

IV. *On Specific and Mimetic Relationships in the genus Heliconius, L.* By H. ELTRINGHAM, M.A., D.Sc., F.Z.S.

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PLATES XI-XVII.

SOME time has elapsed since Professor Poulton first suggested to me that an investigation into the specific relationships of the forms of the genus *Heliconius* would probably be productive of interesting results, and I must admit to having had some hesitation in embarking on such a work in view of the fact that a very lengthy and elaborate monograph of the genus already existed. This memoir, however, is based entirely on external characters, and it appeared that anatomical study might elucidate new facts with regard to the relationships of the forms, more especially as the mimetic phenomena are of an unusually complicated kind.

Perhaps the most valuable feature of the monograph above referred to (Stichel and Riffarth, in "das Tierreich," 1905) is the recognition by Riffarth that the whole genus can be divided into two sections by means of a peculiar character of the fore-wing underside in the male. It was my friend, Mr. W. J. Kaye, who pointed out\* that, having divided the forms by means of the character mentioned, a most remarkable fact was disclosed.

A great number belonging to Section I resemble very closely forms belonging to Section II. In other words, intrageneric mimetic resemblance is of frequent occurrence. I here use the words "mimetic" resemblance in a wide sense as indicating merely a similarity of pattern; the precise nature of the resemblance may be considered later.

The present paper is an attempt to investigate more precisely the specific relationships of the forms of *Heliconius* by means of anatomical study combined with an examination of pattern gradations.

We are rarely able in such investigations to arrive at entirely satisfactory conclusions owing to lack of adequate

\* Proc. Ent. Soc. Lond., p. xiv, 1907.



material and data, and I fear the present effort is no exception. The results may, however, serve to indicate the directions in which future workers, and especially those with facilities for making breeding experiments, may hope to obtain more definite results. For the opportunity of examining and dissecting many rare forms I am indebted to the generosity of Lord Rothschild, Mr. W. J. Kaye, and the Authorities of the British Museum, whilst my friend Professor Poulton has assisted me with his continual encouragement and valuable suggestions. Mr. Kaye has also given me much practical help in sorting specimens and in correspondence, and my friend Dr. F. A. Dixey has rendered valuable assistance in connection with Pierine mimics. Dr. Karl Jordan has kindly looked over most of my microscope preparations and given me the benefit of his views thereon.

Opinions may differ as to the significance of conclusions based on the structure of the male armature. However that may be, probably most naturalists will agree that close resemblance in these structures may usually be regarded as evidence of near relationship, whilst distinct and constant differences will probably generally be accepted as evidence of specific separability.

In the genus *Acraea* it was found that in nearly all cases the species were well defined, and anatomical differences easily recognised. Such is only partially the case in *Heliconius*, as will be seen later, nor are the structures particularly constant within the limits of the same species. It should be understood at the outset that I do not put forward the present paper as a statement of conclusive and final results, hence it is not to be taken as a complete revision of the genus. I do not consider that our knowledge of the forms is yet adequate to such a task. My desire has rather been to indicate the directions in which future effort should be made, and the lines on which, especially, those in the field might profitably direct their observations.

The genus is distinguished from *Eueides* by its much longer antennae. It can be divided, as Riffarth has shown, into two great sections. On the underside of the male fore-wing, from the inner margin to the first branch of the median, is an area which presents a peculiar silky grey appearance. In Section I of the genus this silky surface is continued right up to the median without any visible



change in texture. In Section II there is, adjacent to the median and its branch, a certain amount of dull "mealiness." This amount may be very small, but it is always recognisable, especially after a very little practice. The two sections were designated by the extremely clumsy names of *Opisogymni* and *Opisorhyperi* respectively. For convenience they may be referred to as Section I and Section II. Between these two sections the reputed species are nearly equally divided. In the monograph referred to Section I contains 31 species and 110 subspecies, whilst Section II includes 39 species and 79 subspecies. This division is apparently a natural one, and so far as my preparations go the genital armature of no species of Section I could be mistaken for that of a species of Section II.

Section I may now be further divided, and we will first consider the forms included by Riffarth under the name *Silvaniformes*. These include nearly all those species the patterns of which are composed of yellow, brown, white, and black markings. Generally speaking, it may be said that the ground-colour of one or both wings is brown or yellow, though there are one or two exceptions.

#### *The evidence of the genitalia.*

Whilst the genitalia of nearly all the members of this group are readily distinguishable from those of the rest of the genus, they are by no means so readily separable *inter se*. Moreover, at least one form hitherto regarded as rather widely separated from the *Silvaniformes* must now be included in that group. I refer to *H. atthis*. In the accompanying plates the genitalia have been illustrated by giving a carefully drawn outline of one clasper, as it is from the shape of this part that any conclusions can best be drawn.\* After examination of a large number of preparations, it appears that they may be divided more or less into those which have a dense hairy tuft near the end of the clasper and those which are only moderately pilose. Whether this feature is of real value or not is difficult to decide; if, however, we accept the feature it would seem

\* I much regret the poor quality of these plates. The present necessity for economy has, however, made it impossible to use the beautiful lithographic process by which the figures were reproduced in my paper on *Acraea*.



possible to separate the following reputed species and their forms from the remainder of the *Silvaniformes*.

- H. ismenius*.
- „ *“ silvana ” metaphorus*.
- „ *narcaea*.
- „ *numatus*.
- „ *ethilla*.
- „ *gradatus*.

The first two above are separable from the rest on general differences in the armature, and we may now consider the remainder.

#### *H. narcaea*, Godt.

The typical form of this well-known species occurs in S. Brazil. In Seitz' *ab. connexa* the subapical band is completely separated and surrounded by black. The form *satis*, Weym., has a brown instead of a yellow band in the hind-wing. The form *flavomaculatus*, Weym., has a yellow instead of a white apical spot in the fore-wing, whilst *physcoa*, Seitz, has the fore-wing yellow band much broader than usual. The form *polychrous*, with largely increased black areas, is regarded by Stichel and Riffarth as a subspecies, though apparently occurring in the same localities as *satis*. It cannot be doubted that these are all forms of the same species, as they are for the most part mere colour variations. The outline of the claspers in three of the forms is shown on Pl. XIII. In general structure there is considerable agreement, though there is a marked difference between the actual outlines of the typical form and *narcaea polychrous*.

#### *H. numatus*, Cram.

Of this species some ten forms have been named, and they extend from Guiana across North Brazil to the Western Amazon region and Peru. The claspers of three forms are illustrated on Pl. XIII. The form *guiensis* is merely a variety of the type, but there is a greater difference between its clasper and that of *numatus numatus* than between the latter and *narcaea narcaea*. Indeed, the two last are not appreciably distinguishable. It may be said that they do not occur in the same locality and that thus there is no necessity for the respective armatures to be different.



There may be something to be said for this view, though it will not explain further cases yet to be described.

**H. silvana**, Cram.

Of this form three subspecies are named, and though the genitalia of the group are of little assistance in many of the cases of closer resemblance they seem to show that at least three of the forms hitherto regarded as subspecies of *silvana* do not belong to *silvana* at all, but to two other species. On Pl. XIII I have shown the claspers of two specimens of *silvana silvana* taken at random. One is hardly distinguishable from *numatus guiensis*, whilst the other is but little modified from *narcaea narcaea*. A part of the difference is due to the bending over of the apex of the clasper, but this is not a point of great importance and probably would not occur in a perfectly fresh specimen. Now, *silvana* occurs in Guiana, Venezuela, N. Brazil and Peru. The anatomy of the armature gives no reason to suppose that it is anything but a form of *numatus*, just as the latter on the same grounds appears to be as closely related to *narcaea*.

**H. ethilla**, Godt.

Some twelve forms of this species have been named, ranging through Trinidad, Guiana, Brazil, Venezuela, Colombia, and Panama. Seven illustrations of the claspers are given on Pl. XIII. The two specimens of *ethilla ethilla* are by no means identical, whilst the two of *ethilla tyndarus* are markedly different. One example of *ethilla ethilla* resembles *narcaea satis* and is not unlike *numatus numatus*. The outline of *ethilla aërotome* is very different from one example of *ethilla ethilla*, but not sufficiently distinct from one of *ethilla tyndarus*. My friend Mr. W. J. Kaye, regards *ethilla* as conspecific with *numatus*, a view I am strongly inclined to support, further adding that so far as the armatures are concerned there is no more reason for separating either from *narcaea* and *silvana*.

**H. gradatus**, Weym.

Of this rather rare species I have been able to make only one preparation from its subspecies, *thielei*, Riff. As will be seen from the illustration on Pl. XIII, the clasper



is much less different from that of *ethilla metalilis* than the latter is from some other forms of *ethilla*.

We thus see that on the structure of the genitalia we cannot satisfactorily distinguish between *narcaea*, *numatus*, *ethilla*, and *gradatus* and most of their forms.

We now turn to a large group containing ten reputed species and their forms. They all have at least this feature in common, that there occurs near the end of the clasper a tuft of bristles sufficiently evident to distinguish them from those of the *narcaea* group.

#### **H. novatus, Bates.**

The claspers of the three principal forms are shown on Pls. XIII, XIV, and present a closer agreement than any we have so far examined. The forms are found in Peru and Bolivia. Mr. Kaye informs me that *schantzei*, Riff., is merely the female of *novatus*.

#### **H. hecale, Fab.**

This large black form with a conspicuous white patch on the fore-wing occurs in Dutch and British Guiana. The clasper is shown on Pl. XIV, and differs in scarcely any respect but that of size from those of the last and next species. There is a form named *fulvescens*, Lathy, from Demerara, in which there is a brown basal suffusion in the fore-wing.

#### **H. aristiona, Hew.**

Of this species some twelve subspecies and several forms have been named, ranging through the Amazon region, Peru, Ecuador and Bolivia. I have shown the claspers of seven forms on Pl. XIV, and here again there is considerable general agreement accompanied by a certain variation in actual outline.

#### **H. ithaka, Feld.**

The typical form and two subspecies are all found in Colombia. It would be difficult to distinguish between the clasper shown on Pl. XIV and that of some of the forms of *aristiona*.

#### **H. pardalinus, Bates.**

The type form and four subspecies range through N. Brazil, Peru, Bolivia and probably Ecuador. The clasper



of *pardalinus lucescens* shown on Pl. XIV is shorter and broader than those already considered, yet, except in size, there is no very satisfactory difference between it and that of *anderida zuleika* on Pl. XV, and some forms of *anderida* are barely separable from *aristiona*.

**H. fortunatus, Weym.**

This and two subspecies occur in N. Brazil. I have illustrated a clasper of *fortunatus spurius* on Pl. XIV. It is much more rounded than those so far considered. If every specimen dissected out were identical with this, then we might, perhaps, say that it differed constantly from the other species, but a very small amount of variation would make it as difficult to distinguish as the rest.

**H. quitaleus, Hew.**

The type form and three subspecies range through Peru, Ecuador, Bolivia and N. Brazil. Reference to the drawings on Pl. XIV shows a marked difference between *quitalenus quitaleus* and *quitalenus felix*. The first might well be a variation of one of the forms of *novatus*. If the second differs from these it does so no more than from its own type.

