
Thus, consistency of notation between wings is achieved by designating the first seven peripheral fw veins as p2 to p8, and the last peripheral vein as r5 along its whole length from root to periphery. In fact this vein usually intersects the costa fairly far from the fw apex, so the use of r5 along the whole length is not inappropriate. This, of course, leaves several peripheral veins unnamed, lying between p8 and r5, but being relatively minor branches below the costa it is rarely necessary to pick one out individually. I shall name them collectively the **antecostal veins** (a more natural name would be subcostal, but that name is used for fw vein r4 in some notations).

The atrophied veins on the fw correspond to those on the hw, and are not numbered.

It is important to stress that the numbering system used here differs from the existing conventional system of numbering, as described by Higgins and Riley (1981) or Nijhout (1991).

To compare the two systems (present system first):
hindwing, veins p1, p2, p3, p4 to p9 are v1a, v1b, v2, v3 to v8;
forewing, veins p2, p3, p4 to p8 are v1, v2, v3 to v7.

The conventional system uses names instead of numbers for the root-veins.



Labelling of intervein spaces, *Aricia agestis* (Brown Argus)

The present notation for labelling spaces between the peripheral veins is marked in yellow. The notation it replaces is shown in green. A few peripheral veins are also labelled in a similar way. Space 1 on the hw is hidden by the body. Space 4 (4a and 4b) in the basal region is the cell.

Intervein Spaces

It is the notation for the intervein spaces that really matters in identifying pattern-elements. I shall number spaces rigorously according to their anterior vein (the vein in front of the space in question). In the conventional system spaces are usually, but not invariably, labelled according to the posterior vein, as illustrated.

The inconsistencies of the conventional system are:
on the hw, veins v1b, v1a (concealed) and none-existing are posterior to spaces s1c, s1b and s1a (concealed);
on the fw, v1 and none-existing are posterior to s1b and s1a.
Thus the labelling of spaces does not match the labelling of the veins.

The conventional system also lacks internal consistency between the wings, since spaces s1c and s1b on the hw correspond to spaces s1b and s1a on the fw.

The conventional system also suffers the inconvenience of not having a numerical system for labelling spaces near the root, even though pattern-elements are often found there.

The conventional notation can also be inconvenient in one other particular, when it comes to real spot patterns. The atrophied vein between p2 and p3 often splits pattern-elements in this space. When this happens, it is easy to develop the present notation to label a twin pair of pattern-elements in space s3 as 3a and 3b. In the conventional notation the corresponding unsplit spots are numbered 1c on the hindwing and 1b on the forewing, and there seems to be no felicitous development of this notation to distinguish members a split pair. This point is better appreciated in the context of real patterns, discussed in the sections on the various subfamilies.

Bibliography

As mentioned on p. 3, I have drawn information on distributions, foodplants and habitats, and flight-times from the works of other authors, and have not usually acknowledged them explicitly in the text.

For distributions I have consulted Kudrna (2002) throughout Europe, with backup from Tolman (1997), Henriksen and Kreutzer (1982) in Scandinavia, and García-Barros *et al* (2004) in the Iberian Peninsula; and for foodplants, habitats and flight-times, Tolman (1997) in Europe generally, Henriksen and Kreutzer (1982) in Scandinavia, and Munguira *et al* (1997) in the Iberian Peninsula.

I should also acknowledge that I have used all the *books* listed in the references for a variety of information and would particularly like to mention: Higgins and Riley (1980), for descriptions of species and for wing-sizes; Lewington (1997) for his beautiful paintings; Henriksen and Kreutzer (1982) whose book broke new ground and has been inspirational; Tennent (1996) in North Africa and Manley and Allcard (1970) in Spain for their originality; and Lafranchis (2004) for some original diagnostic characteristics.

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