**H. anderida, Hew.**

The type and six subspecies range through Venezuela, Colombia, Central America, and one form is said to have been taken in Dutch Guiana. The claspers of six forms are illustrated on Pls. XIV, XV, from which it may be seen that there is considerable variation. There is less difference between *anderida holocophora* and *aristiona floridus* than between the former and *anderida anderida*. Kaye is of opinion that *anderida fornarina* is either a good species or a form of *hecale*. The clasper is, however, very near to that of *anderida melicerta*, and though *hecale* has a somewhat different appearance it still seems connected with the other forms of this group.

**H. paraënsis, Riff.**

The two forms of this species are described from Para and Itaituba respectively. A clasper of the form *latus*, Riff., is illustrated on Pl. XIV, and is seen to be not satisfactorily distinguishable from several of the other forms described.



**H. aulicus**, Weym.

I have only had one example of this species to examine. Its clasper is shown on Pl. XV. It has the dense hairy tuft of the *novatus* group, and differs little from that of *aristiona tarapotensis*. The pattern of the wings is also so similar that it seems certain that they are the same species.

All the above seem to constitute a group of forms which cannot be constantly distinguished by the genitalia. Before passing to those species which have claspers of the *ismenius* type there are a few forms which must be separately considered.

**H. "silvana" robigus**, Weym. ; **H. "silvana" ethra**, Hübn.

The form *robigus* occurs in Brazil (Espiritu Santo, Rio de Janeiro, Minas Geraes, etc.). The clasper is shown on Pl. XV. It cannot be placed in the *narcaea* group owing to its form. It is less densely tufted than those of the *novatus* group. Two preparations show much the same structure. It is certainly incorrectly placed in being associated with *silvana*. Apart from the difference in the tuft, the form of the clasper suggests an affinity with *aristiona*, and further reasons for placing it in that association will be given later.

The clasper of "*silvana*" *ethra* shown on Pl. XV is barely distinguishable from that of "*silvana*" *robigus*. It is rather more densely tufted, but must, I think, be regarded as conspecific with *robigus* and probably with *aristiona* and *novatus*.

**H. vetustus**, Butl.

The typical form occurs in British Guiana and the form *metellus*, Weym., in N. Brazil. The clasper (Pl. XV) is of a curiously irregular shape. Except for the dense tuft of bristles it might well be a form of *numatus*.

**H. sergestus**, Weym.

This species occurs at Tarapoto in Peru. I have had but one example to examine, and the clasper is shown on Pl. XV. If its well-rounded and tufted form is constant it may well be regarded as definitely distinct.

**H. atthis**, Doubl.

This species, which has become so profoundly modified in mimicry of *Tithorea pavonii*, occurs in Ecuador. Though



hitherto regarded as related to the Cydnoformes, the structure of the clasper on Pl. XV shows it to belong rather to the Silvaniformes. If it had a denser tuft of bristles it would be difficult to distinguish it from *aristiona lenaeus*.

**H. ismenius, Latr.**

The typical and four subspecies occur in Colombia and Central America. Though the forms are placed near *narcaea* in existing works, I have placed them nearer to the latter part of Section I, since, if the form of the claspers is to be regarded as any indication of relationship, then they are undoubtedly closely allied to the *melpomene* association. The claspers of three forms are shown on Pl. XV, from which it will be noted that there is some variation between them. The clasper of "*silvana*" *metaphorus* is also shown, and is seen to resemble that of *ismenius telchinia* so closely that we cannot doubt that the form is much more closely related to *ismenius* than to *silvana*. Indeed, I am convinced that it is merely another form of *ismenius*.

We have now considered nearly all the reputed species which appear to belong to the group Silvaniformes. Forms of which I have been unable to obtain examples are *ennius*, *sulphureus*, and *hippola*. With so peculiar a genus it may be rash to speculate on the position of forms which have not been examined, but I should expect *ennius* to prove a form of *quitalenus*, and *sulphureus* of *ethilla*. As to the rare species, *hippola*, of which only the type seems to be known, its appearance gives no clue. It will, perhaps, prove to be near *narcaea*.

Assuming the structure of the genitalia to be of any value at all in these forms, we can, therefore, arrange the reputed species in six groups of which it may be said that if the respective members are not conspecific, at least they are extremely closely allied, and are not separable by any constant and recognisable features of the male armature.

I have left for consideration at the end of this group two species which are amongst the most remarkable of all the *Heliconii*. The first is *H. tumatumari*, Kaye, from Guiana. This species resembles *aoede astydamia*, forms of *erato*, and secondarily forms of *melpomene*. It is a tribute to Mr. Kaye's excellent judgment that he did not regard it as a form of *melpomene*, but described it as a separate species. The structure of the male armature is quite



different from that of any form of *melpomene*, and, in fact, has a typically silvaniform appearance. It is nearest to that of a species with which one would not at first think of associating it, viz. *vetustus*: indeed, the only obvious difference between the armature is that in *vetustus* the extremity of the clasper is rather more densely pilose. That the species is, in fact, closely related to *vetustus* I have no doubt, and the further evidence for this will be found under the discussion of patterns. It may here be mentioned that the most obvious difference between *tumatumari* and *melpomene* forms is the occurrence in the former of a sulphur yellow streak on the underside of the hind-wing, this streak being not *on* the costa, but below the costal nervure.

On my pointing out to Mr. Kaye the significance of this yellow line, he kindly brought for examination two *melpomene*-like forms, one of which agrees with *melpomene elevatus*, Nöld., and the other an undescribed female form somewhat like it, from his own collection. Both these had the peculiar yellow line, and without anatomical examination might well have been regarded as geographical forms of *tumatumari*. Microscopic investigation of the male example showed, however, that though it was apparently not a form of *melpomene*, it was equally specifically separate from *tumatumari*. The armature is again of a somewhat silvaniform type, but resembling that of *H. sergestus*. These two species, *elevatus* and *tumatumari*, will be further considered in the discussion of patterns.

Although they are separable from *melpomene* it must not be supposed that they are as markedly distinct from that species as are many of the species of Section II from one another. Preparations of the genitalia of *melpomene* show much individual variation, and whilst there would never be any difficulty in distinguishing the armatures of, say, *anderida* and *melpomene*, there might be more difficulty in separating some preparations of *melpomene* from certain of the Silvaniformes. In other words, the Silvaniformes are not, in spite of their *Melinaea*-like patterns, a markedly separate group, and, in fact, it may be said that all the species belonging to Section I are far less satisfactorily differentiated than those of Section II. This fact would seem to lend support to the view that Section I is of more recent development, as we should expect, since its members are mimics rather than models.



We now pass to those species grouped under the name of the

CYDNOFORMES.

**H. cydno**, Doubl.

The typical and eight subspecies are described with several varietal forms occurring in Central America, Peru, Ecuador, Colombia, and Venezuela. The claspers of five forms are shown on Pl. XV. They show a general resemblance of structure with a certain amount of variation.

**H. weymeri**, Stgr.

Of the typical form of this Colombian species I have had no example to examine, but have dissected out more than one armature from the form *gustavi*, Staud. There is no constant and recognisable difference between the armatures of this and of *cydno* (Pl. XV).

**H. pachinus**, Salv.

This species from Chiriqui and Costa Rica occurs commonly in collections. I have made several preparations which show but little range of individual variation. The pattern of the wings seems at first sight so distinct that it might well be regarded as a satisfactorily defined species, yet the armature (Pl. XVI) shows no distinction from that of *weymeri* and could not be constantly separated from some forms of *cydno*.

**H. heurippa**, Hew.

This species, with which I include *rubellius* of Smith and Kirby, occurs in Colombia. Typical *heurippa* has a striking appearance owing to the large patch of sharply divided yellow and red on the fore-wing. In the form *rubellius* this patch is reduced to very narrow dimensions. The clasper shown on Pl. XVI from a specimen of *heurippa* shows much the same structure as is found in *cydno*, *weymeri*, etc. There can be little doubt that *heurippa* and *cydno* are the same species, and it will be seen later that consideration of the pattern confirms this view.

**H. melpomene**, Linn.

Over fifteen subspecies of this form, with many varieties, are described. They range over the greater part of northern S. America, but have not, so far, been reported



from Colombia and Venezuela. A drawer filled with these forms presents a most bewildering diversity of patterns linked together by intermediate forms. On Pl. XVI I have illustrated eight of the claspers. From these it will be seen that there is a strong tendency for the point of the clasper to be fuller and more rounded than in *cydno* and some of the other forms. Two drawings are shown taken from consecutive specimens of *melpomene thelxiope*. The difference between these is as great as that between the second of them and one of the *cydno* forms, whilst that of *melpomene timareta contiguus* is essentially of the *cydno* pattern.

#### **H. amaryllis, Feld.**

The typical and two subspecies occur in Central America, N.W. Brazil, Peru, Venezuela, Colombia and Trinidad. Of the two claspers shown on Pl. XVI that of *amaryllis rosina euryas* is of the *cydno* type, whilst that of *amaryllis euryades* comes nearer to that of some forms of *melpomene*, showing that here again this reputed species cannot be definitely separated.

#### **H. vulcanus, Butl.**

The typical form occurs in Colombia and Panama, and is rather doubtfully recorded from Guiana. The form *cythaera*, Hew., occurs in Ecuador. Claspers of the two forms are shown on Pl. XVI, and present no clearly distinguishing features.

#### **H. xenoclea, Hew.**

This species appears as *batesi* in Stichel and Riffarth's monograph, Riffarth having thought that *xenoclea* belonged to the second section of the genus. Kaye pointed out the error,\* and has given the name *microclea* to the form in Section II which resembles Hewitson's species. It occurs in Ecuador and Peru, and is distinguished by the two separate rounded spots on the fore-wing.

The clasper figured on Pl. XVI is not distinguishable from several of those already described.

#### **H. nanna, Stich.**

This reputed species occurs in S. Brazil, and a form occurring further north, in which the fore-wing red discal

\* Proc. Ent. Soc. Lond., p. xiv, 1907.



band is less indented, has been named *burchelli* by Poulton. *H. nanna* resembles closely, on the upperside at least, *H. besckei*. The clasper as shown on Pl. XVI is no more distinctive than the others already considered.

*H. besckei*, Ménétr.

This species, occurring in S. Brazil, resembles *nanna* and *erato phyllis*. It is distinguished outwardly by a reddish submarginal line on the underside of the hind-wing. Kaye has expressed the view that it is a form of *H. erato phyllis*, but the structure of the armature precludes this possibility. A clasper is shown on Pl. XVI, and the principal feature in which it differs from the *cydno* and *melpomene* forms is the presence of a dense tuft of bristles near the point. If this be a good character, as has been supposed, in dividing the *Silvaniformes*, then we have grounds for separating the species, and the peculiarity of the hind-wing pattern supports this view.

We thus see that in so far as may be judged from the genitalia there is no reason to suppose that the forms now included under the *Cydnoformes* and *Melpomeneformes*, with the exception of *H. besckei*, really constitute more than one species. The extent to which pattern and other features support such a conclusion will be discussed in a later portion of this paper.

SECTION II.

In this section the structure of the armature provides much more satisfactory evidence of specific distinctions and to a considerable extent confirms the reputed species into which the forms have been divided. Taking these in the order adopted in Stichel and Riffarth's work, we find seven reputed species included in group I, the

HECALESIFORMES.

*H. crispus*, Stgr.

This species resembles *atthis*, but is modified so as to mimic *Tithorea bonplandii descandollesi*. It occurs in the Cauca valley. I have had no specimen to examine.



**H. hecuba**, Hew.

This Colombian species also resembles a *Tithorea*. Seitz regards both *choarinus* and *cassandra* as forms of this species, together with *tolima*, Fassl. I have had *hecuba*, *choarinus* and *tolima* to dissect, and they would certainly appear to be the same species. The claspers of *hecuba* and *choarinus* are shown on Pl. XVI. That of *cassandra* I have not been able to examine.

**H. hecalesia**, Hew.

The typical form occurs in Colombia and the form *formosus* in Guatemala, Nicaragua, Costa Rica, and Panama. I have dissected examples of both, and the clasper is shown on Pl. XVI. It is of quite distinct structure. *H. octavia*, Bates, has exactly the same type of clasper and is certainly the same species. It occurs in Guatemala and Honduras.

Two forms of this group remain, *H. gynaeisus*, Hew., and *H. longareus*, Hew. The first of these Riffarth regards as a form of *hecalesia*. Unfortunately, I have had no example to examine, and the only specimen of *longareus* known to me is the type. My view as to the position of these two forms will be found under the consideration of patterns.

## AOEDIFORMES.

**H. godmani**, Stgr.

This species is included by Riffarth in the Aoediformes, but its appearance suggests an alliance with *gynaeisus*, though this may quite well be due to mimetic resemblance. I cannot express an opinion as to its true position, as the type is, so far as I know, the only specimen in existence. It was taken on the river San Juan in W. Colombia.

**H. metharme**, Erich.

A rather distinctive-looking species occurring in N. Brazil, Peru, Colombia, and doubtfully in Nicaragua. The male armature (Pl. XVI) is quite distinct from that of any other form examined except *aoede*.

**H. aoede**, Hübn.

The typical and three subspecies range through British Guiana, N. Brazil, Venezuela, Peru, and Ecuador. The



claspers of two forms are illustrated on Pl. XVI. They differ from one another considerably, but the differences are just such as to make it difficult to separate them on these structures from *metharme*. In the latter species the peculiar toothed organ on the inner side of the clasper seems intermediate in form between that of *aoede aoede* and that of *aoede astydamia*. Allowance must be made for differences of position, as this organ appears to be movable. The matter will be further considered under the discussion of patterns.

#### XANTHOCLEDOFORMES.

##### *H. xanthocles*, Bates.

Five subspecies and the typical form are described from various parts of northern S. America. The male claspers are distinctive, those of two forms being shown on Pl. XVI. The most interesting feature is the small, upturned projection from the inside of the clasper, suggesting an alliance with *H. hierax*, Hew.\* The only feature of the wing patterns which would support such a view is the row of small, almost marginal white spots on the underside of the hind-wing.

#### EGERIFORMES.

##### *H. egeria*, Hübn.

The typical and three subspecies of this large and handsome form have been described from Guiana and North Brazil. The male clasper is illustrated on Pl. XVI, and could not be confused with that of any other species I have examined, though suggestive of relationship with *burneyi catharinae*.

##### *H. burneyi*, Hübn.

The typical form and three subspecies range through Guiana, N. Brazil, Peru, Bolivia, and Colombia. I have illustrated the claspers of three forms (Pl. XVII) showing a very wide limit of variation, notwithstanding which, the clasper of only one other reputed species could be confused with them. This is *wallacei wallacei*, Pl. XVII, and it is

\* On the clasper alone *hecuba*, *xanthocles*, and *hierax* would appear to be rather difficult to separate. There are certain other differences, however, notably in the shape of the uncus, which enable them to be separated.



difficult to see in the armature any grounds for regarding it as specifically distinct. *H. wallacei* colon shows a similar structure.

**H. doris**, Linn.

The forms of this species have a wide range, being recorded from the whole of northern S. America. It is characterised by the radiate coloured markings on the hind-wing, which may be blue, green, or red, or combinations of these, or even dusted with white. Three subspecies and some varietal forms are described. I have illustrated on Pl. XVII the claspers of only two forms, as further preparations show a similar structure characterised by a large upturned projection of the upper part of the clasper. No other species can be confused with it.

**H. hierax**, Hew.

I have already pointed out that the clasper of this species suggests a close affinity with *H. xanthocles*. It is certainly wrongly placed next to *doris*.

WALLACEIFORMES.

**H. wallacei**, Reak.

The typical and two subspecies are described from northern S. America. As indicated above, the claspers (Pl. XVII) show a near affinity, if not specific identity, with *burneyi*.

SAPHOFORMES.

**H. sapho**, Drury.

The typical and four subspecies are described from Peru, Ecuador, Colombia, Central America, and doubtfully from Jamaica. The claspers of two forms are shown on Pl. XVII, and those of other forms examined show a similar structure. They suggest relationship with the Clysonimoformes, though they are distinguishable from the fact that in the latter the lower inflated part of the clasper is of a thinner chitin. There seems little to separate the *sapho* forms from *antiochus*, *leucadia* and *sara*.



**H. hewitsoni**, Stgr.

This species is remarkable for its resemblance to *H. pachinus*. Though allied to *sapho* forms I think it is certainly distinct, the male armature having several peculiarities (Pl. XVII).

**H. congener**, Weym.

This species is closely allied to the *sapho* forms, but the uncus is much more slender, so that for the present we may keep it separate (Pl. XVII).

ANTIOCHIFORMES.

**H. antiochus**, Linn.

This species and four subspecies are described from Guiana, Brazil, Peru, Ecuador, Colombia, and Venezuela. A remarkable form, *salvinii*, Dew., from the Orinoco delta, has a transverse yellow hind-wing band (Pl. XVII).

**H. leucadia**, Bates.

The type and one subspecies are described from N. Brazil, Peru, Ecuador and Bolivia (Pl. XVII).

**H. sara**, Fab.

Six subspecies of this form are described from various localities ranging through the greater part of northern S. America. Claspers from the above three reputed species are illustrated on Pl. XVII, from which it will be seen that, though varying in size and slightly in form, there is no satisfactory feature to distinguish them either from each other or from *sapho* forms. Also, it may be observed, they approach in structure the *cydno* forms.

ERATOFORMES.

**H. himera**, Hew.

A small and interesting form from Ecuador.

**H. notabilis microclea**, Kaye.

Resembles *H. xenoclea*, Hew., but distinguished by the character of the section. Occurs in Peru and Ecuador. A form with the fore-wing spots more or less white occurs in E. Ecuador.



**H. cyrbia**, Godt.

The typical and two subspecies are described from Ecuador, Colombia, and Bolivia.

**H. favorinus**, Hopff.

A Peruvian form.

**H. petiveranus**, Doubl.

The typical and one subspecies described from Colombia, Venezuela, and Central America.

**H. hydarus**, Hew.

Five subspecies are described. The forms occur in Venezuela, Trinidad, Colombia, and Panama. The forms are remarkable for the great diversity of colour and pattern exhibited.

**H. amphotrite**, Riff.

A Peruvian species closely resembling *erato callycopsis viculata*.

**H. erato**, Linn.

The typical and no less than eleven subspecies are described. Extending over the greater part of northern S. America. It is a species in which pattern and colour seem to run riot much as in *melpomene*.

Claspers taken from the foregoing eight reputed species are illustrated on Pl. XVII. All are characterised by the toothed projection at the outer end of the clasper, which takes the form of a flattened lobe with a peculiar twist, as though it had been taken in forceps and given part of a turn, whilst the rest of the clasper remained fixed. An examination of the figures shows that no satisfactory character differentiates these forms. The figures are only a selection from many preparations, all of which show the same kind of structure. Whether or not all are forms of one species, they certainly cannot constantly be distinguished by the structure of the armature.

One more species of the group remains, viz.—

**H. hermathena**, Hew.

This remarkable species from the Lower Amazon region has the fore-wings of one of the *erato* forms and the hind-



wings of *H. charithonia*. The clasper shows a near relation to *erato*, but there is a peculiar formation below the twisted projection, giving it the appearance of having been pinched (Pl. XVII).

CHARITHONIFORMES.

*H. charithonia*, Linn.

A common and well-known species having a very wide range over S. America and even into southern N. America. The clasper is very small for the size of the insect, and though not very characteristic may probably be regarded as distinct (Pl. XVII). There is one subspecies, *peruviana*, Feld., in which the claspers are similar.

*H. nattereri*, Feld.

Of this rare Brazilian (Bahia) species I have had no example to examine.

*H. fruhstorferi*, Riff.

Resembles the above and is thought to be its female. I have not seen an example.

CLYSONIMOFORMES.

*H. clysonimus*, Latr.

The typical and two subspecies are described from Central America, Colombia, and Venezuela. The principal characteristic feature of the clasper, shown on Pl. XVII, is the compressed appearance of the end of the dilated portion.

*H. hortense*, Guér.

From Ecuador, Colombia, Guatemala, and Honduras. The clasper (Pl. XVII) has a curious little hook-like projection.

*H. telesiphe*, Doubl.

From Peru and Bolivia. A form with yellow instead of white band on hind-wing (*sotericus*, Salv.) occurs in Ecuador. The clasper on Pl. XVII is simple and not very characteristic. Though somewhat resembling *sapho* forms, the uncus (not shown) is of a stouter form and slightly toothed.

We have now considered the apparent relationships of



most of the reputed species of the genus, from the point of view of the structure of the male claspers. In a general way the conclusions suggested show considerable and in some cases remarkable correspondence with the order in which the reputed species have been arranged in existing works. Most of the forms which now appear conspecific have already been placed together as nearly related.

The question of the specific value of the genitalia is difficult and complicated. The claspers have many forms, showing that we are not dealing with a genus in which these organs are of a primitive and simple character. The highly modified form of the armatures in many species supports the view that specific identity alone accounts for the resemblances found between the organs of forms hitherto regarded as distinct. It will be interesting to see to what extent external features help to confirm the conclusions arrived at from anatomical study.

*The evidence of pattern and colour.*

In considering the question of pattern it is important to distinguish between resemblance due to affinity and that due to mimetic influences, and it is just on this point that the evidence of the genitalia affords valuable clues. Thus the resemblance between "*silvana*" *ethra* and *narcaea flavomaculatus* would at first appear to support the theory of the affinity of *silvana* and *narcaea*. We have seen, however, that whilst on anatomical grounds *silvana* and *narcaea* do appear to be conspecific, "*silvana*" *ethra* is not to be regarded as a *silvana* at all. According to Seitz, *ethra* and *narcaea flavomaculatus* fly together at Bahia and are hardly distinguishable from one another. This fact, coupled with the known anatomical difference, points strongly to an instance of mimetic resemblance. As is well known, most of the Silvaniformes are modified to resemble Melinaeas and other butterflies of different subfamilies. Whether in likeness to a common model or to each other, several forms of the Silvaniformes bear strong resemblance to other Silvaniformes. Thus—

<i>ethilla aërotome</i>	resembles	<i>pardalinus lucescens</i> .
<i>anderida melicerta</i>	„	" <i>silvana</i> " <i>metaphorus</i> .
<i>anderida zuleika</i>	„	<i>hecalisia octavia</i> .
<i>anderida holocophora</i>	„	<i>numatus superioris</i> (dark form).



In each of these cases, as in that of "*silvana*" *ethra* and *narcaea flavomaculatus*, the forms which resemble one another are *separable on the anatomical structure*, and the resemblance may be regarded as mimetic without stopping to define the particular class of mimicry to which each case should be referred.

Bearing in mind the above facts, we may now consider the extent to which the patterns support the conclusions formed on the anatomy.

#### The *narcaea* association.

The typical form of this species appears to be very distinct from the other reputed species with which I have associated it, and it cannot be said that pattern affords much support for the conclusions based on the anatomical structure. Other members of the association, however, offer strong support to these conclusions. Comparison of *silvana silvana* with the typical form of *numatus* shows that there is really little difference between their patterns. *H. gradatus thielei* is scarcely separable from forms of *numatus* on pattern. As to *ethilla*, pattern would certainly support the view of a close affinity with *numatus*, especially if the undersides of *numatus numatus* and *ethilla eucomus* be compared. *H. ethilla claudia*, which resembles *anderida melicerta*, stands out rather distinctly from the rest. As we have seen, the claspers of forms of *ethilla* vary greatly, but in *ethilla claudia* they so closely resemble those of *ethilla ethilla* that there can be no doubt of their specific identity. Riffarth's diagnosis of this case was extremely shrewd. With reference to the other reputed species, the claspers of which I have not been able to examine, *H. hippola* must remain very doubtful, though an example of *narcaea satis* with the apical spot suppressed and the discal band darkened to the ground-colour would be difficult to distinguish from *hippola*. It is difficult on mere outward examination to appreciate the grounds on which *sulphureus* has been separated from *ethilla*.

#### The *novatus* association.

The pattern exhibited by the reputed species here associated are extremely diverse, though some of the special features may be traced through several different forms.



1. A tendency to melanism in the hind-wings is seen in *aristiona* and its forms *messene* and *aurora*, and appears again in *ithaka* and *pardalinus lucescens*, reaching a climax in *hecale* and *anderida fornarina*.

2. The undersides of *aulicus* and *aristiona lenaeus* are nearly identical, if we except the central and marginal black markings of the former, which, however, are traceable as vestiges in the latter.

3. The relationship of the underside pattern of *novatus leopardus* to that of *aristiona arcuella* is very evident on careful comparison.

4. The brown markings seen on the underside of *anderida fornarina* are faintly represented in some examples of *hecale*, whilst the yellow markings of the fore-wing upper-side in *fornarina* are partially reproduced in white in *hecale*.

5. Comparison of the hind-wing underside in *pardalinus lucescens* and *aristiona aurora* shows a close relationship of pattern.

6. The pattern of *quitaleus felix* is merely a slight modification of that of *pardalinus tithorides*.

7. The vestigial submarginal yellow spots in the hind-wing of *ithaka* appear to correspond with those in *anderida anetta*.

8. The various *anderida* forms graduate so obviously one into another that a connection between any of them and one of the other reputed species serves as an indirect connection for all.

9. In considering the form of the armature of these species I stated that there was a further reason for connecting "*silvana*" *robigus* with this association. The underside pattern of this form, especially of the hind-wing, is nearly identical with that of *novatus novatus*.

10. The hind-wing underside of *paraensis latus* closely resembles that of *aristiona arcuella*.

11. Similar close resemblances may be observed between examples of *fortunatus* and *pardalinus*.

We thus see that careful comparison of the wing patterns of the *novatus* association tends to support the conclusions based on an examination of the male armatures.

#### H. vetustus.

This species and its subspecies *metellus*, though closely allied to the *novatus* association, may for the present be



kept separate. The forms are rather rare in collections, and I have not been able to examine a large series. It may well prove ultimately to be a member of the *novatus* association.

**H. sergestus.**

The position of this species is obscure. Its pattern suggests a close relationship with *pardalinus*, but the clasper is of a very different form, and it must for the present remain separate.

**H. atthis.**

The structure of the armature of this species shows that it belongs to the Silvaniformes, though the pattern has been profoundly modified in mimicry of a *Tithorea*. The markings show no indication of its affinity, though the claspers are hardly distinguishable from those of *anderida*. They are rather less densely tufted.

**H. ismenius.**

The apparent specific identity of "*silvana*" *metaphorus* with the forms of *ismenius* is one of the surprising results of this investigation. The patterns are very different, though certain similarities may be observed. Thus the white and yellow spots on the underside of the fore-wing apex are practically identical with those in *ismenius telchinia*, and the same may be said of the white spots of the hind-wing underside.

There are two doubtful species included in the Silvaniformes concerning which nothing can be said. They are *H. arcuatus*, Kirby, and *H. euclea*, Godt. Their identity has not been satisfactorily established.

**H. tumatumari, Kaye.**

This peculiar species has already been mentioned in connection with the armature structure. As stated, the anatomy indicates relationship with *H. vetustus*, and whilst I think there are grounds for regarding it as a good species, certain particulars of the pattern support the above view of its affinity. Examination of the fore-wing underside shows in *tumatumari* three subapical spots and a fourth submarginally placed below the extremity of the first branch of the median. Precisely similar white spots are found in *vetustus metellus*. The discal pattern of the



fore-wing evidently bears a close affinity in the two species. If *tumatumari* be carefully examined in a good light, it will be seen that on the hind-wing underside the brown colour above the cell is very dark, whilst beneath this dark area is a paler stripe traversing the cell, its hinder border line passing out of the cell exactly at the origin of the second subcostal branch. The positions of these dark and light areas correspond precisely with those of the black-brown and orange-brown in *vetustus*, whilst there is an orange-brown streak below the cell in *vetustus* corresponding accurately with the distinctive yellow streak in *tumatumari*. Taken singly these points may be small and might be accidental; collectively they appear to me to be very significant.

#### *H. elevatus*, Nöld.

It is scarcely surprising that this species has been regarded as a form of *melpomene*. There is practically no external feature to distinguish it, beyond the yellow streak already referred to, yet it is more nearly related to some of the *Silvaniformes* than to *melpomene*. Three male examples are before me from Chanchamayo, São-Paulo (Amazon), and Beni River (Bolivia) respectively. The first two agree nearly with the description of *elevatus*. The third differs in the following respects. The fore-wing discal yellow fills the outer third of the cell, and extends across the space between the first and second median, and as a suffusion half-way down to the submedian. On the margin of the hind-wing underside it has very distinct white dots, absent in the two other specimens. These dots are described as occurring in the type. In all three the hind-wings above have an orange-red horizontal band passing through the cell and ending beyond the subcostal. This is followed by the usual straight band of black, and seven orange-red internervular "nail-headed" streaks almost reaching the hind-margin.

As has been stated, the armature approaches in structure that of *sergestus*. If there is any real affinity there is no indication of it on the upper surface. On the under surface, when the third specimen described above is compared with *sergestus*, we find that the position and general contour of the fore-wing discal yellow is very similar to that in *sergestus*. The latter furnishes one of the rare cases in which a silvaniform *Heliconius* has a red



spot at the base of the hind-wing, and *elevatus* has an exactly similar spot, though, of course, this feature is only of value in conjunction with the anatomical similarity, as so many of the non-silvaniform *Heliconii* have basal red spots.

These two species, *tumatumari* and *elevatus*, are of extraordinary interest as showing that there is no marked line of division between the Silvaniformes and the other members of Section I. The hind-wing pattern of *elevatus* raises another very interesting point. The "flame pattern" so frequently found in *Heliconius* is of two kinds. In *melpomene* forms (Section I) it is always cut across in a nearly straight line and the rays are of the "nail-headed" type, whereas in the species of Section II in which it occurs, the rays at their inner ends follow the contour of the cell. Why should the pattern of *H. elevatus* be of the nail-headed type? The reply seems to me to be that the characteristic horizontal black bar in the hind-wing of species of Section I is an ancestral pattern of considerable stability. It appears in one form or another in *narcaea*, *silvana*, *numatus*, *ethilla*, *novatus*, *pardalinus*, *quitalenus*, *paraensis*, *aulicus*, forms of *anderida*, etc., and its inner (upper) edge runs across at the level of the cell end. Hence when a "flame" pattern is developed it is cut off straight along the top by this characteristic bar. Thus, if my suggestion be well founded, we should expect any species of Section I which developed a flame pattern to produce the straight-cut, more or less nail-headed type found in *melpomene* and *elevatus*, irrespective of fascies of more recent ancestry. The nearest approach to a flame pattern in any truly silvaniform-patterned species that I know is in an example before me which agrees with Weymer's *H. fortunatus*. Here the usual black band is very distinct, and beneath it is a series of orange internervular marks of the ground-colour which, whilst running off to fine points marginally, are cut off proximally by the black band and have the nail-head pattern, though greatly foreshortened.

Professor Poulton has suggested to me that the black bar may have been developed in Section I of *Heliconius* in mimicry of *Melinaea* forms, doubtless an association of great antiquity. The idea has much to recommend it, since if it were a character of still greater antiquity we should expect it to be common to both sections of the



genus. However that may be, the bar is now a deeply established factor of the pattern, and sufficiently accounts, I think, for the special characteristics of the flame pattern as developed in Section I.

The *melpomene* association.

Some ten reputed species are here included, totalling, with subspecies and varieties, sixty or seventy named forms. On Pl. XI I have figured twenty-six butterflies which exhibit some of the forms included in this association. All the figures are much reduced from natural size, but for convenience of comparison it was desirable to have them all on one plate. The forms of *cydno* exhibit great diversity of pattern. White and lemon-yellow are easily interchangeable in both wings. The broad yellow fore-wing discal band of *cydno* is divided into two separate bands in the form shown at fig. 3, and in fig. 4 there is a submarginal row of white spots, the other fore-wing markings having become white. On the hind-wing of *cydno* there is a white border of medium width, almost marginal. In fig. 3 it is twice as broad, and in fig. 5 it is broad and yellow. In *hermogenes* (fig. 4) it is yellow and considerably separated from the margin, whilst in fig. 7 it is vestigial, but providing a link with the peculiar hind-wing marginal pattern in *vulcanus cythera*, fig. 8. Fig. 2 represents the underside of fig. 1. Note the peculiar pattern of the hind-wing. Two red-brown bands are faintly visible and the white sub-marginal border of the upperside is repeated. In some cases the upper red-brown band is practically horizontal, broad proximally and tapering towards the hind-margin. It is important to bear these variations in mind when comparing the patterns of the other reputed species.

Fig. 14 represents *weymeri*, Stgr., which is separated by Riffarth, but regarded by Seitz as conspecific with *cydno*. The latter view is undoubtedly correct. The fore-wing pattern is only a slight modification of fig. 3, whilst the hind-wing central yellow band is probably a development from the red-brown band of the underside of *cydno*. This central yellow band is a common feature in the genus; it occurs in both sections, and I shall have to refer to it again.

Fig. 15 is the form known as *weymeri gustavi*, Stgr. It has lost the fore-wing markings altogether and become



a remarkable mimic of a species in Section II. An example kindly lent me by Mr. Kaye is to some extent intermediate, having in the fore-wing a white spot above the first median, another below the first subcostal, whilst with a lens white scales can be seen in several other positions. The underside of this specimen is very remarkable, since the dull brown colour is paler all round the margin of the hind-wing over an area corresponding exactly with that of the white border in forms of *cydno*. Moreover, on the fore-wing the discal area is paler, not over an area corresponding with the white marks in *weymeri*, but representing the yellow patch of *cydno*.

We may now turn to *heurippa*, a nearly typical example of which is shown at fig. 10. There is little or nothing to associate it with *cydno*. Fig. 9, however, shows the fore-wing of *heurippa* with the *cydno* band in the hind-wing. This is the form known as *wernickei*, Stgr., and there is a somewhat similar form, *emilius*, Weym., which has the hind-wing band slightly suffused with grey as in some forms of *cydno*. These facts would seem remarkable enough, but there is further and stronger evidence. My figs. 10, 11, and 12 show a regular gradation of pattern, ending in the form at fig. 12, which is very near the stage of having nothing but a red patch on the fore-wing. Now this specimen, which is in the Tring Museum, has on the underside (fig. 13) the "ghost" of the pattern of the *cydno* underside. The delicacy of the shades of brown is difficult to reproduce, but the beauty of the actual specimen is very striking, and I am certain that no one could see it without being convinced of the specific identity of *cydno* and *heurippa*. The specimen shown at fig. 11 is also remarkable from the fact that on the underside of the hind-wing there is a pale horizontal band exactly corresponding to the yellow horizontal band of *weymeri*.

At fig. 16 is a figure of a form of *melpomene* which does not quite correspond with any of those named in the monograph already referred to. The fore-wing has the bicoloured patch of *heurippa*, but in other respects the example resembles *melpomene amandus*, shown at fig. 17. This form approaches *nanna burchelli*, but has more red in the cell. *H. melpomene amandus*, fig. 17, connects *nanna* with *heurippa*, and through the latter with *cydno*. Fig. 18 is *amaryllis rosina*, which is merely a form of *melpomene* with the hind-wing yellow band, whilst fig. 19



is *amaryllis euryades*, lacking the yellow band on both surfaces of the hind-wing, though in the form *euryas* it is present on the underside, and in one example before me from the Rio Dagua there is a trace of a white submarginal band on the hind-wing underside. These forms bring us to *melpomene*, fig. 20, which is merely a modification of the form of *heurippa* shown at fig. 12. All the yellow has disappeared and nothing but the bright red fore-wing patch remains. Occasionally an example of *melpomene* may be found in which the dull brown of the hind-wing underside has a rather lighter appearance corresponding in position to the yellow band of other forms.

Fig. 21 is the form described by Lathy as *xenoclea confluens*. It may be regarded either as a *xenoclea* in which the two patches have run together, or more probably as a *melpomene* with an extended patch not yet separated into two. In any case it connects *melpomene* with *xenoclea*, shown at fig. 22. In fig. 23 the two patches of *xenoclea* are white with a dusting of red. The example shown at fig. 24 exhibits the well-known "flame" pattern in the hind-wings together with basal red in the fore-wing. The flame pattern occurs in many forms of *melpomene* and also in species of Section II, though in the latter the red streaks radiate from the borders of the cell and have not the appearance of being horizontally cut off at their upper end.

Fig. 25 represents *melpomene eulalia*, in which, as in fig. 26, we see a distinct trace of the *heurippa* band in the fore-wing, the flame pattern recurring in fig. 26. Fig. 27 is a remarkable combination of the *melpomene amandus* fascies with the flame pattern superimposed. Finally, fig. 28 shows *H. pachinus*. The genitalia of this cannot be distinguished from those of all the other forms shown on the plate, and as to pattern, the yellow bands appear to be a mere modification of those of the fore-wing of figs. 3 and 6 and the hind-wing of fig. 4. Moreover, on the underside of *pachinus* there is frequently to be seen on the hind-wing a submarginal series of white spots like the vestige of the white border of *cydno*.

I have discussed the *melpomene* association at some length because I happen to have had access to a great number of examples, and these fortunately exhibit remarkable intermediate forms, which, together with the pre-



parations of genitalia, provide, at least in my own opinion, conclusive evidence of the specific identity of all the forms above considered, and divided in Stichel and Riffarth's monograph into ten species. Considered alone, the question of whether all these forms are representatives of one or several species is of little real importance except as a study in variation. The interest of the matter will, however, become apparent when we come to investigate the peculiar mimetic relationships occurring between the two sections of the genus.

#### *H. besckei.*

This species I keep separate both on account of the form of the clasper with its tuft of bristles and also because of the pattern of the hind-wing underside. Kaye was at one time of the opinion that it was a form of *erato phyllis*, though this cannot be maintained in view of the structure of the male claspers. Also I think it is rightly placed in Section I. It should be noted, however, that on the hind-wing underside there are some small whitish spots at the apex, and similar spots are occasionally found in examples of *melpomene*, and the relationship, if not specific, is extremely close.

### SECTION II.

#### *H. crispus.*

I have not been able to examine the armature of this species, and the pattern, being so profoundly modified in mimicry of a *Tithorea*, furnishes little evidence of its identity.

#### *H. hecuba.*

The patterns of *hecuba*, *choarinus*, and *cassandra* support the view that they are all one species, and whilst I have had no example of *longareus* to examine, its pattern indicates that it is conspecific with *cassandra*. If another example of *longareus* is ever discovered I shall be surprised if its locality is not found to be identical with that of *gynaesius*.

#### *H. hecalesia.*

The armature of *hecalesia* is so characteristic that the fact of the same organ in *octavia* being precisely similar leaves no doubt in my mind that they are forms of the



same species. An examination of pattern leaves little doubt that *gynaesius* is also a form of *hecalesia*, since *octavia* forms an almost perfect transition thereto. Indeed, if the basal brown be eliminated from the fore-wing of *octavia* there is no distinction from that of *gynaesius*, whilst a proportionate reduction of the hind-wing brown in *octavia* would leave the hind-wing pattern of *gynaesius*. If Stichel and Riffarth were satisfied that *gynaesius* was a form of *hecalesia* it is strange they should have kept *octavia* separate. It should further be noted that whilst the underside of the hind-wing in *octavia* has a very different appearance from that in *hecalesia*, it is practically identical with that in *hecalesia formosus*, whilst the latter has a trace of the fore-wing basal brown found in *octavia*.

#### H. godmani.

Stichel and Riffarth place this form in their *Aoediformes*, presumably on account of its shape. In other respects it differs little in appearance from *gynaesius*. The structure of the armature would probably settle the point at once, but I know of no example except the type, and this is not available for dissection.

#### H. metharme.

Whilst the difficulty of distinguishing the claspers suggests the specific identity of *metharme* and *aoede*, the difference in the shape of the wings suggests their separation. On the other hand, the radiate red pattern in the hind-wing in *aoede* is repeated on the underside of *metharme*, and there is an example of the latter in the Tring collection, having indications of the flame pattern on the upperside, though it must be remembered that the radiate pattern is common in several undoubtedly separate species. I think we must be content to regard them as doubtful species, but certainly very nearly allied.

#### H. xanthocles, H. hierax, H. egeria.

These three species are sufficiently distinct on the structure of the armature, and need no further comment.

#### H. burneyi.

The suggestion that *burneyi* and *wallacei* are conspecific is strongly supported by their patterns. On the hind-wing



underside the white internervular streaks and fringes are well represented in *wallacei colon*, the peculiar arrangement of the basal red is similar, and the conspicuous precostal yellowish spot is common to both. The base of the fore-wing costa beneath in *wallacei* is deep red, corresponding with a more conspicuous basal red in *burneyi*. Indeed, the hind-wing undersides in *wallacei colon* and *burneyi catharinae* are practically identical, and if a series of the hind-wings of both were mixed together it is difficult to see on what grounds they could be separated.

**H. doris.**

This species and its forms are readily recognised and specifically distinct, as the male claspers show, though many features of the pattern would suggest relationship with *metharme*.

**H. hewitsoni.**

A distinct species, as shown by the armature.

**H. congener.**

Probably distinct, on the structure of the armature.

**H. sapho, etc.**

The forms of *sapho* resemble those of *cydno*, and, as in that species, the two colours, lemon-yellow and white, are remarkably interchangeable. The broad white discal band in *sapho eleusinus* and *sapho leuce* appears as a double yellow band in several other forms, whilst the hind-wing hind-marginal white may vary from a mere fringe in *sapho leuce* to a broad band in *eleuchia*, or become a still broader yellow band in *sapho primularis*. The reputed species *antiochus*, *leucadia*, and *sara* do not show any characteristic differences in the structure of the claspers, and their patterns support the theory of specific identity in the following ways—

1. All have a tendency to white fringes pointed with black at the nervure ends.

2. The fore-wing subcostal and median nervures are generally dusted with pale yellow on the underside, the fore-wing subcostal almost invariably. In *antiochus* this dusting is on the subcostal and median. In many species of *sara* and *leucadia* the yellow scales can be seen on the median with a lens.



3. A very slight modification of the two fore-wing yellow bars in *sapho eleuchia* gives us the characteristic yellow or white bars in forms of *antiochus*.

4. *H. sara theudela* presents only a very slight modification of the pattern of some examples of *sapho primularis*.

5. Some examples of *leucadia pseudorhea* have the rudiments of a hind-wing marginal white border, strongly suggesting that more highly developed in *theudela* and forms of *sapho*.

6. Many forms of *leucadia* and *sara* have on the underside of the hind-wing a variable number of red spots forming a discal row more or less parallel with the hind-margin, though I have not seen any trace of this in *sapho* or *antiochus*.

7. Except for the red subcostal streak in *antiochus*, the hind-wing basal spots on underside of that species are almost exactly like those in *sara*. Moreover, in many examples of *antiochus* there is a yellow spot near the middle of the inner margin on the hind-wing underside. Several specimens of *sara* show the same peculiar yellow spot.

#### H. erato, etc.

The forms and reputed species included in this association present a case somewhat analogous to the great *melpomene* association in Section I.

The following considerations of the patterns support the conclusions based on the structure of the armatures—

1. *himera* may well be a form of *hydarus* with the red and yellow markings reversed.

2. *notabilis microclea*, with its double spots, may be traced to *erato* through a form of *erato estrella*, which has white subapical spots in the fore-wing, exactly the same white spot appearing in *notabilis notabilis*.

3. *hydarus hydarus* (resembling *melpomene*) has several admittedly conspecific forms which are totally unlike. Of these *hydarus colombinus* has a red fore-wing discal band and a central horizontal hind-wing yellow band. Beyond a slight difference in shape of this yellow band there is little to distinguish it from that of *petiveranus*.

4. *hydarus chestertoni* is a glossy blue form with a central horizontal hind-wing yellow band. If *cyrbia* be compared with this, the hind-wing yellow in that form, apparent only on the underside, is quite evidently the same as that



in *hydarus chestertoni*, *cyrbia*'s fore-wing red being obtained from *hydarus hydarus*. The peculiar white-dusted hind-wing border in *cyrbia* is more difficult to account for. It would at first suggest affinity with *sapho*, but the structure of the armature precludes this. The form is, of course, either a mimic or a model of *vulcanus cythera*.

5. *amphitrite* is merely a development of *hydarus*, the armatures being practically identical.

6. *erato* appears in many forms, some of which have developed the flame pattern common in other species. All kinds of intermediates are known, for which some forty-three names are recorded by Seitz. Most of these forms resemble others belonging to Section I, of which they are either the models or mimics. Its variability is, perhaps, even greater than that of *melpomene*, and there is nothing improbable in supposing that the forms I have associated with it are really the same species.

#### H. hermathena.

Closely related to the *erato* association, but apparently distinct. A very remarkable species combining the fore-wing spots of *erato phyllis* with the hind-wing of *charithonia*.

#### H. charithonia.

The true relationship of this common form is rather obscure. It is apparently a good species.

#### H. nattereri, H. fruhstorferi.

Of these I have had no examples to examine. There is, as already stated, some probability that they are male and female of the same species, though whether distinct or merely forms of *charithonia* must remain for the present undecided.

#### H. clysonimus, H. hortense, H. telesiphe.

These three forms are probably distinct species and call for no special comment, except that *clysonimus* is probably related to *antiochus* through forms of *sara*, in which traces of the hind-wing red band can still be seen.

We thus see that examination of the patterns and colours of the various forms dealt with supports in most cases the relationships suggested by the study of the genital armatures. We may, therefore, draw up the following table embodying the results of the foregoing investigation. Forms apparently not specifically distinguished are placed



under one number. Those forms, examples of which have not been available for examination, are marked with an asterisk. Except where otherwise stated, all the subspecies formerly included under a type name are here included also.

## SECTION I.

1. *H. narcaea*, Godt.  
   „ *numatus*, Cram.  
   „ *silvana*, Cram. (not including *metaphorus*, *robigus*,  
     and *ethra*).  
   „ *ethilla*, Godt.  
   „ *gradatus*, Weym.  
   „ *sulphureus*,\* Weym.  
   „ *hippola*,\* Hew. (?)
2. *H. novatus*, Bates (including *schultzei*, Riff.).  
   „ *hecale*, Fab.  
   „ *aristiona*, Hew.  
   „ *ithaka*, Feld.  
   „ *pardalinus*, Bates.  
   „ *fortunatus*, Weym.  
   „ *quitaleus*, Hew.  
   „ *anderida*, Hew.  
   „ *paraensis*, Riff.  
   „ *aulicus*, Weym.  
   „ *ennius*,\* Weym. (?)  
   „ “*silvana*,” *robigus*, (?) Weym.  
   „                   *ethra*, (?)
3. *H. atthis*, Doubl.
4. *H. vetustus*, Butl.
5. *H. tumatumari*, Kaye.
6. *H. sergestus*, Weym.
7. *H. elevatus*, Nöld.
8. *H. ismenius*, Latr.  
   „ “*silvana*,” *metaphorus*.
9. *H. cydno*, Doubl.  
   „ *weymeri*, Stgr.  
   „ *pachinus*, Salv.  
   „ *melpomene*, Linn.  
   „ *heurippa*, Hew. (including *rubellius*, Gr.-Sm.).  
   „ *amaryllis*, Feld.  
   „ *vulcanus*, Butl.  
   „ *xenoclea*, Hew.  
   „ *nanna*, Stich.
10. *H. besckei*, Ménétr.



SECTION II.

11. *H. crispus*, Stgr.
12. *H. hecuba*, Hew.  
     ,, *choarinus*, Hew.  
     ,, *cassandra*,\* Feld.  
     ,, *longareus*,\* Hew.
13. *H. xanthocles*, Bates.
14. *H. hierax*, Cram.
15. *H. hecalesia*, Hew.  
     ,, *octavia*,\* Bates.
16. *H. godmani*, (?) Stgr.
17. *H. metharme*, Erich. } (doubtfully separate).
18. *H. aoede*, Hübn. }
19. *H. egeria*, Cram.
20. *H. burneyi*, Hübn.  
     ,, *wallacei*, Reak.
21. *H. doris*, Linn.
22. *H. hewitsoni*, Stgr.
23. *H. congener*, Weym.
24. *H. sapho*, Dru.  
     ,, *antiochus*, Linn.  
     ,, *leucadia*, Bates.  
     ,, *sara*, Fab.
25. *H. himera*, Hew.  
     ,, *notabilis*, Godm.  
     ,, *cyrbia*, Godt.  
     ,, *favorinus*, Hopf.  
     ,, *petiveranus*, Doubl.  
     ,, *hydarus*, Hew.  
     ,, *erato*, Linn.  
     ,, *amphitrite*, Riff.
26. *H. hermathena*, Hew.
27. *H. charithonia*, Linn.
28. *H. nattereri*,\* Feld. } ? ♂ and ♀.  
     ,, *fruhstorferi*,\* Riff. }
29. *H. clysonimus*, Latr.
30. *H. hortense*, Guér.
31. *H. telesiphe*, Doubl.

One fact is especially striking. If the conclusions arrived at are sound, Section I, containing some 35 reputed species, is reduced to 10, whilst Section II, containing some 37 reputed species, is reduced to 21. Furthermore, when considering the mimetic side of the question, it will appear



TABLE I.--Forms of *Heliconius* and those of other genera which they resemble.

Heliconius	Spp. of other genera	Locality
<div> <div>narcæa narcæa</div> <div>"silvana" ethra</div> </div>	<div> <div>Mechanitis nessea lysimnia, Hübn.</div> <div>Ceratinia daeta, Bo'sd.</div> <div>Melinaea ethra, Gott.</div> <div>Dismorphia astynome, Dalm.</div> </div>	Central Brazil.
narcæa connexa	<div> <div>Ceratinia euryanassa, Feld.</div> <div>? Eresia eunice, Hübn.</div> </div>	S. Brazil.
numatus numatus	<div> <div>Hirsutis harmonia, Cram.</div> <div>Lycorea ceres, Cram.</div> <div>Melinaea mediatix, Weym.</div> <div>Mechanitis pannifera, Butl.</div> </div>	Br. Guiana.
<div> <div>numatus isabellinus</div> <div>? aristiona arcuella</div> <div>quitaleus sisypus</div> </div>	<div> <div>Melinaea flavosignata phasiana, Butl.</div> <div>? Lycorea eva concolor, Staud.</div> <div>Ceratinia maenas, B. Haas.</div> </div>	W. Amazon.
silvana silvana	<div> <div>Melinaea paratva, Reak.</div> <div>Mechanitis silvanoides, Godm.</div> </div>	Guiana, etc.
ethilla ethilla	<div> <div>Protogonius ochraceus, Butl.</div> <div>Hirsutis megara, Gott.</div> </div>	Trinidad.
ethilla metalis	<div> <div>Hirsutis furia, Godm.</div> </div>	Venezuela.
<div> <div>ethilla aërotome</div> <div>pardalinus lucescens</div> </div>	<div> <div>Lycorea cleobaea cinnamomea, Weym.</div> <div>Melinaea maelus cydon, Godm.</div> <div>" madeira, Staud.</div> <div>Mechanitis equicoides, Godm.</div> <div>" egaënsis, Butl.</div> <div>Ceratinia pardalina, Hopf.</div> <div>" fluonia, Hew.</div> <div>" anastina, Bates</div> <div>Dismorphia egaëna, Bates</div> <div>Protogonius castaneus, Butl.</div> </div>	W. Amazon.
<div> <div>ethilla claudia</div> <div>"silvana" metaphorus</div> <div>anderida melicerta</div> </div>	<div> <div>Melinaea idae, Feld.</div> <div>Mechanitis macrinus, Hew.</div> <div>Callithomia beronilla, Hew.</div> <div>Ceratinia philetæra, Hew.</div> <div>Ichomia iphianassa panamensis, Bates</div> </div>	Panama, Colombia, Ecuador, etc.
aristiona aristiona	<div> <div>Mechanitis deceptus, Butl.</div> <div>Melinaea mothone, Hew.</div> <div>Ceratinia honesta bicolora, Hsch.</div> <div>" manaos semifulva, Salv.</div> <div>Napeogenes achæa, Hew.</div> <div>Hypocada fallax, Staud.</div> <div>Eresia murena, Staud.</div> <div>" ithomiola, Salv.</div> <div>Protogonius s-mifulvus, Butl.</div> <div>Eueides acacetes, Hew.</div> <div>Papilio bachus, Feld.</div> <div>Periconis hydra, Butl.</div> </div>	Bolivia, Peru.



	<i>Melinaea messonina</i> , Feld. <i>Mechanitis messenoides</i> , Feld. }		Colombia, Ecuador.
	<i>Melinaea zaneka</i> , Butl.		Ecuador.
	<i>Melinaea menophilus tarapotensis</i> , Haen.		Ecuador.
	<i>Melinaea menophilus menophilus</i> , Hew.		Colombia.
	<i>Melinaea lucifer</i> , Bates <i>Ceratinia soror</i> , Srkr. }		W. Amazon.
	<i>Melinaea flavosignata orestes</i> , Salv.		W. Amazon.
	<i>Hirsutis pinthias</i> , Godm. " <i>duenna</i> , Bates ? <i>Phyciodes ithomoides</i> , Hew. <i>Ceratinia callispila</i> , Bates <i>Napeogenes tolosa</i> , Hew. <i>Callithomia hedila</i> , Godm. " <i>hezia</i> , Hew. <i>Hyposcada adelphina</i> , Bates <i>Eresia nigripennis</i> , Godm. }		Central America.
	<i>Tithorea pavonii</i> , Butl.		Peru.
	<i>Melinaea messatis</i> , Hew. <i>Napeogenes larina</i> , Hew. <i>Hyposcada adelphina</i> , Bates <i>Ithomia candescens</i> , H.-Sch. }		Colombia.
	<i>Ithomia celemia</i> , Hew. <i>Ceratinia fulminans</i> , Hew. }		W. Colombia.
	<i>Melinaea scyllax</i> , Salv. <i>Ithomia plagiota</i> , Butl. " <i>callipsila</i> , Bates. <i>Dismorphia sororna</i> , Butl. (♀) }		Costa Rica, etc.
	<i>Melinaea imitata</i> , Bates <i>Lycorea atergatis</i> , Doubl. <i>Mechanitis doryssus</i> , Bates <i>Ereides cleobaea zorcaon</i> , Reak. <i>Ceratinia dionaea</i> , Hew. <i>Perrhybris malenka</i> , Hew. (♀) <i>Dismorphia praxinoe</i> , Doubl. (♀) <i>Eresia phillyra</i> , Hew. (♀) <i>Protophonus cecrops</i> , Doubl. <i>Pericopis angulosa</i> , Walk. }		Central America.
aristiona lenaeus			
aristiona tarapotensis			
aristiona euphone			
aristiona aurora			
aristiona timaeus			
auderida zuleika hecalesia octavia }			
atthis charithonia peruvianus }			
ismenius ismenius			
ismenius faunus			
ismenius clarescens			
ismenius telchinia			



that all but two species in Section I mimic species of other genera. Intrageneric mimicry occurs between two or three species in Section I and between a much larger number of species in Section II. One species in Section I produces forms which mimic six or seven species in Section II, a phenomenon recalling that of the mimicry of several species of *Planema* by one species of *Pseudacraea*.

Whilst I think that fuller knowledge of the genus is likely to confirm the majority of the conclusions here attained, it must not be forgotten that cases occur in which Lepidoptera quite undistinguishable on the armature structure are, nevertheless, known from other characters to be distinct species, and it seems probable that instances of this condition will also be found in the present genus.

#### The mimetic relationships of *Heliconius*.

The species and forms included under the group *Silvaniformes* nearly all resemble species of other genera and subfamilies. They are members of great mimetic associations which include species of widely separate affinities. It is not within the scope of the present paper to study in detail all these associations. They are fairly well known, and have been referred to by many authors. Beyond the fact that *hecalesia octavia* resembles *anderida zuleika*, the forms of *Silvaniformes*, excluding the intermediate *tumatumari* and *elevatus*, do not, as a rule, resemble those of members of Section II of the genus. The accompanying table (Table I) gives some of the more striking associations to which forms of the *Silvaniformes* belong.

As already stated, Mr. W. J. Kaye has pointed out\* that, having once separated the forms of the genus into their two sections, we find that many of those of Section I resemble forms of Section II. In order more fully to illustrate this remarkable parallelism, I have prepared Pl. XII. The figures, as in Pl. XI, are much reduced, but will suffice to illustrate the patterns. The examples shown in the second and fourth columns are all forms belonging to *melpomene*—that is, accepting the conclusions already arrived at, are all the same species. The specimens figured in the first and third columns are all members of Section II, and belong to several species.

Fig. 1 is *egeria egerides*, fig. 2 *melpomene funebris cybele*.

\* *Loc. cit.*



Both occur in Guiana and North Brazil as far as the Rio Negro. Figs. 5 and 6 are *burneyi hübneri* and *melpomene penelope*, both from Bolivia. Figs. 9 and 10 represent *hewitsoni* and *pachinus* from Panama. Figs. 13 and 14, 17 and 18, 21 and 22 represent respectively three forms of *sapho* and three of *cydno*. Figs. 25 and 26 are *himera* and *melpomene timareta contiguus*. In this case the patterns are by no means so alike as in most of the other examples, but that of the hind-wing of the *melpomene* form is the more interesting in that it shows the crowding together of the flame pattern rays in order to produce a resemblance to the band of *himera*.

Figs. 3 and 4 are *notabilis microclea* and *xenoclea* respectively, and beneath them (figs. 7 and 11) are *notabilis notabilis* and *erato rothschildi*, to which correspond the two *melpomene* forms, figs. 8 and 12. Figs. 15 and 16 are *hydarus chestertoni* and *weymeri gustavi*. These, I am told, have not the same vertical distribution, though possibly their enemies may not be correspondingly separated. Figs. 19 and 20 are *hydarus colombinus* and *amaryllis rosina* from Bogota. Figs. 23 and 24 represent *erato phyllis* and *melpomene amandus*, the latter example approximating to the form *nanna burchelli*, Poulton. It has been pointed out by Professor Poulton (Ann. Mag. Nat. Hist., p. 33 et seq., 1910) that where *nanna* occurs within the range of *erato phyllis* the red bar of the fore-wing is deeply toothed at the lower outer edge, just as in *erato phyllis*, whereas in his form *burchelli* the red bar is of less irregular outline. Finally, at figs. 27 and 28 are shown peculiar forms of *erato* and *melpomene* from Bolivia.

Adhering to our previous conclusions, we have, then, on Pl. XII, fourteen forms of *one* species of Section I which, whilst differing widely from one another, present respectively a remarkable resemblance to fourteen forms of Section II belonging to *six* different species. The examples shown by no means exhaust the subject. It would be possible to fill another plate with corresponding forms of *erato* and *melpomene*; *aoede*, *xanthocles* and *doris*, all have forms which could be included, and whilst so many forms in Section I mimic others in Section II, some of those in the latter seem to mimic each other. The nature of this mimicry is somewhat difficult to define. Mr. Kaye (*loc. cit.*) has himself pointed out its peculiarities. The comparative rarity of the forms of Sections I and II is not constant.



Thus *nanna* and *rosina* are much rarer than *phyllis* and *colombinus*, whilst, on the other hand, *xenoclea* is much commoner than *notabilis microclea*. He points out, however, the possibility that in some or, perhaps, most of the localities, members of one section may be always more dominant than the other. Also that the exact times of appearance may not coincide.

Hitherto it has been the custom to assign all such cases of mimicry either to the Batesian or Müllerian category. Those of us who have heard Mr. Swynnerton's remarks on his experiments in South Africa, given some time ago before the Linnean and Entomological Societies, know that the relative distastefulness of insects is a variable character dependent on factors not entirely related to the insect itself. Mr. Swynnerton's papers are not yet published, so that I cannot utilise his results for the present discussion. Meanwhile, we know that, although no direct experiments have been made with *Heliconius*, the genus gives great evidence of being a distasteful one, and we may therefore regard the existing resemblances as being of a Müllerian character. We are, however, faced with the difficulty of the multiplicity of patterns. If Section II contains the models it would appear to be a great disadvantage to the forms to have so many different appearances, since each form is not necessarily confined to a special locality but considerable overlapping occurs. Where mimicry occurs between separate species of separate genera, then multiplicity of patterns in the models may be compensated for by diversity of habit of the different species. Thus Mr. Kaye, in discussing mimetic groups in the Potaro district of British Guiana, states that the species of *Heliconius* with patterns resembling *Ithomiinae* frequent flowers of a certain plant, whilst other species of *Heliconius* are never, in his experience, found on these flowers. This is an extremely valuable point and one which should be remembered in considering mimetic phenomena.

It does not, however, seem probable that forms of the same species will have different habits corresponding to those of their respective models. Apart from the preferences of insectivorous enemies, whether absolute or conditional, the unpalatability of the insect is, of course, a relative factor. Thus resemblance of a species of *Heliconius* in Section I to a species in Section II may be a measure of protection to both, assuming the two species



to possess a certain degree of distastefulness. Another species of *Heliconius* may resemble a *Melinaea* or a *Lycorea*. We know that in most cases the *Melinaeas* are much more numerous than *Heliconius*, and we may suppose that the former are so much more unpalatable than the latter that, in spite of the degree of distastefulness in *Heliconius*, the latter may be practically a Batesian mimic of the *Melinaea*. At the same time it is, perhaps, inappropriate to use the term Batesian in this connection, since it was the mimicry of *Heliconius* which Bates himself felt unable to explain on his own theory. To understand more fully the relationships of models to mimics in *Heliconius* we require much more information concerning geographical distribution, and also as to comparative rarity of forms and other bionomic factors. S. America is a very large area, and the commonest type of data on our labels is "Upper Amazon," "Colombia," "Peru," and even sometimes "Brazil." We might as well be told that a certain insect occurs in Europe.

Including the examples figured on Pl. XII the following is a list of some of the most remarkable instances of intrageneric mimicry in the genus.

SECTION I.

*cydno chioneus*  
 „ *epicydnides*  
 „ *galanthus*  
 „ *alithea*  
*weymeri gustavi*  
*pachinus*  
*melpomene funebris cybele*  
 „ *equadoriensis*  
 „ *vicinus*  
 „ *funebris deinea*  
 „ *penelope*  
 „ *penelope margarita* (?)  
 „ *timareta contiguus*  
 „ *aglaope* f.  
*xenoclea corona*  
*amaryllis rosina*  
 „ *euryades*  
*vulcanus cythaera*  
*xenoclea*  
*nanna nanna*

SECTION II.

*sapho eleusinus*  
 „ *eleuchia*  
 „ *leuce*  
 „ *primularis*  
*hydarus chestertoni*  
*hewitsoni*  
*xanthocles*  
 „ *melior*  
 „ *melete*  
*burneyi catharinae*  
 „ *hübneri*  
*erato anacreon ottonis*  
*himera*  
*erato rothschildi*  
*notabilis notabilis*  
*hydarus colombinus*  
 „ *hydarus*  
*cyrbia cyrbia*  
*notabilis microclea*  
*erato phyllis*



## SECTION II.

<i>doris delila</i>	<i>burneyi hübneri</i>
„ <i>metharmina</i>	<i>metharme</i> }
	<i>sara</i> ff. }

Of the genus *Eueides*, Seitz remarks that it may be said that no *Eueides*, without any exception, has a character of its own. Some copy *Heliconius*, others *Lycorea* and *Actinote*, and in some species the male copies one species whilst the female resembles another. A few of such resemblances are given below.

<i>Eueides</i> .	<i>Heliconius</i> .
<i>ricini</i> , Linn. }	<i>clysonimus</i> }
<i>procula</i> , Doubl. }	<i>hortense</i> }
<i>eanes</i> , Hew.	<i>erato lativitta</i>
<i>eanes eanides</i> , Stich.	<i>melpomene aglaope</i> f.
<i>dianasa</i> , Hübn.	<i>narcaea</i>
„ <i>decolorata</i> , Stich.	„ <i>satis</i>

All the numerous forms of *E. isabella*, Cram., resemble various forms of *Heliconius* of the *Silvaniformes* group.

In addition to the mimetic associations above tabulated there are further instances of considerable interest. Thus the resemblance of *Colaenis telesiphe* to *H. telesiphe* is well known. They fly together and cannot be distinguished on the wing. In Ecuador the *Heliconius* has the hind-wing band yellow instead of white and broader than in the typical form. The *Colaenis* in the same region is correspondingly modified. Several *Papilios* present *Heliconoid* patterns, notably *P. zagreus*, Doubl., and its form *P. bachus*, Feld., which have an appearance recalling that of species of the *Silvaniformes*. *P. pausanias* is a mimic of *H. sara* and is also said to imitate the *Heliconius* flight.

*P. euterpinus*, Godm., though it can only be said to be a rough mimic of a *Heliconius*, presents the *melpomene* pattern which, as Dr. Dixey has shown, may be traced over a large area and through many species, including many forms of *Heliconius*, *Eresia castilla*, Feld. *Adelpha lara*, Hew., *Agrais amydon*, Hew., *Siderone* spp., *Catagramma euomia*, Hew., *Callithea davisii*, Butl., *Daedalma* sp., several species of *Pereute*, *Catasticta tentamis*, Hew., and a number of



moths, including Arctiids, Hypsids and Syntomids. With regard to *H. erato phyllis*, Seitz (Macrolepidoptera) records that, whilst it occurs all the year round in Rio and Santos, it becomes comparatively scarce in January and February, at which season only worn specimens are found. At the same time *Eresia lansdorfi* appears, a species which, as may be seen from its pattern, copies not a fresh, but a worn and faded *phyllis*. Several forms of *Heliconius* resemble species of *Tithorea* and *Hirsutis*. Some have already been mentioned, as *H. atthis*, etc. *H. crispus* flies with *T. bonplandii descandollesi* in the Cauca Valley. *H. hecuba* mimics *T. humboldti*, and *H. hecuba tolima* is a copy of *T. bonplandii*. *H. hecalesia* resembles *T. hecalesina*, *Ceratinia peridia*, *Callithomia tridactyla*, and others which form a large association, whilst its Central American form, *formosus*, resembles *T. pinthias*.

It is remarkable that *H. charithonia*, perhaps the commonest species of *Heliconius*, should have no close imitators. Professor Poulton points out to me that the females of *Catonephele nyctimus* approach this pattern, as also do those of *C. acontius*. The latter has a wider eastward range than *charithonia*, but the former is the better mimic in that the hind-wing yellow band is broader, though in both cases the resemblance is very slight. The *peruvianus* form of *charithonia* is evidently a modification in the direction of *Tithorea pavonii*, Butl., the marginal and sub-marginal spots being white instead of yellow. In one respect it is a better mimic of the *Tithorea* than is *H. atthis*, since the fore-wing yellow band is broader, as in the *Tithorea*, and curves down, not up, as in *Atthis*. The ♀ of *Pieris viardi*, Boisd., is also modified in the direction of *H. charithonia*, whilst *P. mandela tithoreides*, Butl., approaches *Tithorea pavonii* in the same way as does *H. charithonia peruvianus*.

Some of the most interesting *Heliconius* mimics occur amongst the *Pierinae*, such cases being the more noticeable since the normal Pierine fascies are so unlike those of *Heliconius*. Thus, *Euterpe bellona hyrnetho*, Fruhst., ♀, from Bolivia, has black wings with a fore-wing discal yellowish patch and a radiate red pattern on the hind-wing, thus resembling similar forms of *H. erato*. *Euterpe bellona cutila*, Fruhst., ♀, also shows the incipient stages of such a pattern. *E. bellona negrina*, Feld., ♀, bears on the underside a very good copy of the underside of *H. erato venusta*.



It is interesting to note that the flame pattern in these Pierines is a copy of that occurring in the species of *Heliconius* belonging to Section II, and not those of Section I. *Pieris mandela locusta*, Feld., ♀, and the form *noctipennis* resemble to some extent *H. sapho leuce*, whilst *Pereute charops*, Boisd., ♀, resembles *H. hydarus*. On the underside of the hind-wing (all that shows when at rest) the female of *Perrhybris lorena* is very like *H. antiochus aranea*, though the upperside is more like one of the Silvaniformes. A similar silvaniform appearance is also presented by several females of *Perrhybris*, though the resemblance is probably secondary, both being influenced by Ithomiine models. It seems unnecessary further to enumerate special cases of mimicry connected with the genus. An examination of any large collection will convince the observer of the prevalence of mimetic patterns.

Apart from a few exceptional instances, it appears to be the rule that, whereas species of *Heliconius* belonging to Section I are mimetic and constitute members of large associations of which they are not themselves the dominant models, species of Section II act as models and are imitated either by forms of Section I or by butterflies of other genera, and moths. The *melpomene* forms of Section I seem to be all one species, whereas their counterparts in Section II belong to several. Again, where a butterfly of another genus appears to be a *Heliconius* mimic, its model will almost always be found in Section II and not in Section I. Thus *Eueides* finds its models in Section II. Even *Napeogenes duessa* is apparently an incipient mimic of an *erato* form which is very perfectly imitated by a moth of the genus *Pericopis*. Moths of this genus come into mimetic associations of which silvaniform *Heliconii* are fellow members, but the moths are certainly not the models, though *Pericopis* is doubtless a protected genus. Distastefulness is a relative factor, and we are, of course, quite justified in speaking of model and mimic, even in Müllerian associations. The model is the form which, from whatever cause, not necessarily palatability, has attained to a greater predominance, and in the genus *Heliconius* it would appear that, generally, the species of Section II have in some way evolved a degree of such predominance superior to that enjoyed by the species of the other half of the genus. It is interesting to see an independent property of this kind correlated with recognis-



able differences of internal anatomy and a slight, though evident, external characteristic.

It remains to consider certain points in connection with the modifications which occur in various geographical areas. Several exhibits have been made and papers read on this subject. Mr. W. J. Kaye read a paper in 1906,\* in which he described and illustrated the many forms of *Melinaea*, *Heliconius*, etc., forming a great characteristic group in the Potaro District of British Guiana. In this group were found to occur the following forms:—

NYMPHALIDAE.

*Ithomiinae*.

*Melinaea* 4

*Mechanitis* 2

*Ceratinia* 2

*Heliconinae*

*Heliconius* 4

*Eueides* 3

*Nymphalinae*

*Eresia* 1

DANAIDAE

*Lycoreanae*

*Lycorea* 2

ERYCINIDAE

*Lemoniinae*

*Stalachtis* 1

together with the outlying members of the group not up to that time actually taken on the Potaro, *Tithorea harmonia*, Cram., *Protopogonius hippona*, Cram., *Dismorphia amphione*.

The dominant member of the group was *Melinaea mneme*, Linn., which occurred in "prodigious numbers." The *Heliconius* forms were found to be by far the closest mimics of the *Melinaea*, whilst at the same time they were comparatively rare.† Great variation was observed in the banding of the hind-wing from a narrow bar to almost entirely black. A careful and interesting analysis is made of the degree of blackening observed in the various forms, with the result that there is found to be a closer agreement on the underside than on the upper. Only two species

\* Notes on the dominant Müllerian group of butterflies from the Potaro District of British Guiana. Trans. Ent. Soc. Lond., p. 411 et seq., 1906.

† See also Proc. Ent. Soc., p. liv, 1903.



showed a large proportion with heavy black underside. The tendency to melanism was found to be more prominent on the upperside. The author concludes that the forces of selection are now acting more forcibly on the underside pattern, as might be expected from the sedentary habits of the group, and that these forces are now tending to produce forms with less blackening. A further point of great interest was that already mentioned—namely, that all the members of the group are commonly found feeding on the white flowers of *Eupatorium macrophyllum*, and that whilst there are many other differently coloured forms of *Heliconius* in the neighbourhood, they are never, in the author's experience, found on these flowers. This point is worthy of special remark as showing how the advantages of similarity of pattern may be increased by the development of a common habit.

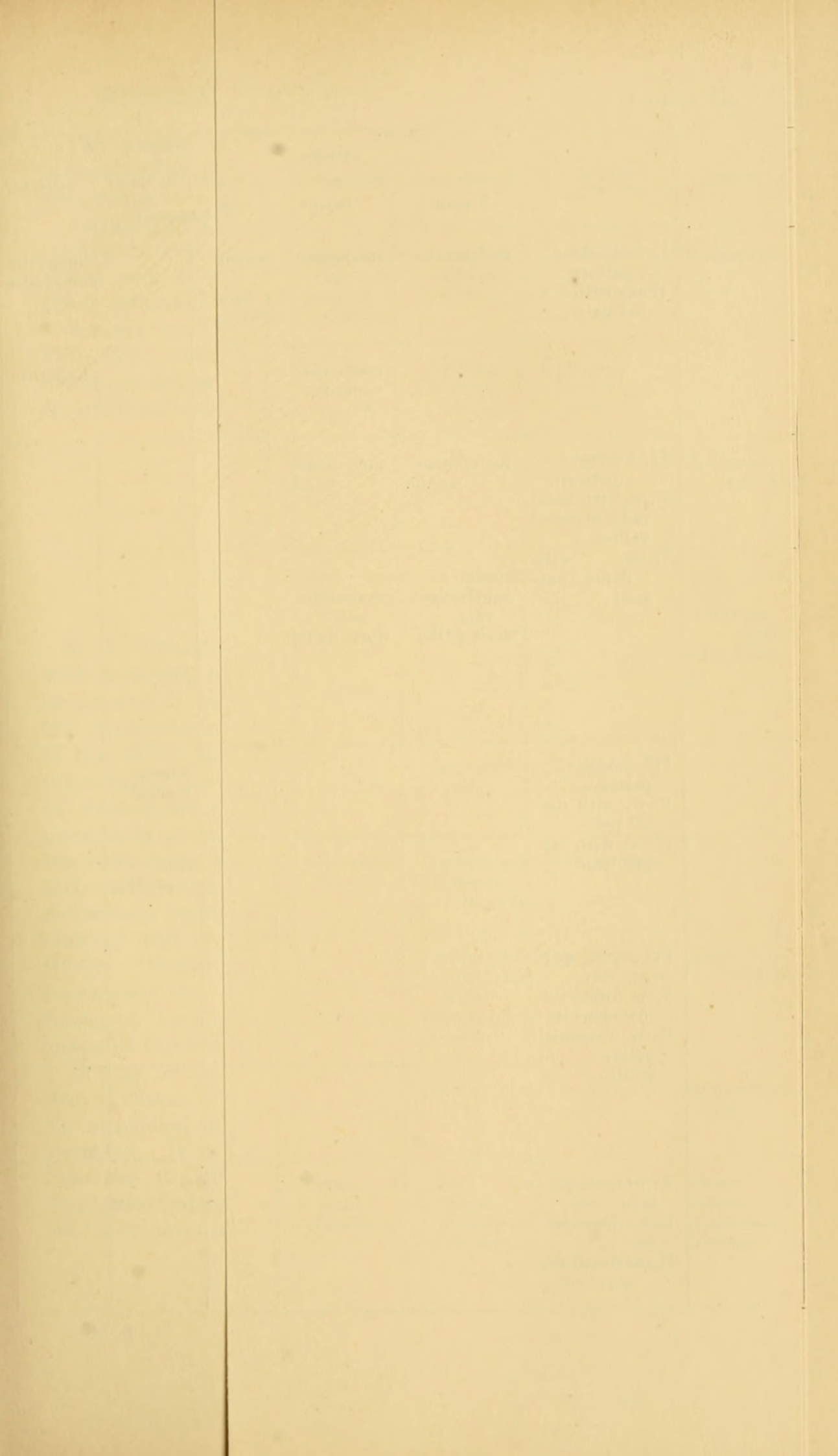
In 1908 Mr. J. C. Moulton read a paper "On some of the principal Mimetic (Müllerian) Combinations of Tropical American Butterflies" (Trans. Ent. Soc., p. 585 et seq., 1908) in which he described four great associations of mimetic forms, including *Ithomiinae*, *Heliconinae*, and members of other subfamilies. Association I is classed as the North Central American type from Guatemala, Honduras, and Nicaragua. The typical pattern is here that of *Melinaea imitata*, which is closely copied by *H. ismenius telchinia*, the rest of the group including—

*Ithomiinae* 5  
*Danainae* 1  
*Nymphalinae* 2  
*Heliconinae* 1  
*Pierinae* 2  
*Hypsidæ* 1

Association II is described as the East Brazilian type and is divided into two subgroups (a) having the fore-wing subapical spots yellow and (b) having the same spots white. The first is centred round *Melinaea ethra*, Godt., and includes *H. "silvana" ethra* and other species of the following subfamilies:—

*Ithomiinae* 4  
*Danainae* 1  
*Nymphalinae* 2  
*Heliconinae* 1  
*Pierinae* 1







Peru	Bolivia	E. Amazon	W. Amazon	E. Brazil	S. Brazil	Trinidad
				(S. of Amazon)		
melpomene amaryllis euryades		melpomene				amaryllis euryades
amphitrite		erato cally- copsis				hydarus
melpomene aglaope	melpomene penelope	melpomene thelxiope melpomene aglaope	melpomene aglaope			
xanthocles melior doris delila erato deme- ter erato lati- vitta	aoede lucre- tius xanthocles melete doris delila erato venusta erato lati- vitta	aoede doris delila erato ama- zona	aoede bart- letti doris delila erato lati- vitta			
amaryllis					nanna besckei	
erato phyllis	erato phyllis				erato phyllis	





Eltringham, Harry. 1916. "IV. On Specific and Mimetic Relationships in the genus *Heliconius*, L." *Transactions of the Entomological Society of London* 64, 101–148. <https://doi.org/10.1111/j.1365-2311.1916.tb03123.x>.

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